Journal: Ecology

Manuscript type: Article

Running Head: Avian trophic cascades

Do birds help trees grow? An experimental study of the effects of land-use intensification on avian trophic cascades

Scott H. Harris[1,4], Urs G. Kormann[1], Thomas D. Stokely[1], Jake Verschuyl[2], Andrew J. Kroll[3],
Matthew G. Betts[1]

[1]Department of Forest Ecosystems & Society, Forest Biodiversity Research Network, Oregon State
University, Corvallis, Oregon 97331 USA

[2]National Council for Air & Stream Improvement, Anacortes, Washington 98221 USA

[3]Weyerhaeuser 785 N 42nd Street, Springfield, OR, 97478 USA

Accepted Article

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/ecy.3018

This article is protected by copyright. All rights reserved

Accepted Article

ABSTRACT

By regulating populations of herbivores, predators can indirectly influence plant production. However, the factors influencing the strength of this type of trophic cascade are still unclear. We hypothesized that changes to plant community structure would affect the number of avian predators, thereby mediating cascade strength. Using a 4-year, blocked split-plot experiment, we independently manipulated both predators (birds) and plants in an early seral managed forest system in western Oregon, USA, and measured abundance across three trophic levels. We applied herbicides, as a surrogate for land-use intensification, to recently clearcut stands to establish an experimental gradient in plant abundance and species richness, and excluded birds using 28, 225 m^2 exclosures. In total, we counted and identified 94,738 arthropods of 141 families in paired control and bird exclosure plots. On average, insectivorous birds reduced arthropod abundance by 16% and plant damage by 14%, and some well-known pests (e.g., *Adelges cooleyi*) of crop trees (mostly *Pseudotsuga menziesii*) in our system were reduced by as much as 30%. However, this effect did not translate into a trophic cascade that increased crop-tree growth in the presence of birds. We experimentally reduced plant abundance and diversity by 67% and 55% respectively in the most intensive herbicide treatment in relation to untreated controls, but reduced vegetative resources did not change the strength of the direct effect of birds on arthropods or the indirect effect of birds on plants.

Key words: trophic cascades, ecosystem services, temperate forests, forest management, birds, arthropods, land-use intensification, herbicides

INTRODUCTION

Decades of empirical studies provide ample evidence for the existence of trophic cascades, yet critical questions remain about the mechanisms that determine cascade strength. Trophic cascades, indirect species interactions that start with predators and propagate downward through food webs (Paine 1980, Ripple et al. 2016), are influenced by both bottom-up (producer driven) and top-down (consumer driven) controls over the abundance of organisms at each trophic level (Hunter and Price 1992). The relative roles of these controls in mediating cascade strength have occupied much of the research on trophic dynamics (Borer et al. 2006). The bottom-up view is described in classic trophic theory (Elton 1927, Lindeman 1942). The *ecosystem exploitation* hypothesis (Fretwell and Barach 1977, Oksanen et al. 1981) refines classic theory by describing how the number of trophic levels

This article is protected by copyright. All rights reserved

Accepted Article

increases with plant productivity, consequently strengthening trophic cascades. In contrast, the *green world* hypothesis (Hairston et al. 1960) explains that the abundance of herbivores is regulated by the top-down control of predators, and not by the abundance of plants. Our understanding of the relative roles of top-down and bottom-up controls over trophic cascades is limited due a paucity of studies that experimentally manipulate multiple trophic levels (Borer et al. 2006). Additionally, many previous trophic studies have limited inferential power because they are conducted over short time spans, at small scales, and lack information on the abundance of organisms across trophic levels. Here, we address these knowledge gaps and shortcomings by manipulating both the predator and plant communities in a replicated, four-year, broad-scale experiment, and by measuring relative abundance in three trophic levels: plants, arthropods, and vertebrate predators.

Land-use intensification alters plant community structure and composition and has been shown to reduce the complexity of trophic interactions, and therefore has the potential to affect the ecosystem services provided by trophic cascades, such as arthropod pest control provided by birds (Tscharntke et al. 2005, Tylianakis et al. 2007, Thies et al. 2011). Land-use intensification has also been shown to negatively impact the abundance and diversity of birds (Donald et al. 2001). Plantation forests, a form of intensive land use, account for approximately 7% of global forested areas (Keenan et al. 2015), are increasing at a rate of approximately 2% per year (Sloan and Sayer 2015), and constitute an increasingly important contribution to the global demand for wood products (Meyfroidt and Lambin 2011, d'Annunzio et al. 2015). The value of trophic-induced biological pest control in temperate forests has been estimated to be US$235 per hectare per year (de Groot et al. 2012), but the degree to which this service is altered by land-use intensification remains unclear. In plantation forests, herbicides are often used to control competing vegetation. If trophic cascades are mediated by plant community changes, then managers can potentially manipulate inputs to maximize desired ecosystem services. These manipulations could also include activities to further bird conservation, if it is shown that birds play important roles in these trophic cascades. In our study, we examine whether avian-induced trophic cascades are affected by herbicide use, which we use as a surrogate for land-use intensification in plantation forests.

Exclosures are often used to quantify how vertebrate predators reduce herbivore abundance and indirectly affect plant damage, biomass, and growth. Meta-analyses of such studies provide consistent

This article is protected by copyright. All rights reserved

and strong evidence that arthropods are less abundant in the presence of predators, but that the additional indirect effect of predator exclusion on plants is either attenuated or insignificant (Borer et al. 2006, Whelan et al. 2008, Van Bael at al. 2008, and Mooney et al. 2010, Mäntylä et al. 2011). For example, the presence of predators has been shown to reduce plant damage, but with smaller effect sizes than the reduction of arthropods (Van Bael et al. 2008, Mooney et al. 2010). Effects on plant biomass are generally further attenuated (Mooney et al. 2010, Mäntylä et al. 2011).

In this study, we examine factors that trophic theory suggests will mediate the strength of trophic cascades: the abundance of predators (top-down control by birds) and plants (bottom-up control). We used four herbicide treatment levels to establish a gradient in plant abundance, and manipulated bird access with exclosures that were sufficiently large (225 m^2) to reflect arthropod community dynamics (Englund 1997, Jia et al. 2018) (Fig. 1). In order to isolate the effects of birds from the plant community changes caused by herbivorous ungulates, our exclosures excluded deer and elk (Stokely et al. 2018). We suggest that the controls over bird abundance are the primary mechanisms affecting the strength of trophic cascades. More intensive use of herbicides modifies the plant community by reducing plant diversity and the abundance of non-crop plant species, especially deciduous trees and shrubs. If bird abundance is affected by the availability of foraging and nesting resources at the forest stand scale (MacArthur and MacArthur 1961, Haddad et al. 2011), then trophic cascade strength should be weaker with more intensive herbicide use due to reduced vegetation and consequently reduced bird abundance. We term this the *local trophic cascade* hypothesis (Fig.1). Alternatively, if birds are not affected by the plant community changes caused by herbicides, then bird abundance should remain relatively constant across our four herbicide levels. In this case, birds would be more abundant in relation to arthropods in the intensively managed stands (where food for arthropod herbivores is assumed to be scarce), leading to stronger trophic cascades with increasing use of herbicides. We term this the *evenly-distributed trophic cascade* hypothesis (Fig. 1). Finally, under an Ideal Free Distribution (Fretwell and Lucas 1969, Haché et al. 2013) bird abundance should adjust to the density of arthropod prey. This relatively constant ratio of birds to arthropods would result in no change in cascade strength across the herbicide levels or changes in the plant community; we term this the *ratio-dependent trophic cascade* hypothesis (Fig. 1).

Accepted Article

This article is protected by copyright. All rights reserved

Accepted Article

METHODS

Study site and experimental design

Our study area encompasses managed forest plantations of the Oregon Coast Range, one of the most productive temperate forest ecosystems and a prominent timber producing region in the United States (Adams and Latta 2007). The climate consists of cool, wet winters and mild, dry summers. Forest plantations here are dominated by nursery-stock Douglas-fir (*Pseudotsuga menziesii*), along with other naturally regenerating conifers, deciduous trees, shrubs, and herbs. See Stokely et al. (2018) for a detailed description of the study area.

Our experiment employed a split-plot, randomized complete block design with two treatment factors: herbicide intensity (three levels plus a control without herbicides, replicated over seven blocks) and bird exclusion. From a list of stands scheduled for clearcut harvest in 2009, we assigned 4 stands to each of 7 blocks. Blocks were evenly distributed across a 100 km wide study area and ranged in elevation from 210 to 710 m. Stands within blocks were all within 5 km of each other and at least 1 km apart to minimize within-block variation. Stands were 10 to 19 hectares in size. Following harvest, we randomly assigned one of 4 herbicide treatment levels to each of the 4 stands within a block: (1) a no-herbicide control, (2) a light treatment, (3) a moderate treatment, and (4) an intensive treatment. Our herbicides targeted species that compete with the conifer crop and the treatments were designed to create four levels of non-crop plant abundance. The moderate treatment represents typical current industry practices and the intensive treatment represents an extreme case that attempts to suppress all vegetation except the conifer crop (Betts et al. 2013). Chemicals and applications were relatively consistent across stands for each treatment level. In the winter of 2011, all stands were planted with 2-year-old bare-root nursery Douglas-fir at approximately 1,100 trees/ha (Kroll et al. 2017). Appendix S1 shows the study geography, a diagram of the experimental design, and photos of stand conditions. Appendix S2 provides detailed descriptions of the type, rate, and timing of herbicide applications.

In the early seral stages of stand regeneration following harvest (2012), we constructed two adjacent 15m x 15m exclosures: one fenced and one fenced and netted. By using the fenced exclosure as our control, we eliminated the variation in measured responses that are caused by large mammalian herbivores (deer and elk) altering the plant community (Borer et al. 2005, Stokely et al. 2018). Our

This article is protected by copyright. All rights reserved

Accepted Article

exclosures were relatively large in relation to previous studies, as smaller exclosures (e.g., a single branch or plant) fail to measure arthropods within a community setting that includes the effects of arthropod emigration and immigration (Englund 1997, Jia et al. 2018). Numerous terrestrial taxa prey on arthropods, yet our focus was on birds. Our netted exclosure excluded both birds and bats. However, bats in our study region have been shown to utilize old-growth forest and water as nesting and feeding sites at much higher rates than young-growth forest (up to 10.3 times, Thomas 1988, Clare et al. 2011). The *Myotis* bats that comprise the majority of the bat species in our study area are also more likely to feed on flies and aquatic insects (Waldien et al. 2000), and not the arthropods for which we found strong exclosure effects (see Results). Therefore, birds likely comprise the majority of vertebrate predators in this experiment. Each exclosure consisted of a 2.4 m high fence with a mesh size of 10cm x 8cm. The netted exclosure also included a net with mesh size 18mm x 18mm that was stretched over the top of the fence and draped over the sides, extended to the ground. Exclosures were randomly placed at least 50 m from stand edges, occurred on a wide range of slopes, covered all aspects, and avoided riparian areas, logging trails, and logging debris piles. Nets were removed in the winter to avoid snow loading and reinstalled in the spring.

Arthropod Sampling

We sampled arthropods in each exclosure, once in July and once in August in 2012, 2013, 2014, and 2015 (3 to 6 years following harvest) using methods intended to sample a wide range of substrate and arthropod feeding guilds: sweep net, pitfall trap, and a restricted leaf-turning method. For the sweep net, an observer walked three evenly-spaced parallel transect lines across the length of the exclosure, sweeping a net at ankle- to waist-height with sufficient force to dislodge arthropods while not damaging the vegetation. Three pitfall traps, using a 9 cm diameter plastic cup with rain cover, were evenly spaced across the middle of the exclosure and remained in place for 24 hours. For the leaf-turning method, one representative specimen of the five most abundant tree and shrub species in the plots, one representative of bracken fern (*Pteridium aquilinum*), one representative of sword fern (*Polystichum munitum*), and all Douglas-fir (*Pseudotsuga menziesii*), were sampled. Each sample consisted of examining a fixed number of leaves per plant for deciduous species and five 30 cm branch segments for Douglas-fir. Sampled deciduous tree and shrub species included California hazelnut (*Corylus cornuta*), oceanspray (*Holodiscus discolor*), vine maple (*Acer circinatum*), big-leaf

This article is protected by copyright. All rights reserved

maple (*Acer macrophyllum*), cascara (*Rhamnus purshiana*), red alder (*Alnus rubra*), *Rubus* spp., *Vaccinium* spp., salal (*Gaultheria shallon*), and Oregon grape (*Mahonia nervosa*), depending on site. We detected no difference in the number of Douglas-fir trees in the fenced (Mean = 19.5, SE = 4.6) and netted (Mean = 20.7, SE = 5.1) exclosures (paired t-test, $t_{27} = -1.48$, $P = 0.15$).

Arthropods were identified to the family level in most cases and assigned to a feeding guild (predator, herbivore, detritivore, mixed). For arthropods that were difficult to identify, we assigned a higher taxonomic rank: Chilopoda (class), Acari and Collembola (sub-class), Isopoda, Microcorphyia, and Opiliones (orders); microwasp and midges (sub-orders). The length of each arthropod was measured prior to live release in the center of each plot. No vegetation was removed to sample arthropods. The composite count from the sweep net, pitfall trap, and leaf-turning methods from the two surveys (July and August) represents the relative arthropod abundance for that year.

Vegetation and bird measurements

For each year of the study, we estimated the percent cover of each vascular plant species in twelve 1m x 1m quadrats evenly spaced throughout each plot. The average among the quadrats represents the percent cover for each species each year and total plant cover is the summed cover of all plant species in each plot. Total plant cover can exceed 100 percent due to overlapping canopies.

For each year of the study, we calculated the wood volume of all cultivated Douglas-fir trees in each plot using measurements of height and basal diameter and the formula for the volume of a simple cone. For the years 2013, 2014, and 2015 (2012 data was not available), we calculated needle damage as the proportion of needles damaged by arthropods on marked branches. In our system, needle damage in the form of disfigured, discolored, or partially missing needles is primarily caused by the Cooley spruce gall adelgid (*Adelges cooleyi*).

Relative bird abundance at the stand scale was quantified by point count surveys (Ralph et al. 1995). Four times during the breeding bird season, ten-minute counts were conducted at three points that were evenly distributed throughout each stand with a minimum distance of 150 m between points. All birds detected by sight or sound within a 50 m radius circle were recorded to species. We restricted our analysis to data from insectivorous and omnivorous bird species as defined by Ehrlich et al. (1988).

Statistical Analysis

This article is protected by copyright. All rights reserved

Accepted Article

To examine the cumulative effects of arthropods over the study period, we pooled annual survey data across all four survey years as follows: arthropod and bird relative abundances were summed and total plant cover and Douglas-fir needle damage (both proportional measures) were averaged. We calculated the volume change of Douglas-fir as the difference in volume between the last and first years of the study. By pooling data in this way, our analysis represents cumulative bird and arthropod effects on plants (Mooney and Linhart 2006). To assess the appropriateness of this method, we conducted tests for each individual year (Appendix S3). Initially, we estimated arthropod biomass using a biomass-length regression developed for this study (Loehle et al. 2019), but chose to use arthropod abundance for all subsequent tests due to the high correlation between length and biomass (adjusted $r^2 = 0.91$). We compared our estimates of relative bird abundance calculated from raw data with estimates calculated from a multi-species N-mixture model (described in Appendix S4) that modelled detection as a function of plant cover, date, and year (Yamaura et al. 2012, Pearson et al. 2015). The Pearson correlation (Pearson's r) between estimates of stand-level bird abundance calculated from raw data and detection-corrected data was 0.82. Because of this close correlation and the restrictive assumptions of using N-mixture abundance estimates (Link et al. 2018), we chose to use the relative abundance estimates calculated from raw data for further analysis.

We first tested whether herbicides altered the plant community by modelling total plant cover, plant species richness, and the change in wood volume of Douglas-fir as a function of herbicide intensity. We then tested whether the abundance of arthropods, herbivory damage to Douglas-fir needles, and wood volume change of Douglas-fir (the three response variables) were affected by bird exclusion and whether the strength of this effect changed with either herbicide intensity, total plant cover, or bird abundance. We modelled each logged response variable as a function of bird exclusion and either herbicide level, total plant cover, or bird abundance, and their interaction. We used mixed-effects models (Pinheiro and Bates 2000) using package *nlme* (Pinheiro et al. 2018) in R (R Core Team 2018) and implemented a random effect structure of 1|block/stand/exclosure, corresponding to an intercept with exclosure (n=2 per stand) nested within stand (n=4 per block), nested within block (n=7). We assessed model fit by visual evaluation of residual plots for equal variance and homoscedasticity and then used F-tests to assess the evidence for how each fixed effect and interaction influenced the response variable.

Accepted Article

Accepted Article

To estimate an effect size for trophic strength, we calculated the log-response ratio (LRR) with pairwise comparisons of the treatment factors using the *emmeans* package in R (Russell 2018). Because our response variable was log-transformed, the pairwise comparison between the responses in the presence versus absence of birds results in LRR:

$$\ln[N_{B+}] - \ln[N_{B-}] = \ln[N_{B+} / N_{B-}] = \text{LRR}$$

where N_{B+} and N_{B-} are the mean responses in the presence (fenced exclosure) and absence (netted exclosure) of birds, respectively. The log-response ratio is frequently-used in trophic studies to estimate cascades strength (Hedges et al. 1999, Mooney et al. 2010). Data and the r-code used for statistical tests are provided as supporting information in Data S1. Results of statistical tests are provided in Appendix S5.

RESULTS

Herbicides substantially reduced total plant cover ($F_{3,18} = 18.11$, $p < 0.0001$) and plant richness ($F_{3,18} = 31.43$, $p < 0.0001$), and increased the wood volume of crop trees ($F_{3,18} = 10.15$, $p = 0.0004$) (Fig. 2). Plant cover and richness decreased by 67% (95% CI: 40 to 82%) and 55% (95% CI: 42 to 65%), respectively, in the intensive herbicide treatment in relation to unsprayed controls. The unsprayed controls had the lowest four-year wood volume increase for Douglas-fir.

We collected and identified 94,738 arthropods to the taxonomic level of family (see Methods for taxon exceptions) with 141 different families. The sweep net, pitfall traps, and restricted leaf-turning methods accounted for 64%, 6%, and 30% of the total sample, respectively. The Cooley spruce gall adelgid (*Adelges cooleyi*), a known pest of Douglas-fir, comprised 21% of all sampled arthropods. Larval forms of arthropods were rare in our samples (0.04% of total). We detected 6,004 aerial and leaf-gleaning insectivorous and omnivorous birds, representing 54 species.

Averaged across all herbicide levels, birds reduced arthropod abundance by 16% (95% CI: 6 to 24%) and biomass by 20% (95% CI: 2 to 35%) (Fig. 3). Using a length threshold of 3mm, we found no difference between the effects of bird predation on short and long arthropods. We had considered long arthropods to be more at risk of direct predation (Hagar et al. 2007, Karp and Daily 2014). Birds reduced the abundance of predaceous and herbivorous arthropods 13% (95% CI: 0 to 24%) and 21% (95% CI: 12 to 31%), respectively, but did not affect the abundance of detritivores. Among the families with species known to be pests of Douglas-fir (Goheen and Willhite 2006), birds reduced

This article is protected by copyright. All rights reserved

Acrididae (grasshoppers) by 41% (95% CI: 28 to 51%), *Curculionidae* (a large family that includes bark beetles) by 34% (95% CI: 9 to 53%), and *Adelgidae* by 30% (95% CI: 17 to 41%). *Diprionidae* (sawflies), *Aphididae* (aphids), and *Geometridae* (moths) showed little evidence of an exclosure effect.

Even though birds reduced arthropod abundance, and herbicides substantially influenced the vegetation community, the strength of top-down effects did not change with herbicide intensity (Fig. 4) or with total plant cover. We found little evidence for an interaction between exclusion and herbicide level ($F_{3,24} = 1.63$, $P = 0.21$) or exclusion and total plant cover ($F_{1,25} = 0.003$, $P = 0.96$) on the abundance of arthropods. The presence of birds reduced needle damage by 14% (95% CI: 5 to 23%), but this effect did not change with herbicide intensity ($F_{3,24} = 1.56$, $P = 0.22$). We did not find evidence for an exclosure effect on wood volume change. Averaged across all herbicide levels, wood volume in the presence of birds increased 5% but confidence intervals were broad and bounded zero (95% CI: -14 to 29%).

Similarly, even though bird abundance increased with total plant cover ($F_{1,20} = 11.22$, $P = 0.003$, Fig. 5), we found little evidence that increased bird abundance altered the top-down control (predation) on arthropods ($F_{1,26} = 0.93$, $P = 0.34$).

DISCUSSION

We experimentally manipulated two trophic levels (predators and plants) and quantified the abundance of organisms across three levels (birds, arthropods, and plants). We found that birds reduced the number of arthropods and arthropod-induced plant damage, but this trophic cascade did not result in the ecosystem service of increased crop-tree growth. Our finding that neither herbicide intensity nor plant cover, our surrogate for vegetation abundance, mediated cascade strength contradicts theory following from the *ecosystem exploitation hypothesis* as well as our *local trophic cascade* and *evenly-distributed trophic cascade* hypotheses, but is consistent with our *ratio-dependent trophic cascade* hypothesis – that bird abundance should adjust to the density of arthropod prey (Fig. 1c). Therefore, our study provides important insight into the interacting roles of top-down and bottom-up controls over trophic cascades

The relative abundance of all arthropods in our experiment was reduced by 16% in the presence of birds. This effect size is smaller than averages reported in other studies. For instance, in a meta-

Accepted Article

This article is protected by copyright. All rights reserved

analysis of 113 vertebrate predator exclusion studies (Mooney et al. 2010), average arthropod abundance was reduced by 38%. The smaller effect size we calculated could be due to several factors. Variability in effect sizes reported in the exclosure literature has been attributed to contextual differences such as experimental design, ecosystem, taxa, and how responses were measured (Karp et al. 2018, Jia et al. 2018). For example, Borer et al. (2005) found that effect sizes were weakest among endothermic predators compared to other taxa. Also, bird abundance may be suppressed in in our study area due to low landscape-scale abundance of arthropod prey. In our study area, industrial plantation forests comprise at least 40% of the landscape (Ohmann et al. 2007) and arthropod abundance and diversity has been shown to be reduced in plantations compared to other forest types (Schowalter 1995).

Several explanations exist for why bird-induced trophic cascades may not have led to changes in wood growth. Many studies have measured plant biomass, but only a few (for trees) have measured growth or the ultimate ecosystem service of changes in yield. Trophic cascades may increase plant biomass (Marquis and Whelan 1994, Schmitz et al. 2000, Borer et al. 2006, Mooney et al. 2010, Mäntylä et al. 2011) and the yields of commodities such as apples (Mols and Visser 2002), coffee (Kellerman et al. 2008, Karp et al. 2013), and cacao (Maas et al. 2013). However, we are aware of only two studies that found increases in wood growth; for conifers (Mooney and Linhart 2006) and deciduous trees (Bridgeland et al. 2010). Biomass represents all plant material including leaves and therefore it can be expected to decrease due to herbivory. The effects on yield were observed in systems where tissue-boring insects directly damaged annual fruits or when herbivory was caused by large numbers of non-native arthropods. In our system, the commodity crop grows over a period of up to 60 years before being harvested (Adams et al. 2005). Therefore, long-term experiments may be required to rigorously examine the effect of trophic cascades on timber production.

The strength of trophic cascades could also vary by year and growing conditions, as suggested by Bridgeland et al. (2010). They found a significant bird-induced trophic cascade on trunk growth in a year with higher precipitation, tree growth, and arthropod abundance compared to the second year of their study. Similarly, Meserve et al. (2003) found evidence for shifting trophic effects due to precipitation in a 13-year exclosure study in a semi-arid setting. In our study, the cumulative 4-year effect of excluding birds was a reduction in arthropod abundance, but this result also varied by year

Accepted Article

This article is protected by copyright. All rights reserved

Accepted Article

(see Appendix S3). An experiment that excludes birds throughout the entire harvest cycle of up to 60 years (for plantation forests in Oregon) would provide stronger inference. Unfortunately, such an experiment would be logistically and economically challenging (e.g., draping exclosure nets over trees that exceed 30 m in height). Nevertheless, it seems unlikely that bird-induced trophic cascades will benefit tree growth to the same degree as release from interspecific plant competition that occurs as a result of herbicide applications.

Trophic theory predicts that intraguild predation, when birds consume both predaceous and herbivorous arthropods, will weaken trophic cascades (Polis and Holt 1992). Under intraguild predation, excluding birds releases predaceous arthropods from consumption, resulting in increased predation upon herbivorous arthropods. In a manipulative experiment in a pine ecosystem influenced by an ant-aphid mutualism, Mooney and Linhart (2006) found that when insectivorous birds fed as intraguild predators, there were no detectable effects on plant biomass, but an increase in wood growth occurred without intraguild predation. In our study, birds likely acted as intraguild predators because we found little difference between the exclosure effect on predaceous and herbivorous arthropods (Fig. 3). Therefore, our finding that wood volume was not influenced by bird exclusion is consistent with Mooney and Linhart (2006).

Chemical defense mechanisms of conifers may also explain the lack of a detectible wood-volume change in this experiment. Defense mechanisms of *Pinaceae* have evolved in concert with their herbivorous mammalian and arthropod pests. These defenses include constitutive and induced chemical compounds, typically terpenoids, which can decrease herbivory, oviposition, survival, and fecundity (Schmitz et al. 2000, Mumm and Hilker 2006). Additionally, fungal endophytes in the needles of Douglas-fir reduce the forage quality of vegetation for some herbivores (Omacini et al. 2001).

Finally, under the conditions of our study, herbivorous arthropods may not detectably constrain wood growth of the crop species. The most-closely monitored pests of Douglas-fir, Cooley spruce gall adelgid (*Adelges cooleyi*) and bark beetles (in the *Curculionidae* family), were significantly reduced by the presence of birds. These taxa are not currently considered by managers to be of concern for the overall health of Douglas-fir plantations in Oregon (Oregon 2017). However, adelgids occasionally cause enough damage to warrant concern in intensively-managed Christmas tree plantations (Goheen

This article is protected by copyright. All rights reserved

and Willhite 2006). Adelgids are quite small (approximately 1 mm in length) and we have no direct evidence of bird predation on adelgids. However, we know that birds consume other very small insects. For example, Dixon (1960) found 100 aphids in one chickadee bird stomach. Bark beetles can negatively impact tree growth and cause mortality directly or by acting as vectors for black stain root disease (*Leptographium wageneri*), a lethal fungal pathogen that appears to have increased in recent years in the Oregon Coast Range (Oregon 2017). Douglas-fire beetles can increase infestation rates when large amounts of downed wood are present (which was not the case for our study), such as from large-scale disturbance or thinning (Ross et al. 2006). Therefore, in a scenario where changing environmental or management conditions could lead to an increase in the densities of these pests, the trophic effects of bird predation may become more valuable to crop-tree production.

Although our findings that trophic cascades were not mediated by herbicide intensity or vegetation abundance contradict the *ecosystem exploitation hypothesis*, they align with a meta-analysis that found no consistent relationship between primary productivity and cascade strength (Borer et al. 2005). The lack of significant herbicide or vegetation effects on the strength of trophic cascades may be attributed to the combined effects of defensive mechanisms of plants and intraguild predation.

CONCLUSION

For the temperate forest plantations we studied, our experiment provides important contributions to our understanding of trophic dynamics: birds reduced herbivorous arthropods and plant damage, increased herbicide use (our surrogate for land-use intensification) did not change the magnitude of these reductions, and birds did not detectably increase wood growth of the crop species over four years. Even though we did not find that birds helped our crop trees grow, birds still provided the important ecosystem services of pest control and the associated reduction in plant damage, services that can potentially increase in importance under different management and environmental conditions. Birds provide additional ecosystem services we did not study such as seed dispersal, pollination, recreation, and cultural services, in addition to having intrinsic value (Şekercioğlu et al. 2016). Therefore, birds serve important roles in forest systems. Our finding that herbicides did not detectably alter the strength of trophic effects may provide more options for manipulating management inputs in

Accepted Article

This article is protected by copyright. All rights reserved

plantation forests, but longer-term studies will be necessary to more completely elucidate the trophic role of birds in these systems.

ACKNOWLEDGMENTS

This work was supported by the National Science Foundation Graduate Research Fellowship (No. 1840998) to S. Harris. Funding for the experiment was provided by grants from the USDA Agriculture and Food Research Initiative (AFRI-2009-04457, AFRI-2015-67019-23178), the National Council for Air and Stream Improvement, the Oregon Forest Industries Council, and the Oregon State University (OSU) College of Forestry (Giustina Family Research grant, Noble fund, Fish and Wildlife Habitat in Managed Forests grant, and Institute for Working Forest Landscapes). We gratefully acknowledge access to study sites and implementation of treatments provided by Weyerhaeuser Company, Hancock Forest Management, Plum Creek Timber Company, and the Oregon Department of Forestry. Ariel Muldoon provided valuable statistical advice. Melissa Scherr was the lead entomologist.

LITERATURE CITED

Adams, W. T., S. Hobbs, and N. Johnson. 2005. Intensively managed forest plantations in the pacific northwest: introduction. Journal of Forestry 103:59–60.

Adams, D. M., and G. S. Latta. 2007. Timber trends on private lands in western Oregon and Washington: a new look. Western Journal of Applied Forestry 7.

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.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? Ecology 86:528–537.

Borer, E. T., B. S. Halpern, and E. W. Seabloom. 2006. Asymmetry in community regulation: effects of predators and productivity. Ecology 87:2813–2820.

Bridgeland, W. T., P. Beier, T. Kolb, and T. G. Whitham. 2010. A conditional trophic cascade: birds benefit faster growing trees with strong links between predators and plants. Ecology 91:73–84.

Accepted Article

This article is protected by copyright. All rights reserved

Accepted Article

Clare, E. L., B. R. Barber, B. W. Sweeney, P. D. N. Hebert, and M. B. Fenton. 2011. Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). Molecular Ecology 20:1772–1780.

d'Annunzio, R., M. Sandker, Y. Finegold, and Z. Min. 2015. Projecting global forest area towards 2030. Forest Ecology and Management 352:124–133.

de Groot, R., L. Brander, S. van der Ploeg, R. Costanza, F. Bernard, L. Braat, M. Christie, N. Crossman, A. Ghermandi, L. Hein, S. Hussain, P. Kumar, A. McVittie, R. Portela, L. C. Rodriguez, P. ten Brink, and P. van Beukering. 2012. Global estimates of the value of ecosystems and their services in monetary units. Ecosystem Services 1:50–61.

Dixon, K. L. 1960. Additional data on the establishment of the chestnut-backed chickadee at Berkeley, California. Condor 62:405–408.

Donald, P. F., R. E. Green, and M. F. Heath. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:25–29.

Elton, C. S., 1927. Animal Ecology. Sidgwick and Jackson. London, UK.

Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. Ecology 78:2316–2325.

Ehrlich, P., D.S. Dobkin, and D. Wheye. 1988. The Birder's Handbook. Simon and Schuster. New York. NY, USA.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fretwell, S. D., and A. L. Barach. 1977. The regulation of plant communities by the food chains exploiting them. Perspectives in Biology and Medicine 20:169–185.

Goheen, E. M., and E. A. Willhite. 2006. Field guide to common diseases and insect pests of Oregon and Washington conifers. R6-NR-FID-PR-01-06, USDA Forest Service Pacific Northwest Region, Portland, OR, USA.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, and D. Tilman. 2011. Plant diversity and the stability of foodwebs. Ecology Letters 14:42–46.

Hagar, J. C., K. M. Dugger, and E. E. Starkey. 2007. Arthropod prey of Wilson's warblers in the understory of Douglas-fir forests. The Wilson Journal of Ornithology 119:533–546.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response rations in experimental ecology. Ecology 80:1150–1156.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. The American Naturalist 94:421–425.

Jia, S., X. Wang, Z. Yuan, F. Lin, J. Ye, Z. Hao, and M. S. Luskin. 2018. Global signal of top-down control of terrestrial plant communities by herbivores. Proceedings of the National Academy of Sciences 115:6237–6242.

Karp, D. S., C. D. Mendenhall, R. F. Sandí, N. Chaumont, P. R. Ehrlich, E. A. Hadly, and G. C. Daily. 2013. Forest bolsters bird abundance, pest control and coffee yield. Ecology Letters 16:1339–1347.

Karp, D. S., and G. C. Daily. 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. Ecology 95:1065–1074.

Karp, D. S. et al. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proceedings of the National Academy of Sciences 115:E7863–E7870.

Keenan, R. J., G. A. Reams, F. Achard, J. V. de Freitas, A. Grainger, and E. Lindquist. 2015. Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management 352:9–20.

Kellermann, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. Conservation Biology 22:1177–1185.

Kroll, A. J., J. Verschuyl, J. Giovanini, and M. G. Betts. 2017. Assembly dynamics of a forest bird community depend on disturbance intensity and foraging guild. Journal of Applied Ecology. 54:784–793

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–417.

Link, W. A., M. R. Schofield, R. J. Barker, and J. R. Sauer. 2018. On the robustness of N-mixture models. Ecology 99:1547–1551.

Accepted Article

This article is protected by copyright. All rights reserved

Accepted Article

Loehle, C., M. Scherr, and J. Verschuyl. 2019. Foliage arthropod biomass equations for open vegetation conditions of the Pacific Coast Range. Northwest Science 93:155.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Mäntylä, E., T. Klemola, and T. Laaksonen. 2011. Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia 165:143–151.

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of White Oak through consumption of leaf-chewing insects. Ecology 75:2007–2014.

Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutiérrez. 2003. Thirteen years of shifting top-down and bottom-up control. BioScience 53:633.

Meyfroidt, P., and E. F. Lambin. 2011. Global forest transition: prospects for an end to deforestation. Annual Review of Environment and Resources 36:343–371.

Mols, C. M., and M. E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology 39:888–899.

Mooney, K. A., and Y. B. Linhart. 2006. Contrasting cascades: insectivorous birds increase pine but not parasitic mistletoe growth. Journal of Animal Ecology 75:350–357.

Mooney, K. A., D. S. Gruner, N. A. Barber, S. A. Van Bael, S. M. Philpott, and R. Greenberg. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proceedings of the National Academy of Sciences 107:7335–7340.

Mumm, R., and M. Hilker. 2006. Direct and indirect chemical defense of pine against folivorous insects. Trends in Plant Science 11:351–358.

Ohmann, J. L., M. J. Gregory, and T. A. Spies. 2007. Influence of environment, disturbance, and ownership on forest vegetation of coastal Oregon. Ecological Applications 17:18–33.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. The American Naturalist 118:240–261.

Omacini, M., E. J. Chaneton, C. M. Ghersa, and C. B. Müller. 2001. Symbiotic fungal endophytes control insect host–parasite interaction webs. Nature 409:78–81.

Oregon. 2017. Forest health highlights in Oregon - 2016. Oregon Department of Forestry and USDA Forest Service. Portland, OR, USA.

This article is protected by copyright. All rights reserved

Accepted Article

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. The Journal of Animal Ecology 49:666.

Pearson, S. F., J. Giovanini, J. Jones, and A. J. Kroll. 2015. Breeding bird community continues to colonize riparian buffers ten years after harvest. PLOS One 10:e014324.

Pinheiro J. and D. Bates. 2000. Mixed-Effects Models in S and S-PLUS. Springer, New York, NY, USA.

Pinheiro J., D. Bates , S. DebRoy, D. Sarkar, R Core Team. 2018. nlme: linear and nonlinear mixed effects models. R package version 3.1-137.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology & Evolution 7:151–154.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ralph, C. J., S. Droege, and J. S. Sauer. 1995. Monitoring bird populations by point counts. General Technical Report PSW-GTR-149, U.S. Department of Agriculture, Forest Service, Albany, CA, USA.

Ripple, W. J., J. A. Estes, O. J. Schmitz, V. Constant, M. J. Kaylor, A. Lenz, J. L. Motley, K. E. Self, D. S. Taylor, and C. Wolf. 2016. What is a Trophic Cascade? Trends in Ecology & Evolution 31:842–849.

Ross, D. W., B. B. Hostetler, and J. Johansen. 2006. Douglas-fir beetle response to artificial creation of down wood in the Oregon Coast Range. Western Journal of Applied Forestry 21:117–122.

Russell, L. 2018. emmeans: estimated marginal means, aka least-squares means. R package version 1.2.3.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. The American Naturalist 155:141–153.

Schowalter, T. D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. Forest Ecology and Management 78:115–125.

Şekercioğlu, C. H., D. G. Wenny, and C. J. Whelan (eds.). 2016. Why Birds Matter. University of Chicago Press. Chicago, IL, USA.

This article is protected by copyright. All rights reserved

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Sloan, S., and J. A. Sayer. 2015. Forest resources assessment of 2015 shows positive global trends but forest loss and degradation persist in poor tropical countries. Forest Ecology and Management 352:134–145.

Stokely, T. D., J. Verschuyl, J. C. Hagar, and M. G. Betts. 2018. Herbicides and herbivory interact to drive plant community and crop-tree establishment. Ecological Applications 28:2011–2023.

Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. The Journal of Wildlife Management 52:619.

Thies, C., S. Haenke, C. Scherber, J. Bengtsson, R. Bommarco, L. W. Clement, P. Ceryngier, C. Dennis, M. Emmerson, V. Gagic, V. Hawro, J. Liira, W. W. Weisser, C. Winqvist, and T. Tscharntke. 2011. The relationship between agricultural intensification and biological control: experimental tests across Europe. Ecological Applications 21:2187–2196.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8:857–874.

Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. Nature 445:202–205.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology 89:928–934.

Waldien, D. L., J. P. Hayes, and E. B. Arnett. 2000. Day-roosts of female long-eared Myotis in Western Oregon. The Journal of Wildlife Management 64:785–796.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134:25–60.

Yamaura, Y., J. A. Royle, N. Shimada, S. Asanuma, T. Sato, H. Taki, and 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.

Accepted Article

This article is protected by copyright. All rights reserved

Accepted Article

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/xxxxxxxxxx/suppinfo.

FIGURE CAPTIONS

Figure 1. Bird exclosures in the first year of a 4-year study in forest plantations in the Oregon Coast Range, USA in the a) no herbicide control and b) intensive herbicide treatments. c) Conceptual diagram of three alternative hypotheses to describe trophic cascade strength as a function of herbicide intensity and vegetation abundance. In our experiment, vegetation abundance is directly influenced by the intensity of herbicide use, reflecting a gradient in management intensity.

Figure 2. Vegetation responses over 4 years to an experimental gradient in herbicide application intensity in forest plantations in the Oregon Coast Range, USA. Increasing intensity of herbicide resulted in: (a) a decrease in total plant cover ($F_{3,18} = 18.11$, $p < 0.0001$), (b) a decrease in plant species richness ($F_{3,18} = 31.43$, $p < 0.0001$), and (c) an increase in wood volume change of the target crop species, Douglas-fir ($F_{3,18} = 10.15$, $p = 0.0004$). Statistical tests relaxed the assumption of equal variance among herbicide treatments. The control has no herbicide application. Points and boxplots (mean, 1st and 3rd quartiles) are from raw data (n=7 for each herbicide level). Total plant cover is the mean cumulative cover of all plant species over 4 years. Richness is the mean richness over 4 years. Volume change is the mean difference between the 2015 and 2012 wood volume of all planted Douglas-fir trees.

Figure 3. The cumulative trophic effects of bird exclusion over 4 years, shown on the bottom axis as the natural log response ratio, ln[presence of birds / absence of birds], and 95% unadjusted confidence intervals, on arthropod abundance (by family, ecological, and life history characteristics) in forest plantations in the Oregon Coast Range, USA. Negative values indicate a lower value in the presence of birds. The number of individual specimens are provided in parentheses. The arthropod families shown are known pests of Douglas-fir (Goheen and Willhite 2006). The top axis shows the effect size as percent change in the presence of birds.

Figure 4. The cumulative trophic effects of birds over 4 years in forest plantations in the Oregon Coast Range, USA. Shown on the left axis is the natural log response ratio, ln[presence of birds / absence of birds], and 95% unadjusted confidence intervals. Negative values indicate a lower value in

This article is protected by copyright. All rights reserved

the presence of birds. Averaged across all levels of herbicide intensity, in the presence of birds: (a) arthropod abundance was reduced by 16% ($F_{1,24} = 11.39$, $P = 0.003$), (b) plant damage was reduced by 14% ($F_{1,24} = 9.87$, $P = 0.004$), and (c) there was no evidence for an effect on the change in wood volume ($F_{1,24} = 0.29$, $P = 0.59$). For all response variables, there was also no evidence that the trophic effect strength changed with herbicide level. Plant damage is the ratio of damaged Douglas-fir needles. Wood volume change is the change in volume of planted Douglas-fir trees between 2012 and 2015. The right axis shows the effect size as percent change in the presence of birds.

Figure 5. Relationship between cumulative total plant cover and cumulative bird abundance from a 4-year study on forest plantations in the Oregon Coast Range, USA. The gray band depicts the 95% confidence intervals around the predicted values from linear mixed model regression. Raw data points are shown, color-coded for herbicide treatment level.

Accepted Article

This article is protected by copyright. All rights reserved

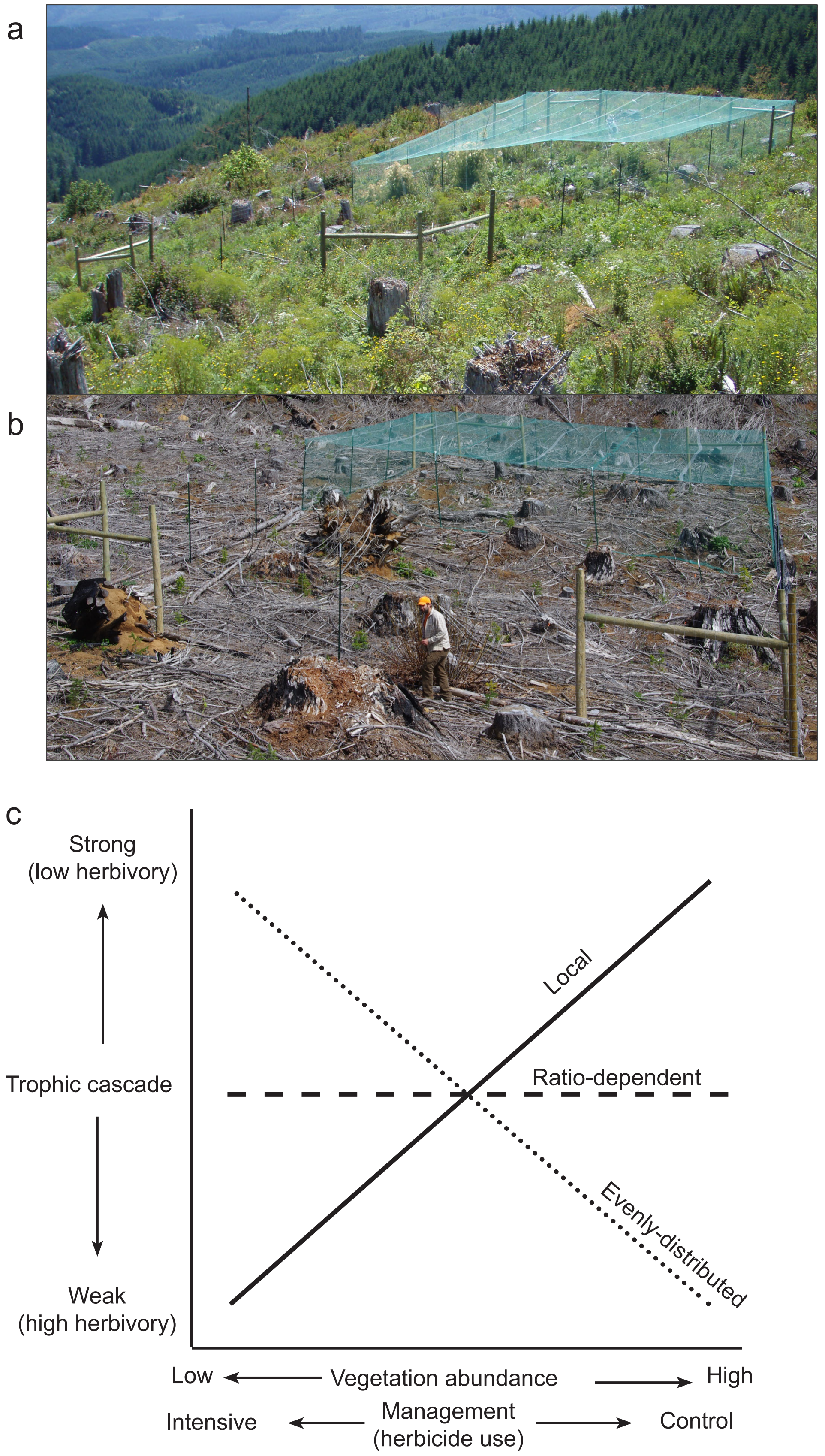
a
b
c
Strong
(low herbivory)
Trophic cascade
Weak
(high herbivory)
Local
Ratio-dependent
Evenly-distributed
Low
Vegetation abundance
High
Intensive
Management
(herbicide use)
Control

Figure 1.

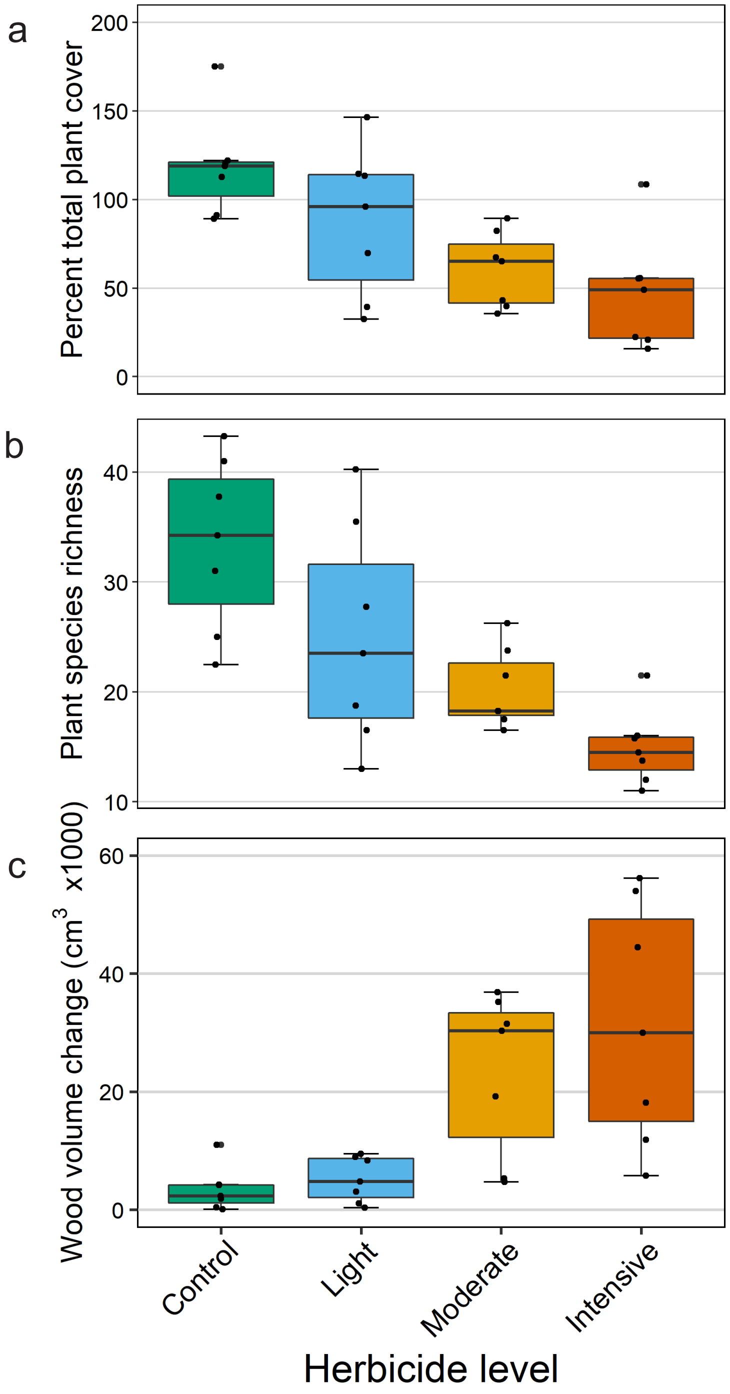
a
Percent total plant cover
200
150
100
50
0
b
Plant species richness
40
30
20
10
c
Wood volume change (cm^3 x1000)
60
40
20
0
Control
Light
Moderate
Intensive
Herbicide level

Figure 2.

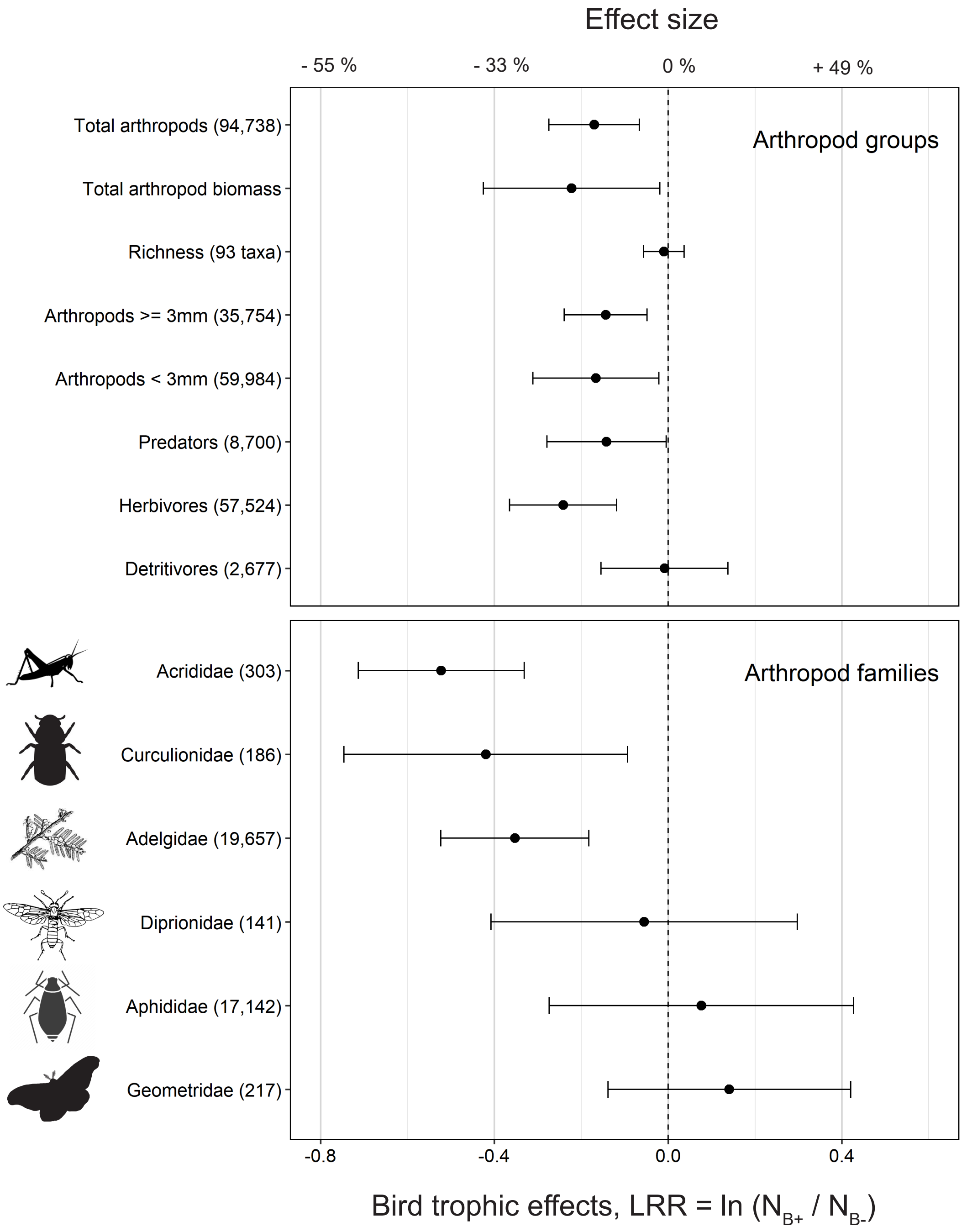
Effect size
- 55 %
- 33 %
0 %
+ 49 %
Arthropod groups
Total arthropods (94,738)
Total arthropod biomass
Richness (93 taxa)
Arthropods >= 3mm (35,754)
Arthropods < 3mm (59,984)
Predators (8,700)
Herbivores (57,524)
Detritivores (2,677)
Arthropod families
Acrididae (303)
Curculionidae (186)
Adelgidae (19,657)
Diprionidae (141)
Aphididae (17,142)
Geometridae (217)
-0.8
-0.4
0.0
0.4
Bird trophic effects, LRR = ln (N_B+ / N_B-)

Figure 3.

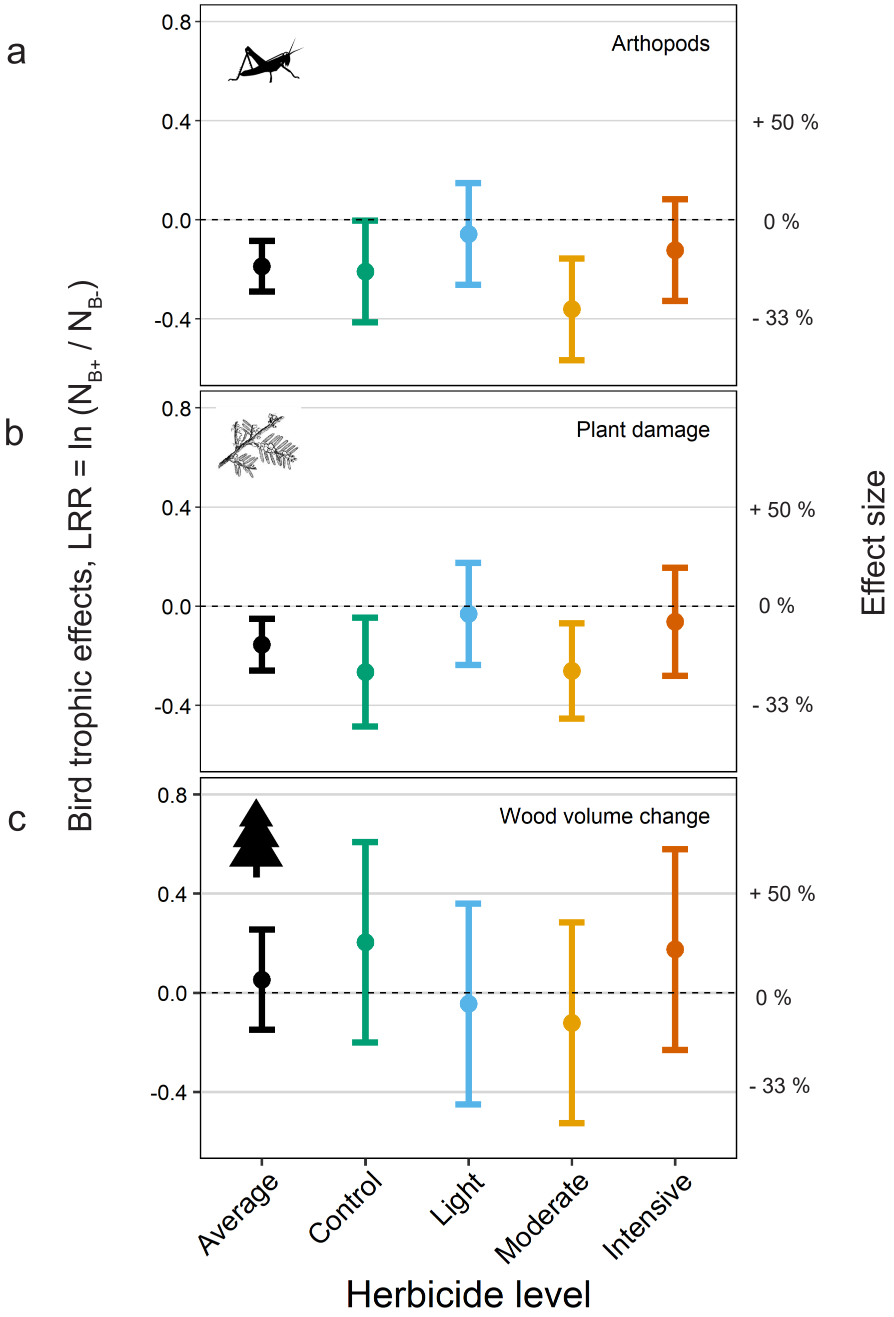
a
b
c
Arthopods
Plant damage
Wood volume change
0.8
0.4
0.0
-0.4
+ 50 %
0 %
- 33 %
Bird trophic effects, LRR = ln (N_{B+} / N_{B-})
Effect size
Average
Control
Light
Moderate
Intensive
Herbicide level

Figure 4.

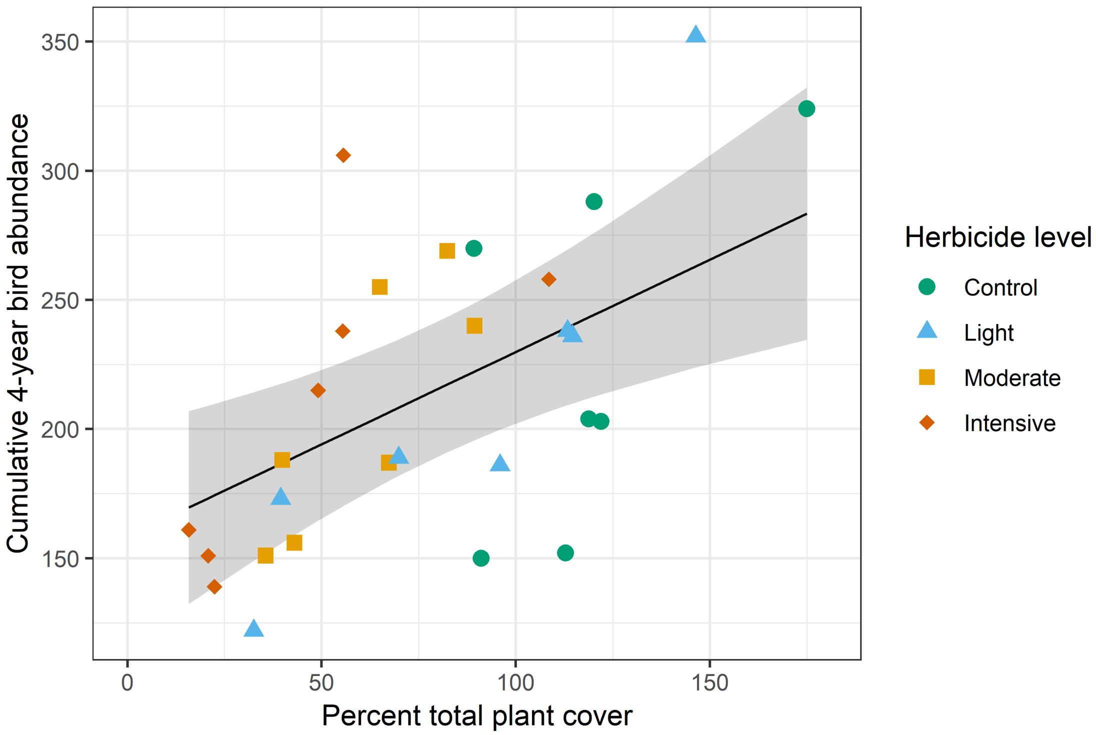
Cumulative 4-year bird abundance
350
300
250
200
150
0
50
100
150
Percent total plant cover
Herbicide level
Control
Light
Moderate
Intensive

Figure 5.