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RESEARCH ARTICLE

Bird response to disturbance varies with forest productivity in the northwestern United States

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Abstract Huston's Dynamic Equilibrium Hypothesis predicts that the response of biodiversity to disturbance varies with productivity. Because disturbance is thought to break competitive advantage of dominant species in productive ecosystems, species richness is predicted to increase with disturbance frequency in productive systems. Recovery of plant biomass following disturbance is also predicted to be faster in productive systems. Here we provide the first test of Huston's hypothesis in the context of setting harvest rates in managed forests for achieving biodiversity objectives. We examined predictions relating to vegetation and bird response to disturbance and succession in productive and less productive forests in western Oregon and Washington, USA. We found that measurements of understory cover and shrub diversity were higher in young, productive stands than less productive stands of similar age. Later-seral forests in productive environments (mean age = 67 years) had less variable and more complete canopy closure than similar-age forests in less favorable settings. At the stand scale, bird abundance and richness decreased with canopy closure in highly productive forests whereas bird abundance and richness increased with canopy closure in less productive forests. At the landscape scale, bird abundance and richness within stands increased with increasing levels of disturbance in the surrounding landscape within highly productive forests, whereas bird abundance and richness decreased with increasing disturbance in the surrounding landscape within less productive forests. Our results indicate that bird response to disturbance varies across levels of productivity and suggest that bird species abundance and associated species richness will be maximized through relatively more frequent disturbance in highly productive systems.

Keywords Disturbance · Productivity · Dynamic equilibrium · Intermediate disturbance hypothesis · Competition · Forest ecology · Forest management · Birds · Diversity

Introduction

A major question in forestry is how to manage levels of disturbance at the landscape scale to accomplish biodiversity and other goals (Seymour and Hunter 1999; Lindenmayer and Franklin 2002). In addition to wood production goals, levels of timber harvest are often set to best balance the requirements of species

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specializing on particular seral stages or forest structural conditions. On federal lands in the northwestern United States, emphasis has been placed on maintaining habitats for species dependent upon late-seral habitats, such as the northern spotted owl (*Strix occidentalis caurina*). Thus, logging has been reduced to retain old-growth forest habitats (Tuchmann et al. 1996). However, federal managers are required by the National Forest Management Act (1976) to retain viable populations of all native wildlife including early-seral specialists (Nelson et al. 1983). On private forest lands, wood production is often favored by short-rotations and harvest rates are set partially based on the constraints imposed by voluntary and/or legal biodiversity mandates which specify providing habitats for both early and late-seral species (Loehle et al. 2002). Thus, both federal and private forest managers in the northwestern United States strive to set harvest levels to provide habitats for some combination of early and late-seral species.

Much of the theoretical basis of using timber harvest to manage forest diversity comes from the Intermediate Disturbance Hypothesis (Connell 1978; Kohm and Franklin 1997). This hypothesis suggests that species diversity is often highest at intermediate levels of disturbance because habitats are maintained for both early and late-seral species. The hypothesis is supported by empirical evidence indicating that individual species abundances and forest community diversity are strongly influenced by gradients in seral-stage and structural complexity (Kohm and Franklin 1997; Harris 1984; McElhinny et al. 2005). Natural disturbance regimes differ among ecosystems as determined by climate, soils, forest productivity, disturbance type, and other factors (Pickett and White 1985; Spies and Turner 1999). Because organisms are often adapted to natural disturbance and landscape dynamics, natural range of variation is sometimes used as a guide for determining intermediate disturbance rates (Landres et al. 1999).

It is not yet widely appreciated in forestry, however, that the effects of disturbance on biodiversity may vary across gradients in forest productivity. Huston (1979, 1994) predicted that the response of species richness to disturbance varies with ecosystem productivity such that richness increases with increasing disturbance in productive systems (Fig. 1). The premise of the Huston's Dynamic Equilibrium Hypothesis (DEH) is that in productive environments a few species are able to dominate the community in the absence of disturbance and competitively exclude other species, thus depressing diversity. Disturbance breaks this competitive dominance, frees resources that allow for rapid recovery of post-disturbance communities and increases functional heterogeneity (spatial and temporal variability in biological legacies and physical conditions, Odion and Sarr 2007) and associated species diversity. Alternatively, recovery following disturbance occurring in low productivity environments is predicted to be slow and more variable as resources and conditions limit species growth rates. Disturbance events in these environments typically compounds physiological stress that organisms experience where resources are already limited resulting in decreased species richness (Huston 2004). Hence, depending on the setting, disturbance may act to enhance diversity by breaking competitive dominance and limit diversity through environmental stress (Odion and Sarr 2007).

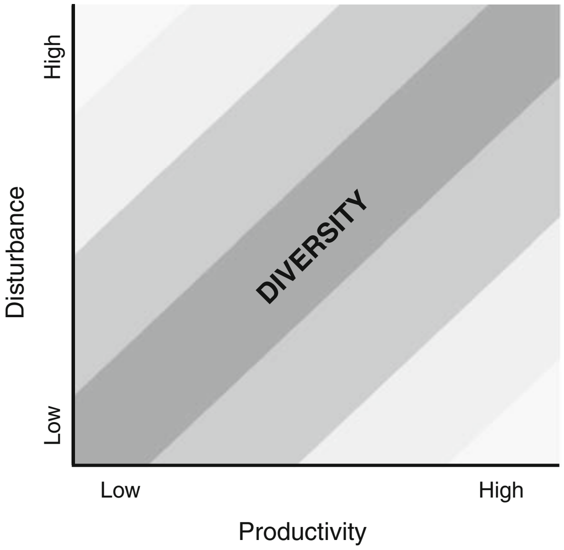


Fig. 1 Theoretical representation of the predictions of the dynamic equilibrium hypothesis (Huston 1979, 1994) for species diversity in relation to productivity and mortality-causing disturbance. High diversity is represented by *darker shading* with the highest diversity along the diagonal. Figure adapted from Huston (1994)

In the northwestern United States, evolutionary conditions have led to the dominance of large stature coniferous forest species, especially in the more productive west-side Cascades (Waring and Franklin 1979). The potential for competitive dominance is thought to be greater in productive environments where the onset of competitive exclusion is rapid (Huston 1979). Data support this premise as diversity across taxa groups is negatively correlated with older, even-aged conifer dominated stands in highly productive forests (Verschuyl et al. 2008; Hayes et al. 2005). Conversely, in less-productive east-side Cascade sites, species diversity is limited by harsh abiotic conditions that act to control species diversity (Verschuyl et al. 2008; Swenson and Waring 2006). These west and east-side Cascade landscapes provide an ideal setting for considering how disturbance may act to both enhance and limit species diversity across a gradient in productivity.

Huston's DEH has been tested empirically for microbial communities (Rashit and Bazin 1987) grassland communities (Huston 1980), plants (Bakker et al. 2006; Osem et al. 2002; Proulx and Mazumder 1998) and for other ecological communities (Worm et al. 2002; Cardinale et al. 2006; Widdicombe 2001). We know of no studies, however, testing Huston's DEH in the context of setting harvest rates in managed forests for achieving biodiversity objectives. Based on the DEH, timber harvest as a form of disturbance in forests is expected to affect species diversity and individual species recovery differently in highly productive environments than less productive environments. Specifically, we expect that recently disturbed forest stands in productive west-side Cascades will experience rapid vegetative recovery supporting high levels of biomass and greater functional heterogeneity in plant communities than in forest stands in a less productive environment. Bird abundance and diversity are expected to follow this response in vegetation through two mechanisms. First, rapid vegetative recovery and high levels of plant biomass following disturbance in productive stands will facilitate bird abundance and richness through the "more individuals hypothesis", which suggests that higher levels of plant biomass and food resources for birds allow for more individuals in populations, fewer population extinctions, and more species in a community (Hurlbert 2004; Monkkonen et al. 2006). Second, increased disturbance would reduce competitive exclusion by dominant plants, increasing functional habitat heterogeneity favoring higher bird diversity, a relationship well supported for birds (Carey et al. 1999; Hunter 1999; Sallabanks et al. 2006).

The primary purpose of this paper is to investigate how vegetation structure and bird community response to timber harvest varies across levels of ecosystem productivity. The effects of competitive dominance by trees in late-seral forests and rates of recovery of vegetation following disturbance are predicted to strongly shape vegetation structure and influence bird abundance and diversity. Testing the DEH is important in the context of forestry because it suggests that effective management of biodiversity through timber harvest, including the balance of early and late-seral species, should be tailored to local settings varying in productivity. We tested the following predictions.

1. In productive settings, open canopy stands recover more rapidly and develop more vegetative cover than in low productivity settings.
2. Consistent with the mechanisms of competitive exclusion by dominant trees, late-seral stands have higher canopy closure and less variation in canopy closure in productive settings.
3. At the stand scale, bird species richness and abundance within stands is positively related to recent disturbance in a productive landscape and is negatively related to recent disturbance in a less productive landscape.
4. At the landscape scale, due to the first three predictions, bird species richness will increase with increasing disturbance in the landscape surrounding survey stands.

Methods

Study area

The study included two landscapes in the northwestern United States: Springfield, Oregon, a productive low elevation landscape located in the foothills of the west-side Cascades surrounding the Willamette Valley; and Cle Elum, Washington, a less productive landscape east of the Cascade crest. Landscape selection emphasized forest sites that contained a similar pool of bird species across gradients in forest productivity and forest disturbance. Similar gradients in forest structural conditions and forest edge density are represented within each site.

Springfield, OR

Weyerhaeuser's Springfield and Cottage Grove tree farms and surrounding BLM and USFS lands are located east of Eugene, Oregon, in the western foothills of the Oregon Cascades (Fig. 2; Table 1). This area is within the *Tsuga heterophylla* Forest Zone (Franklin and Dyrness 1988) and dominant species are Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and grand fir (*Abies grandis*). However, hardwood species become more abundant on drier microsites at the southern end of the study landscape (e.g. oak [*Quercus* spp.], chinquapin [*Castanopsis chrysophylla*] and Pacific madrone [*Arbutus menziesii*]). Land ownership is a checkerboard of Bureau of Land Management (BLM) and private lands bordered by the Willamette National Forest and the H.J. Andrews Experimental Forest. The Springfield landscape is comprised of mostly second and third growth forests with a wide range of structural conditions.

Cle Elum, WA

The Cle Elum landscape is located along the I-90 corridor in Washington's Central Cascades (Fig. 2; Table 1). Plum Creek Timber Company's ownership totals roughly 57,000 ha distributed in a checkerboard pattern with Mount Baker-Snoqualmie and Wenatchee National Forest land. This area is within the *Abies grandis* and *Pseudotsuga menziesii*, *Abies lasiocarpa*, and *Pinus ponderosa* Forest Zones (Franklin and Dyrness 1988) and the dominant tree species are grand fir, Douglas fir, subalpine fir (*Abies lasiocarpa*), and ponderosa pine (*Pinus ponderosa*). Similar to the Springfield landscape, land ownership is a checkerboard of public (US National Forest) and private lands (Plum Creek Timber) and forests are mostly second growth.

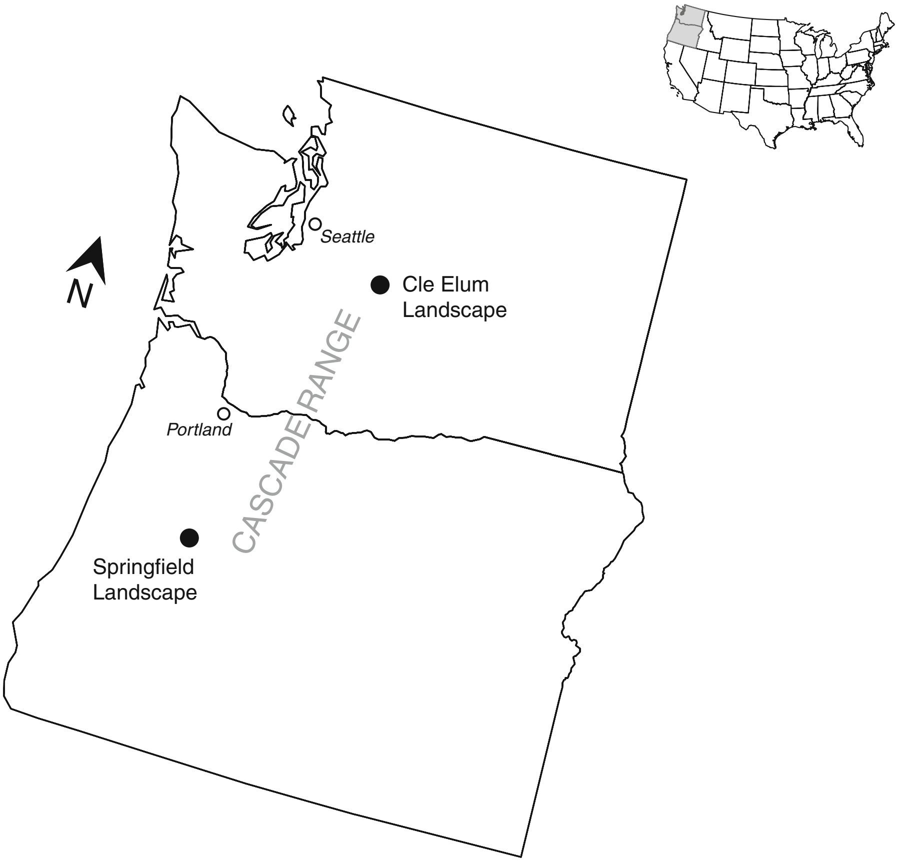


Fig. 2 Location of two study landscapes, Springfield, Oregon and Cle Elum, Washington, USA

Table 1 Environmental and structural characteristics of each landscape

	Springfield	Cle Elum
Elevation range	300–1000 m	600–1800 m
Annual precipitation	120–200 cm	50–200 cm
Range of % recently disturbed forest	0–45%	0–64%
Landscape pattern	Mean (SD)	Mean (SD)
Edge density (m/ha)	23.55 (10.87)	29.54 (13.67)
Connectivity index	0.91 (0.15)	0.94 (0.03)
Total core area (ha)	158.98 (46.63)	127.46 (55.62)
Percent landscape forested	78.93 (12.27)	72.38 (14.50)
Productivity (g Cm^{-2} day^{-1})	Range = 12.9–18.5 Mean = 14.2 SD = 1.1	Range = 5.6–10.9 Mean = 9.2 SD = 1.2
Forest zone (Franklin and Dyrness 1988)	*Tsuga heterophylla*	*Abies grandis* and *Pseudotsuga menziesii*, *Abies lasiocarpa*, *Pinus ponderosa*
Dominant tree species	Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), grand fir (*Abies grandis*)	Grand fir (*Abies grandis*), Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), ponderosa pine (*Pinus ponderosa*)
Land ownership	Weyerhaeuser, BLM and USFS	Plum Creek Timber Co. and USFS
Basal area	Mean (SD)	Mean (SD)
Shrub-sapling (SS)	2.58 (0.61)	3.63 (1.76)
Small-tree (ST)	4.99 (1.57)	4.18 (1.39)
Mature-tree (MT)	7.86 (2.86)	6.57 (1.71)
Large-tree (LT)	11.57 (4.50)	7.20 (2.01)

Study design

To test our hypotheses we first compared vegetative structural conditions in recently disturbed (mean stand age = 7 years) and later-seral forests (mean stand age = 67 years) across sites varying in productivity. We then quantified how bird abundances and richness in the sampled stands varied with increasing canopy closure within these stands and separately with the area of recently disturbed forest within a 1-km circular radius surrounding these stands. Bird richness within stands was then regressed against the proportion of the surrounding landscape recently disturbed by timber harvest. We then compared the slopes of these relationships between the high and lower productivity landscapes. We defined productivity as the rate at which vegetative biomass accumulated at a given site and used remotely derived estimates of gross primary productivity (g $Cm^{-2}day^{-1}$, MODIS satellite sensor) to represent productivity (Running et al. 2004).

Data

Bird data

We sampled birds at Springfield and Cle Elum during the breeding season in 2003, 2004, and 2005, with 2 years of sampling completed at each bird census point. Five bird census points were averaged to represent a forest stand and were positioned along a transect with 150-m separation between adjacent points. All census points were located greater than 150 m from any stand edge. During each survey year, each stand of five points was sampled three times during the breeding season (15 May–10 July). We sampled a total of 48 stands in Springfield and 64 stands in Cle Elum. Stands were typically several kilometers away from other stands and were greater than 20 ha in area. The ample number of surveys used to represent each stand increased the likelihood that rare birds with low detectability would still be adequately sampled. The survey order and observer were varied throughout the season to avoid associated biases.

The manner in which data were recorded was consistent with the point count survey guidelines described by Ralph et al. (1995) within a 10-min time interval. Every bird seen or heard was recorded with an associated first detection distance from the census point. Distances were measured using a laser range-finder distance tool which estimates distance to objects with an accuracy of ±2-m. Analysis of detection probabilities using program DISTANCE (Thomas et al. 2002) revealed that the probability of detection did not change within 50 m for approximately 80% of species. For bird species where detectability was low, we found that detectability did not vary between habitat types or seral stage. Analyses were done across all bird species and for a subset of species considered to be at risk. Partners in Flight (PIF) has identified bird species of regional concern for the Northern Pacific Rainforest Bird Conservation Region based on habitat requirements, threats to habitat, population trends, and other factors (Panjabi et al. 2005). Analyses were done on these species of regional concern to evaluate if species at risk responded to disturbance differently than the bird community at large and are identified in the results.

Vegetation and forest structure data

We sampled vegetation at each point-count station once during the 2 years of survey work. To capture characteristics of the entire survey stand we established four sub-plots 20 m from each of the 5 survey stations in the four cardinal directions. Within each of the four sub-plots, attributes were measured within either a 0.25-m^2 sub-plot located 2-m north of the center of each plot, or within a 2, 4, or 8 m radius around the sub-plot center. Forest structure data represented variation in size and horizontal distribution of trees, shrubs, and snags, as well as canopy and understory measures (Table 2).

Landscape pattern mapping

Our goal was to map the proportion of the landscape in the early stages of recovering from even-aged timber harvest. Thus, we used aerial photographs to delineate two patch types, recently disturbed and recently undisturbed based on tree size class, stand age and understory conditions and the percent canopy cover of dominant canopy trees. Recently disturbed patches (harvested within the last 10 years) consisted of very young forests (mean dbh = 8 cm, mean age = 7 - years) dominated by shrub communities and seedlings of small stature and low percentages of overstory canopy cover (mean percent canopy cover = 11%). Later-seral patches were dominated by canopy trees with larger mean size classes (mean dbh = 48 cm, mean age = 67 years), and higher mean percent forest canopy cover (mean percent canopy cover = 74%). At both sites, recently disturbed stands were most commonly created by even-aged timber harvests where removal of vegetation was almost complete. Thus, successional trajectories were fundamentally reset for harvested stands in each landscape.

Minimum patch size for mapping was >50 m wide in the narrowest dimension, and >1 ha in area. This area roughly corresponds to the smallest estimated home range of bird species found in the study area (Brown 1985). The minimum width was determined to avoid delineating narrow patches that might skew quantification of landscape patch pattern with small patches that are likely less important to birds. We obtained forest patch attribute information from

Table 2 Vegetation and forest structure predictors and area of inventory

Predictor	Definition	Area of inventory
Herbaceous cover	Percent understory cover that is herbaceous recorded as a decimal	20 0.25 m^2 plots
Total understory cover	Percent understory cover total recorded as a decimal	20 0.25 m^2 plots
Shrub diversity	Mean Shannon-Weiner shrub species diversity. calculations (across 4 subplots): $-\sum(p_i * \ln(p_i))$ where p_i = proportion of trees in size class i	20 2-m radius plots
Abundance of large shrubs	Number of shrubs larger than 2 cm basal diameter	20 2-m radius plots
Canopy closure	Percent canopy closure	Densiometer at 80 points

digital layers of stand age, dominant canopy species, ownership, and management history and validated the information with field visits. Using Weyerhaeuser and USGS digital orthophotos, we digitized forest patches manually and used field information to validate forest patch attribute information.

Landscape predictor data

The area of the landscape surrounding each survey stand disturbed by harvest (in recent years) was calculated using FRAGSTATS software (McGarigal and Marks 1995). Harvests consisted of even-aged cuts (mean harvest size = 27 ha) where small numbers of trees were retained for riparian and wildlife purposes. The proportion of recently disturbed forest was calculated within a 1-km radius surrounding survey stands. The percent of the landscape occupied by recently disturbed forest ranged from 0 to 45% in Springfield and 0 to 64% in Cle Elum.

Site productivity

Forest productivity was represented by MODIS satellite derived estimates of gross primary productivity (GPP [g $Cm^{-2}day^{-1}$]). Remotely derived estimates of GPP allowed us to derive predictor data at large scales and best represented productivity across our survey network for several reasons. A comparison of net primary productivity (NPP) (g $Cm^{-2}day^{-1}$) and GPP as predictors of regional and continental-scale bird richness showed that GPP was a much stronger predictor of bird richness than NPP (Phillips et al. 2008). Accuracy assessments of remotely sensed energy and productivity predictors are included in Heinsch et al. (2003, 2006). Productivity data were averaged over the years 2003–2005 to correspond with the bird sampling. A comparison of mean and range of values of GPP for each landscape showed little overlap.

Data analysis

Vegetation and forest structure

We evaluated our first two hypotheses: (1) vegetative recovery following disturbance would be more rapid within a productive landscape (Springfield) than a less productive landscape (Cle Elum); and, (2) later-seral forest stands would have higher levels of canopy closure and less variation in canopy closure in a more productive landscape, by comparing mean vegetation and forest structural values for different aged stands at each landscape. We tested our predictions by comparing mean values of vegetation and forest structural values between the Springfield and Cle Elum landscapes using a student's *t*-test. Vegetation and forest structural variables included in analyses were: herbaceous cover, total understory cover, shrub diversity, the number of large shrubs, and percent canopy closure.

Bird species richness and abundance

To test our third hypothesis: bird species richness and abundance within stands will be greatest in recently disturbed stands where productivity is high, we first compared mean bird species abundances within stands across four seral stages (shrub-sapling, small tree, mature tree, large tree) at each landscape. We then used linear regression to evaluate the relationship between bird species richness and within stand canopy closure at each landscape and Tukey's Honest Significance Difference test (Yandell 1997) to compare mean bird abundances within stands across seral stages for each landscape (TukeyHSD function, R Development Core Team 2007).

We evaluated our fourth prediction: that bird species richness would increase with increasing disturbance in the landscape surrounding survey stands by modeling the response of bird richness to the amount of recently disturbed forest in the landscape surrounding surveyed stands. In separate analyses, we regressed richness of all native bird species and richness of Partners In Flight (PIF) bird species of regional concern on the proportion of recently disturbed forests at both sites. We fit both linear and quadratic models to determine the best functional relationship between species richness and diversity and landscape disturbance extent.

Results

Prediction 1

Comparisons of indicators of vegetative recovery following disturbance showed that Springfield, the more productive landscape, had higher rates of vegetative recovery in recently disturbed stands (shrub-sapling seral stage) than Cle Elum, the less productive landscape. Mean herbaceous cover, total understory cover, mean shrub diversity, and the mean number of large shrubs were greater in recently disturbed stands in the productive landscape than in comparable stands in the less productive landscape (Table 3).

Prediction 2

Mean measurements of percent canopy closure were greater in later-seral stands (mature and large-tree seral stages) in the productive landscape (81.09, SD 12.86) than in the less productive landscape (74.41, SD 15.65) ($P = 0.047$).

Prediction 3

Mean bird abundances (total count across 5 survey points per stand) were higher in recently disturbed stands in the productive landscape (169.50, SD 32.86) than all other seral stages (small tree, 133.83, SD 29.98, mature tree, 125.17, SD 25.06, large tree, 119.58, SD 20.56) whereas mean bird abundances were lowest in recently disturbed stands in the less productive landscape (91.81, SD 29.44). In the less productive landscape, mean abundances were higher in the small-tree, (99.84, SD 24.04) mature-tree, (117.13, SD 29.64) large tree (98.13, SD 23.83) seral-stages although only mean abundances between recently disturbed and mature-tree seral stages were statistically different ($P = 0.048$) (Fig. 3).

Bird species richness decreased with increasing canopy closure within stands in the productive landscape ($P = 0.050$, R-squared $= 0.079$, Fig. 4). In the less productive landscape, bird species richness increased slightly with increasing canopy closure then decreased at the highest levels of canopy closure ($P = 0.094$, R-squared $= 0.061$, Fig. 4).

Prediction 4

Bird species richness increased linearly as the percent of recently disturbed forest increased across a 1-km radius landscape surrounding surveyed stands in the more productive landscape (Fig. 5). Bird richness decreased with increasing recently disturbed forest cover in the less productive landscape (Fig. 5). Both models were statistically significant (Springfield, $P = 0.005$, R-squared $= 0.159$, Cle Elum, $P = 0.036$, R-squared $= 0.298$), explaining 16% percent of the variance in bird richness in the productive landscape and 30% of the variance in bird richness in the less productive landscape. The same result also held true for Partners In Flight species of regional concern richness, but the relationship was slightly weaker (Fig. 6).

Discussion

Huston (1979) suggested that the relationship between disturbance and species diversity at local scales (0.01 to 10,000 km^2) is contingent on site productivity because competitive exclusion is influenced by both disturbance regimes and the processes regulating the rate at which dominance develops. Supporting the idea that productivity levels influence vegetation structure and composition following disturbance at the stand scale, recently disturbed stands within a productive landscape had higher levels of herbaceous cover, total understory cover, and number of large shrubs than a less productive landscape. Given that stands in both landscapes were harvested at similar levels of severity and were of similar ages

Table 3 Mean vegetation and forest structure measurements in recently disturbed stands

	Springfield ($n = 48$)	Cle Elum ($n = 64$)	P
Herbaceous cover	5.05 (1.70)	2.52 (1.16)	<0.001
Total understory cover	7.22 (1.64)	5.37 (1.74)	0.004
Shrub diversity	0.74 (0.31)	0.33 (0.22)	0.010
Abundance of large shrubs	6.23 (8.18)	1.71 (2.85)	0.025

Data represent the mean value recorded across four vegetation plots at five survey points per stand across all recently disturbed stands (standard deviation shown in parentheses). Last column shows P-value from student's t-test comparing mean values between landscapes

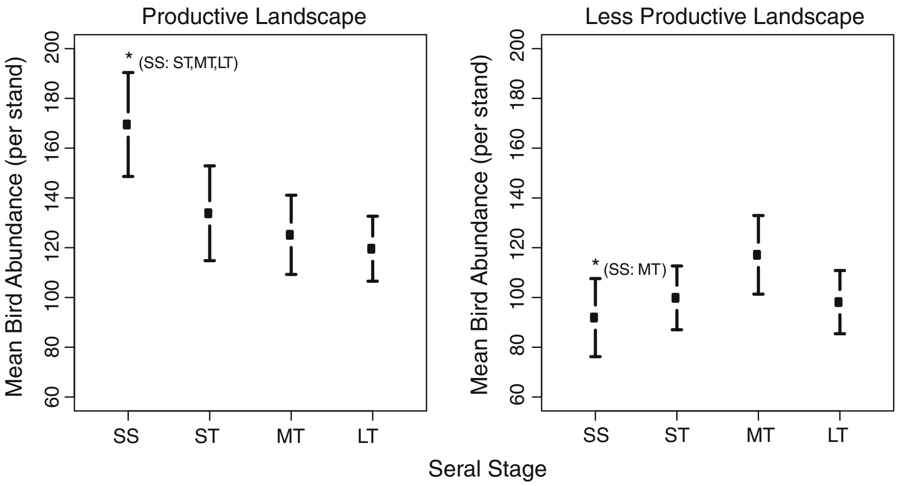


Fig. 3 Mean bird abundance (within stands) across seral stages for each landscape. *Asterisk* indicates mean abundance is significantly different ($P < 0.05$) than other seral stages

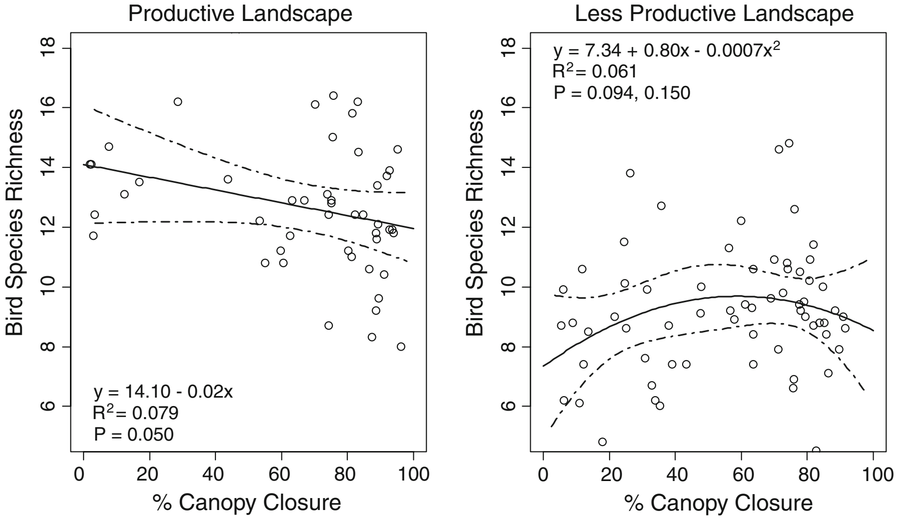


Fig. 4 Plot of bird species richness within a sampled stand as a function of mean percent canopy cover within the surveyed stand. Fitted regression and 95% confidence intervals shown

at the time we sampled them, these data suggest vegetative recovery was faster in the more productive landscape. Additionally, later-seral stands in the productive landscape had higher levels of canopy closure and less variation in canopy closure than the less productive site, suggesting that competitive exclusion may be greater here.

Bird abundance and richness was significantly higher in more open, recently disturbed stands and stands surrounded by landscapes with higher levels of disturbance than older stands with more complete canopy closure, and stands surrounded by landscapes with little disturbance. Conversely, in the less productive landscape, bird abundances and richness increased with canopy closure and were higher in mature stands and stands surrounded by landscapes with low levels of disturbance than more open, recently disturbed stands and stands surrounded by high levels of disturbance. Moreover, patterns of bird species richness within stands are consistent with the

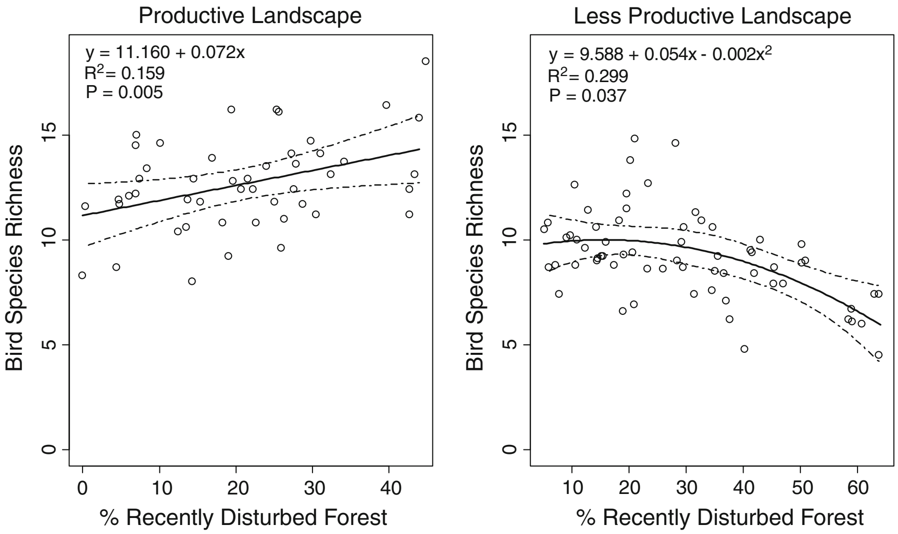
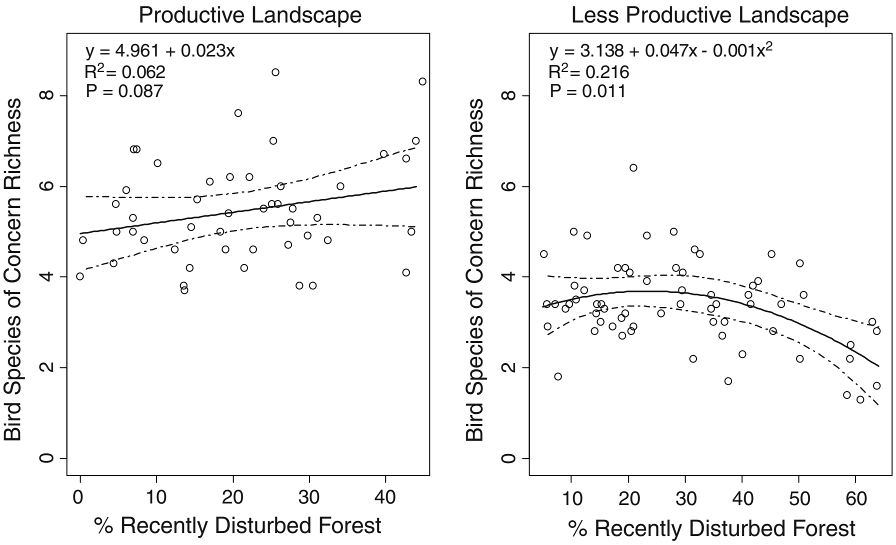


Fig. 5 Bird species richness within a sampled stand as a function of percentage of the surrounding landscape (1-km radius) in recently disturbed forest. Fitted regression and 95% confidence intervals shown

Fig. 6 Sensitive species richness within a sampled stand as a function of percentage of the surrounding landscape (1-km radius) in recently disturbed forest. Fitted regression and 95% confidence intervals shown



mechanism of competitive exclusion by dominant trees in that bird species richness within stands had a hump-shaped relationship with increasing canopy closure in the less productive landscape. These results suggest that rapid vegetation recovery in productive forests support significantly higher bird abundances and high levels of bird species richness compared to similar forests in a less productive environment. Contrary to expectations that understory shrub diversity would decrease with canopy closure, especially in the productive landscape, shrub diversity varied little across seral stages in both landscapes. This may suggest that rapid recovery of vegetation and high biomass of understory plants (Fig. 7) is more important than understory diversity in supporting bird abundance and diversity. Functional characteristics of shrubs and levels of food they support for birds (Hagar et al. 2004; Hagar 2007) may also influence bird abundance and diversity more than overall understory plant diversity. Thus, at least in relation to biomass accumulation, ecosystem productivity appears to influence bird response to both stand and

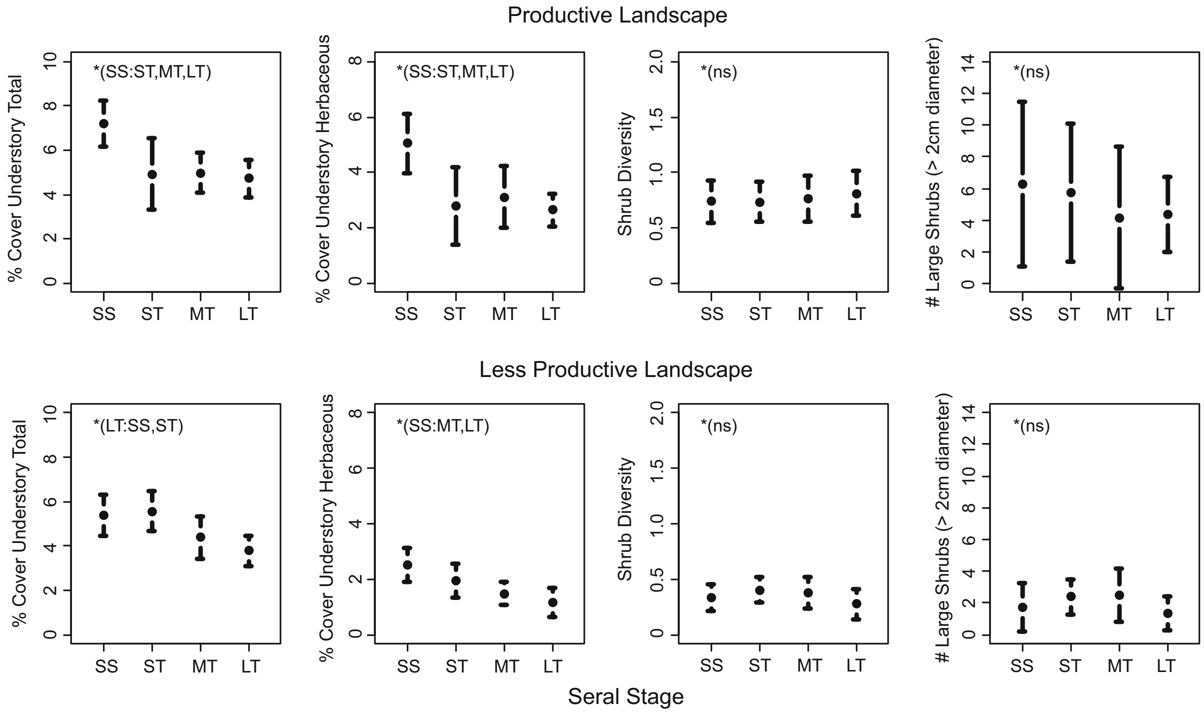


Fig. 7 Measurements of mean understory structural characteristics (within stands) across seral stages (shrub sapling-SS, small tree-ST, mature tree-MT, and large tree-LT) for the productive landscape (*top row*) and the less productive landscape (*bottom row*) with 95% confidence bars around means (*Asterisk* indicates within landscape means are significantly different between seral stages noted in parentheses, $P < 0.05$)

landscape level disturbance and this comparison provides evidence for the hypothesis that bird response to disturbance is moderated by productivity, both at the stand and landscape scale.

These results add to those of previous studies in supporting the hypothesis that disturbance may act to reduce competitive exclusion, increasing local diversity (Proulx and Mazumder 1998; Petraitis et al. 1989; Davis et al. 1988; Sousa 1979) and are the first to test the Dynamic Equilibrium Hypothesis in forested ecosystems. Timber harvest has the potential to break competitive dominance that is often observed in productive forests (Rajaniemi 2003; Wohlgemuth et al. 2002) by freeing resources from living organisms and reducing competition from dominant canopy trees. Assuming that harvest does not lead to significant soil erosion, nutrient loss and reduced soil fertility, the removal of the overstory provides more resources for surviving organisms promoting high understory plant biomass and functional heterogeneity. Hence, where productivity is high, timber harvests may act to increase the abundance and richness of organisms (especially early-seral species) dependent on vegetation for food and other requirements.

Our study provides a reasonable first test of Huston's Dynamic Equilibrium Hypothesis in the context of forest management; however, there are some limitations to this approach. Previous research testing Huston's hypothesis typically involved experimental tests subjecting communities to different levels of disturbance (e.g. Proulx and Mazumder 1998). Our design samples birds within forest stands and analyzes the effects of both within stand and landscape level patterns of forest succession and canopy closure. The approach uses correlation to infer the influence of both within stand and landscape level disturbance and assumes that bird diversity within a stand is influenced by the characteristics of vegetation succession both within stands and in the landscape surrounding stands.

Differences in conditions other than productivity could potentially explain why bird response to disturbance differed across the two landscapes and a consideration of these other factors is important. A comparison of vegetation structural characteristics including understory diversity and stand structural complexity indicate that variation in these characteristics within and between the two landscapes correspond poorly with bird response to disturbance at both stand and landscape scales (Fig. 7). Shrub diversity, while generally higher in all stands in the more productive landscape, varies little across seral stages in both landscapes suggesting that the relationship between understory species diversity and overall bird richness is weak. Structural complexity increases with stand age in both landscapes which should contribute to bird richness as stands move beyond the stem exclusion stage. Bird richness declines, however, in the productive landscape despite this increase in structural complexity. The abundance of non-coniferous understory vegetation that is known to benefit some early-seral associated bird species (Hagar 2007; Hagar et al. 2004) is highest in young stands in the productive landscape then declines significantly as stands mature. In the less productive landscape, the abundance of non-coniferous vegetation in young stands is much lower than the productive landscape and not significantly different across stand ages.

In the context of Huston's model, we interpret these results to suggest that the flush of early-seral vegetation in productive landscapes and high resource availability associated with younger vegetation is strong enough to overcome high structural diversity in productive older landscapes and that low levels of biomass in young forests in the less productive landscape coincide with low structural complexity to depress overall bird abundance and diversity there. In support, several measurements of understory growth show high shrub and herbaceous growth following harvest. Total understory cover, herbaceous cover and conifer cover is highest in the productive landscape in younger stands (Fig. 7) and significantly higher than for young stands in the less productive landscape where there is no difference in understory cover for total, herbaceous, and conifer cover across the shrub-sapling, small-tree and mature-tree seral stages. Shrub diversity varies little with stand development in both landscapes which suggests that vegetative biomass and overall quality and type (e.g. non-coniferous) of shrub habitat resulting from a newly opened canopy may have a more direct impact on overall bird abundance and diversity than overall understory or shrub diversity.

We also considered differences in the abundance and diversity of bird guilds at each landscape and how these differences may influence overall bird response to disturbance. Variation in bird guild richness (cavity, foraging, nesting, and species of concern (SOC) guilds) suggests that the response of birds in different guilds only weakly influences overall bird response to disturbance across the two landscapes (Fig. 8). Cavity guild richness increases with stand development in each landscape, there is no significant difference in nesting or foraging guild richness across stand age in both landscapes, and species of concern richness is slightly higher in small-tree seral stage than other stand ages in the productive landscape and in old stands in the less productive landscape. Thus, variation in bird guild richness is also poorly correlated with bird richness.

The intensity and type of timber harvest at each landscape may explain why birds respond differently to disturbance across the two landscapes and the particular methods used for clearcutting, removing timber and replanting stands may influence stand development and associated bird richness as stands mature. Vegetation data suggest, however, that other than measurements of early-seral growth, stands of comparable age represent a similar range in vegetation structural conditions (Verschuyl et al. 2008). Similarly, while the extent to which landscapes were disturbed varies between the two landscapes, (Springfield, 0–45%; Cle Elum, 0–64%) the relationship between bird richness and disturbance is consistent with our hypotheses where this range overlaps (Figs. 3, 4, 5, 6).

The variation in bird species richness explained by disturbance in our models was modest, although the variation is relatively high given that the different measurements of vegetation structure outlined above already explain some of the variation in bird richness and previous research shows that climatic and within-stand structural predictors are known to influence bird species abundance and community diversity (Verschuyl et al. 2008). Using canopy closure alone, these models explain a substantial amount of variation in bird species richness when compared to models that include both climate and structural variables. Thus, our results provide a reasonably strong first test of

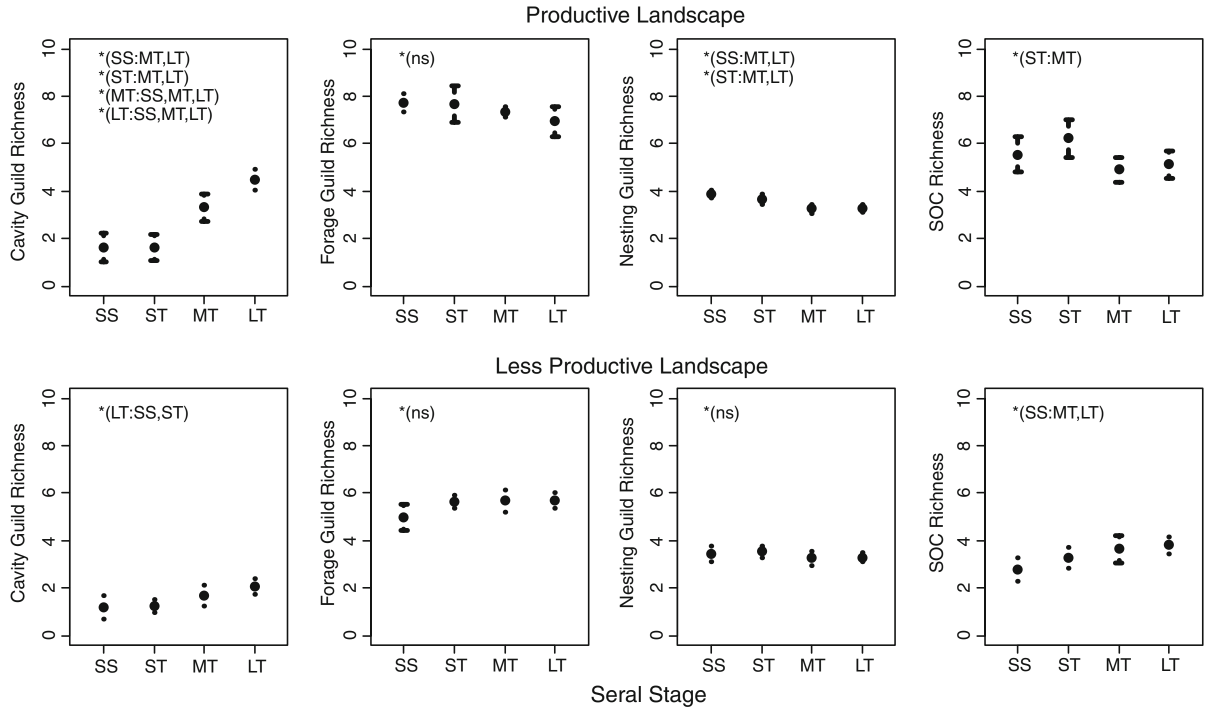


Fig. 8 Measurements of mean guild and species of concern (SOC) richness (within stands) across seral stages (shrub sapling-SS, small tree-ST, mature tree-MT, and large tree-LT) for the productive landscape (*top row*) and the less productive landscape (*bottom row*) with 95% confidence bars around means (*Asterisk* indicates within landscape mean richness values are significantly different between seral stages noted in parentheses, $P < 0.05$)

the Dynamic Equilibrium Hypothesis in a forested ecosystem.

It is also important to emphasize that our study only examined landscapes with <65% of the landscape occupied by recently disturbed forests. It is likely that diversity will drop even in productive sites when mid/late-seral forests fall below some threshold level in the surrounding landscape (Flather and Bevers 2002; Fahrig 2002). Further study is needed to determine at what level such thresholds may exist. Finally, our study included areas representing two levels of productivity. A more robust test of the hypothesis would consider several levels of productivity and attempt to find thresholds in productivity where the relationship between disturbance and diversity changes between positive and negative slopes.

Timber harvest is an important form of disturbance in many environments worldwide; we recognize, however, that timber harvest may influences ecosystem processes differently than natural disturbances, particularly in the removal of biomass that would be recycled and used by organisms in a number of different forms. Nonetheless, considering vegetation and bird response to timber harvest in different environments is important because harvest is the primary agent leading to the disruption of successional pathways and is the primary cause of significant mortality of dominant vegetation in many forested environments. We expect that our predictions would hold if vegetation and bird response to natural disturbance across gradients in productivity were considered.

Management implications

The differing responses of bird communities to logging in the two study landscapes results, we speculate, from differences in long term dynamics between the two systems. In many of the world's forests, natural disturbance regimes are influenced by the same factors that drive ecosystem productivity (White and Jentsch 2001). Thus, natural disturbance and productivity likely covary across forest ecosystems and interact to influence the traits of species and communities. Knowledge of these differences provides a basis for more effective management along the productivity gradient.

Maintaining adequate habitat for early-seral species likely requires more frequent disturbance in productive systems because competitive exclusion of dominant trees and canopy closure from small tree stage on tends to exclude these species. Consequently, if disturbed areas recover vegetation biomass quickly, they quickly become suitable habitat for early-seral species. More species likely specialize on each-seral stage in productive systems because these stages differ much in structure and microclimate. Under these conditions, harvesting as a form of disturbance could be used to reduce strong competition for resources, facilitating rapid growth and colonization of recently disturbed sites by early-seral plant communities and generalist and early-seral associated bird species. Historically, natural disturbances maintaining earl-seral habitats were commonly large, infrequent events (Wimberly et al. 2004; Whitlock et al. 2003; Wimberly 2002). Thus, early-seral species would have had to disperse or migrate over large distances to find suitable habitat and persist between disturbance events. More species were associated with early-seral forests at both sites, 64% of the 60 most abundant species in Springfield and 57% in Cle Elum. Importantly, long-term trends show population declines for 30% of the early-seral associated bird species at both sites whereas less than 1% of the later-seral associated species show declining population trends (Sauer et al. 2005, Table 4). Thus, it seems particularly important to maintain some percentage of early-seral forests for both maximizing diversity and supporting species associated with young forests in productive settings. In less productive settings, retaining biomass in young forests should help support early-seral associated species and diversity.

Management of early-seral forests should also consider how harvest type and severity impact the development of plant understory structure and composition. Research in Cascade forests indicates that the composition of understory plants plays an important role in supporting species associated with younger forests. For example, well-developed assemblages of non-coniferous understory vegetation in young stands provide higher levels of food resources for birds than young forests dominated by coniferous shrubs, enhancing the abundance of some early-seral associated species (Hagar 2007; Hagar et al. 2004). Additionally, high-quality shrub habitat in heavily managed stands of the Cascades persists for only a few years before being replaced by tree seedlings. Management could address the short duration of high-quality shrub habitat in young stands by ensuring that non-coniferous shrubs are represented in young stands across the landscapes. Hence, maintaining younger forests in more productive landscapes to support species diversity should include consideration of how treatments influence the quality and duration of non-coniferous shrub development.

Structurally complex old-growth forests are expected to develop more quickly in productive ecosystems. As a result, there may be greater opportunities to facilitate these conditions in productive managed forests than in many public forests located in less productive environments. In productive ecosystems, managing with multiple rotation ages for different areas in the forest would likely best maintain habitat important to a wide array of wildlife (Seymour and Hunter 1999; Lindenmayer and Franklin 2002). This could be done thru either (a) late-seral reserves that are set aside and not logged combined with short rotation stands that maintain open-canopy habitat, or (b) a mosaic of both short and long rotation stands that are dispersed across the landscape representing the entire gradient in seral-stage structural conditions.

Management of forests in less productive settings should account for slow rates of vegetative recovery that follow disturbance. To maintain adequate levels of vegetative biomass necessary for supporting viable populations of bird species, disturbance should be less frequent and smaller in area. Early-seral species are often able to utilize later-seral habitat because forests in less productive settings experience lower levels of competitive dominance. Consequently, fewer recently disturbed areas are needed to maintain early-seral species. In some settings, smaller disturbance sizes and more focus on retaining understory and canopy structure would allow more rapid recovery of vegetation following harvest. Similarly, because old growth does not rapidly develop in these

Table 4 Bird guild associations and population trends 1966–2005

Species Code	Guild	PIF	BBS trend	P	Species code	Guild	PIF	BBS trend	P
AUWA	Closed^a	–	**1.128**	**0.009**	WISA	Generalist	–	−1.761	0.224
BCCH	Closed^a, OG	–	−0.811	0.380	WIWA	Generalist	–	**−0.984**	**0.005**
BRCR	Closed^a	–	−1.118	0.155	AMGO	Open^a	–	**−1.430**	**0.043**
CBCH	Closed^a, OG	PIF	**−1.569**	**0.027**	AMRO	Open^a	–	**−0.389**	**0.075**
GCKI	Closed^a	PIF	**−2.795**	**<0.001**	BEWR	Open^a	–	0.013	0.991
GRJA	Closed^a	–	0.701	0.525	CEDW	Open^a	–	0.897	0.215
HAFL	Closed^a	–	**1.741**	**0.035**	COYE	Open^a	–	**3.399**	**<0.001**
HEWA	Closed^a	PIF	0.048	0.963	DEJU	Open^a	–	**−0.961**	**0.021**
PIWO	Closed^a	–	0.601	0.599	DUFL	Open^a	PIF	**1.526**	**0.087**
PSFL	Closed^a	PIF	**−1.210**	**0.018**	HOWR	Open^a	–	−0.456	0.523
RBNU	Closed^a	–	−0.038	0.925	LAZB	Open^a	–	−0.427	0.629
RBSA	Closed^a	PIF	−0.333	0.802	MGWA	Open^a	PIF	−0.742	0.213
TOWA	Closed^a	PIF	0.518	0.451	MODO	Open^a	–	**−1.114**	**0.002**
VATH	Closed^a	PIF	−0.880	0.203	MOUQ	Open^a	PIF	1.004	0.199
WBNU	Closed^a	–	**1.876**	**0.075**	OCWA	Open^a	PIF	**−1.443**	**0.057**
WETA	Closed^a	–	**0.948**	**0.066**	OSFL	Open^a	PIF	**−3.604**	**<0.001**
WIWR	Closed^a		**0.731**	**0.038**	RUHU	Open^a	PIF	**−2.240**	**0.003**
BTYW	Closed	PIF	0.282	0.762	SOSP	Open^a	–	−0.318	0.332
CORA	Closed	–	**2.344**	**0.005**	SPTO	Open^a	PIF	−0.200	0.614
HETH	Closed	–	−0.639	0.219	WAVI	Open^a	–	0.319	0.479
HETO	Closed	–	na	na	WCSP	Open^a	–	**−2.316**	**0.002**
STJA	Closed	PIF	0.387	0.235	WIFL	Open^a	PIF	**−2.210**	**0.008**
BHGR	Generalist	–	0.495	0.416	WREN	Open^a	PIF	−1.074	0.186
BTPI	Generalist	PIF	−1.064	0.254	BHCO	Open	–	**−0.874**	**0.047**
HAWO	Generalist	–	−0.194	0.649	BUSH	Open	–	**−2.194**	**0.089**
HUVI	Generalist	PIF	0.612	0.412	PUFI	Open	PIF	**−1.417**	**0.007**
MOCH	Generalist	PIF	**−1.371**	**<0.001**	PUMA	Open	–	1.500	0.600
NAWA	Generalist	–	**−1.356**	**0.011**	RSFL	Open	–	**−0.838**	**0.004**
SWTH	Generalist	–	**−0.849**	**0.024**	VGSW	Open	–	−0.286	0.689
WEBL	Generalist	–	−0.363	0.563	YWAR	Open	–	**−1.153**	**0.014**

Guild designations based on literature review. ^{a} = species where significant difference in abundance between open and closed canopy stands; OG = species where abundances where significantly higher in old-growth stands (average d.b.h. >53 cm); PIF = Partners In Flight Birds of Regional Concern (Panjabi et al. 2005); BBS Trend = coefficient for trend in abundance models for the period between 1966 and 2005, trends with $P < 0.01$ highlighted in bold (Sauer et al. 2005)

less productive settings, longer rotations, smaller harvest units and retention of forest structure promoting legacy tree conditions is appropriate.

The overall conclusion from this work is that management aimed at supporting forest biodiversity will be most effective if tailored to local biophysical conditions. Regional climate, topography, and soils influence forest productivity, disturbance and the ecological response to disturbance. Rotation ages, harvest unit size, and harvest type and severity can be designed for local ecosystem conditions to most effectively meet biodiversity objectives. This research provides guidance for both federal land managers and private land foresters on management strategies to maintain the combination of early-seral species, late-seral species, and total species richness they deem appropriate for their lands.

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