Impacts of the Northwest Forest Plan on forest composition and bird populations

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Edited by Janet Franklin, University of California, Riverside, CA, and approved December 20, 2018 (received for review August 5, 2018)

The Northwest Forest Plan (NWFP) initiated one of the most sweeping changes to forest management in the world, affecting 10 million hectares of federal land. The NWFP is a science-based plan incorporating monitoring and adaptive management and provides a unique opportunity to evaluate the influence of policy. We used >25 years of region-wide bird surveys, forest data, and landownership maps to test this policy's effect on biodiversity. Clearcutting decreased rapidly, and we expected populations of older-forest–associated birds to stabilize on federal land, but to continue declining on private industrial lands where clearcutting continued. In contrast, we expected declines in early-seral–associated species on federal land because of reduced anthropogenic disturbance since the NWFP. Bayesian hierarchical models revealed that bird species' population trends tracked changes in forest composition. However, against our expectations, declines of birds associated with older forests accelerated. These declines are partly explained by losses of older forests due to fire on federal land and continued clearcutting elsewhere. Indeed, the NWFP anticipated that reversing declines of older forests would take time. Overall, the early-seral ecosystem area was stable, but declined in two ecoregions—the Coast Range and Cascades—along with early-seral bird populations. Although the NWFP halted clearcutting on federal land, this has so far been insufficient to reverse declines in older-forest–associated bird populations. These findings underscore the importance of continuing to prioritize older forests under the NWFP and ensuring that the recently proposed creation of early-seral ecosystems does not impede the conservation and development of older-forest structure.

bird population trends | public policy | avian conservation | old-growth forests | early-successional ecosystems

Monitoring and adaptive management have been proposed as tools to enable environmental decision-making in the presence of high uncertainty and ecosystem complexity (1). A critical component of adaptive management lies in the evaluation of ecosystem responses following policy change (2), but this has proved to be a weak link in the approach (3, 4). Challenges with policy evaluation include scarcity of high-quality data at appropriate spatiotemporal scales, the influence of concurrent factors unrelated to the policy, mismatches between policy intent and implementation, and emergence of unintended consequences (5–7). Nevertheless, monitoring and analyzing how species populations have responded to policy are essential for providing feedback to enable future plan adaptations (2).

The Northwest Forest Plan (NWFP) provides a unique opportunity to understand how an abrupt policy change has affected biodiversity. The NWFP was adopted in 1994 at the behest of President Clinton following court injunctions that halted logging on federal forests to provide for species viability under the 1982 National Forest planning rule, and it shifted the primary management objective on 10 million ha of federal land (Fig. 1*A*) to sustaining and restoring older forests and their species (8). The NWFP was unusual in that it explicitly incorporated adaptive management into its design, with considerable resources invested in monitoring, although the formal adaptive management program was ended after a few years (2). The NWFP had two main conservation components: conserving old-growth forests in reserves for species such as the Northern Spotted Owl *Strix occidentalis caurina* and using restoration silviculture such as variable-density thinning in young plantations to accelerate development of old-growth forest structure and restore structural and compositional diversity (8, 9). On federal land covered by the NWFP, 41% was allocated to reserves, in addition to the 36% already protected in wilderness areas, national parks, and administratively withdrawn lands (8). Timber harvest, using alternatives to clearcutting, could occur on ~20% of the remaining unreserved ("matrix") area. The NWFP projected that timber harvest would be reduced to 25% of that in previous decades.

However, following implementation of the NWFP, most clearcutting on federal land ceased by the mid-1990s (*SI Appendix*, Fig. S1). The NWFP did not change the drivers of demand for timber, and as a result of this and other factors, ~43% of the foregone harvests on public lands shifted to private lands elsewhere in the

Significance

The Northwest Forest Plan (NWFP) ended clearcutting of old-growth forest on federal land across western Washington, Oregon, and California in the early 1990s. We provide a test of how this dramatic change affected bird populations—a commonly used biodiversity indicator. Although the NWFP greatly reduced losses of older forests to logging, losses to wildfire have increased, and declines in birds associated with older forests have amplified. The area of early-seral ecosystems with broadleaf trees stabilized on federal land, but declines continue for some associated species. Creation of early-seral vegetation may be justified in some landscapes where wildfires are mostly suppressed, but should not impede development of older forests, the gradual recovery of which remains critical for the long-term success of the NWFP.

Author contributions: B.T.P. and M.G.B. designed research; B.T.P., J.M.N., Z.Y., and M.G.B. performed research; B.T.P., J.M.N., Z.Y., J.S.R., T.A.S., and M.G.B. analyzed data; and B.T.P., J.M.N., Z.Y., R.L.D., J.S.R., T.A.S., and M.G.B. wrote the paper.

Conflict of interest statement: T.A.S. was involved in formulating the Northwest Forest Plan (NWFP) and part of the NWFP Science Synthesis team. M.G.B. was an external reviewer of the NWFP Science Synthesis.

This article is a PNAS Direct Submission.

Data deposition: The data reported in this article have been deposited in the Mendeley database in shapefile format at dx.doi.org/10.17632/k5nj539vc2.1.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1813072116/-/DCSupplemental.

Published online February 4, 2019.

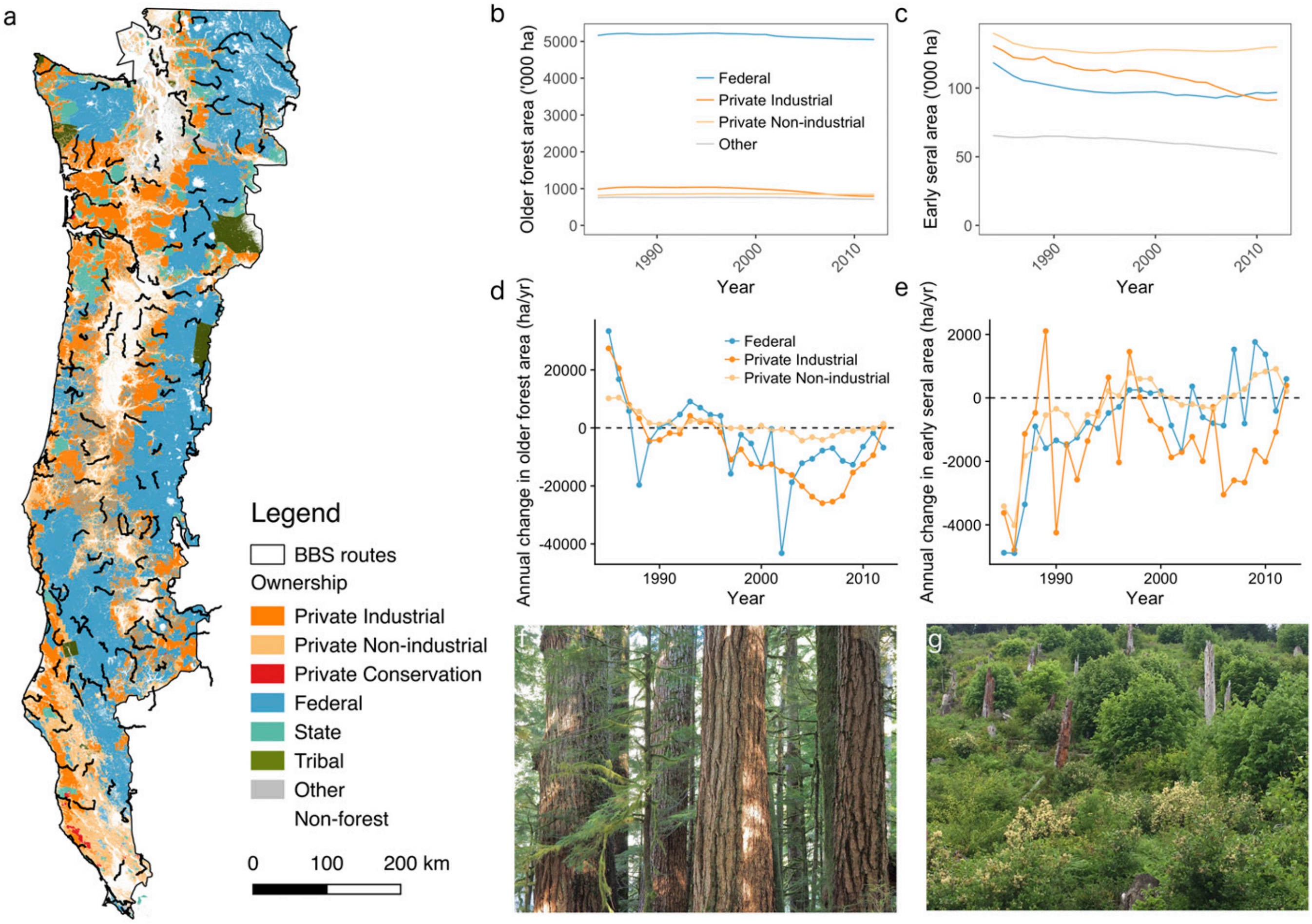

Fig. 1. (*A*) Forest land ownership in the NWFP region. The BBS routes used in the analysis are outlined in black. Nonforest is shown in white. (*B*) Area of older forests (OGSI > 80), on federal, private, and other land within the NWFP area from 1985 to 2012. (*C*) Area of diverse early-seral ecosystems (mean tree diameter <10 cm and >20% hardwood basal area). (*D*) Annual changes in the area of older forests. (*E*) Annual changes in the area of early-seral ecosystems. Photos show typical examples of (*F*) older forest and (*G*) diverse early-seral ecosystems.

western United States, and ∼41% elsewhere in North America (10). Harvests were lower than anticipated on federal lands (and lower than expected under a counterfactual scenario without the NWFP), while increasing slightly on private industrial land in the NWFP region, ending a decade of decline (11).

The NWFP was conceived as a 100-y plan, but also one that would adapt to changing ecological and social conditions and knowledge. National forests in the NWFP region are undertaking forest plan revisions under the new 2012 planning rule (12). Managers may revise forest plans to address new concerns such as increasing losses of older forests to wildfire, the threat posed to Northern Spotted Owls by an expanding Barred Owl *Strix varia* population, and lack of timber to support rural economies. In addition, concerns have been raised about declines of species associated with high-quality "complex" early-seral ecosystems (13) that may be scarcer given widespread suppression of wildfire (12). Some of the characteristic bird species of these ecosystems have declined by ∼3% per year in the NWFP region (14). "Ecological forestry" has been proposed as a way to balance both timber production and conservation, using forest management to create diverse early-seral ecosystems (15, 16). Indeed, one federal agency, the Bureau of Land Management, is already undertaking efforts to create complex early-seral ecosystems (17). However, such techniques are still untested and could have unintended negative ecological impacts (18). Critical issues, then, are whether the NWFP has already had positive effects on older forests and associated species and whether such putative conservation gains are coming at the expense of early-seral ecosystems and species.

Often, policy evaluation is hampered by a lack of appropriate data. In the Pacific Northwest, however, there are detailed, large-scale, long-term datasets on bird populations (19), forest structure and composition (20), and forest disturbance (21) for substantial periods before (1985–1993) and after (1994–2012) the NWFP (and 1968–2015 for birds). Using these datasets, our objective was to understand how populations of bird species associated with complex early-seral ecosystems and older forests have changed on federal lands. In the Pacific Northwest, federal lands are interspersed with private industrial and nonindustrial forest lands, which are outside the jurisdiction of the NWFP. We compared trends on private lands, where clearcutting has continued, with those on federal lands to estimate the effects of alterations to federal forest management triggered by the NWFP.

We established several a priori expectations about how forest structure and bird populations might respond to the NWFP on federal and private land. First, we hypothesized that the loss of older forests has slowed after the early 1990s because of the decline in timber harvesting; this should have resulted in a deceleration in the decline, or even recovery, of species associated with dense older forests. One caveat is that the NWFP anticipated older forests to continue declining for some decades as a result of wildfire, thinning, and regeneration harvests (22), such that 20 y might be insufficient to detect a recovery.

Second, we expected an ongoing decline in older forests on private industrial land consistent with sustained harvests and increasing management intensification (e.g., shorter rotations) in response to restructuring of the industry and increasing competition in wood products markets (23). As a result of continued harvest, we expected that on private land, declines in bird species associated with older forests should be consistent between the pre- and post-NWFP period.

Third, on federal land, we expected diverse early-seral ecosystems to show the reverse pattern to that of older forests: we anticipated decreases in early-seral ecosystems because of both forest succession in areas disturbed in previous decades and reduced harvest. As a potential consequence of this change, we expected a post-NWFP acceleration in the rate of decline of birds associated with early-seral ecosystems. We defined diverse early-seral ecosystems as hardwood/mixed stands with low densities of large live trees (*Materials and Methods*). Limitations of remote-sensing data precluded identification of other characteristics of complex early-seral ecosystems (13) such as snags and fallen dead wood.

Fourth, we expected changes in forest management on private industrial land to exacerbate declines of bird species associated with early-seral ecosystems (13, 14, 24). These changes, aimed at maximizing timber yields, include shorter rotations, use of herbicides and fertilizers, and densely planted trees (25). Shortening rotations can increase the proportion of open vegetation in the landscape, but clearcuts lack habitat features of complex early-seral ecosystems. Herbicides are used on industrial forestlands to control competing vegetation during tree establishment, favoring conifer growth over hardwoods. Tree planting and control of competing vegetation accelerate canopy closure, reducing the time span within which open conditions persist (26, 27).

Underlying these expectations is the assumption that bird populations respond to changes in breeding habitat over the long term, which is not necessarily the case given the well-known role of nonbreeding season habitat on populations of migratory bird species (28). We tested this assumption by examining whether variation in habitat amount (of early-seral ecosystems or older forests) could predict variation in the abundance of birds associated with these vegetation types.

Results and Discussion

Changes in Forest Structure and Composition. Older forests make up a larger portion of the NWFP region (7,393,211 ha) than diverse early-seral ecosystems (370,289 ha) (*SI Appendix*, Fig. S2). The area of both vegetation types has declined across the region (Fig. 1). Currently, most remaining older forests are on federal land (Fig. 1*B*). Their area declined by 2% on federal land between 1984 and 2012; surprisingly, older forests increased overall immediately before the NWFP (perhaps because of dampened harvests during the recession of the mid-1980s and succession from younger age classes) but declined during the two decades afterward under all ownerships. Later declines on federal lands were largely a result of increases in the occurrence of large wildfires related to drought (29), but were no more severe than anticipated under the NWFP (22) (*SI Appendix*, Fig. S3). The area of older forests declined by 19% on private industrial land between 1984 and 2012 and increased slightly overall (3%) on private nonindustrial land.

Between 1984 and 2012, the early-seral ecosystem area declined on federal land by 18%, on private industrial land by 30%, and on private nonindustrial land by 7% (Fig. 1*C*). Counter to our expectations, declines in diverse early-seral ecosystems on federal land came to an end, likely because of large wildfires (*SI Appendix*, Fig. S4) (29). However, diverse early-seral ecosystems continued to decline on private industrial land (Fig. 1*C*).

Bird Population Trends in Relation to Ownership and Vegetation. Overall, losses in vegetation types (diverse early-seral, older forests, or both) along survey routes tended to result in decreases of associated bird populations, while gains in those vegetation types resulted in increases in associated bird populations (*SI Appendix*, Fig. S5). This relationship supports our expectation that changes in breeding habitat have strong influences on both migratory and resident species.

Across the 170 Breeding Bird Survey (BBS) routes in the NWFP region, most of the 24 species meeting our criteria for examination (*SI Appendix*, *Supplementary Text*) declined in one or both time periods. There was little evidence of consistent ownership effects on declines in early-seral-ecosystem–associated species (Fig. 2*A*) or in species associated with both early-seral ecosystems and older forests (Fig. 2*B*). Species associated with older forests showed more consistent changes in trends; all of these 12 species had more negative trends on federal land (and overall) in the post-NWFP period than during the pre-NWFP period (Fig. 2*C*). This is in contrast to our expectation that the status of older-forest–associated species should have improved on federal land. On routes with a high proportion of other ownerships, there was also some evidence of steepening post-NWFP declines, but these trends were less consistent.

The results above initially pose several apparent contradictions. First, why do many early-seral-ecosystem–associated species continue to decline when diverse early-seral ecosystems are no longer declining in most ownerships across the Pacific Northwest? Second, given that declines in older forests have been small (at most 0.8% per year on federal land and on average just 0.2% per year after 1994), why have declines of older-forest–associated bird species amplified post-NWFP? These patterns are especially perplexing given the observed tight relationship between habitat amount and bird abundance (*SI Appendix*, Fig. S5). One possibility is that vegetation change along BBS routes, which are all located along roads, does not represent the broader region (30). This explanation falls short: trends in diverse early-seral ecosystems on BBS routes tracked those across the NWFP region, and loss of older forests was actually greater in the NWFP region as a whole, perhaps because of more active fire suppression near roads (*SI Appendix*, Fig. S6). This would suggest even greater overall habitat-mediated declines in birds associated with older forests than we estimated using BBS data. Furthermore, although BBS routes were on average cooler

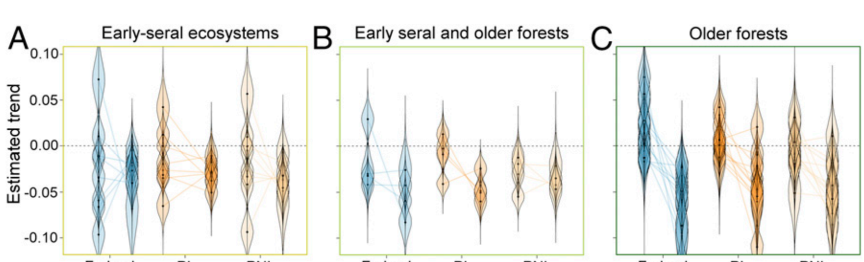

Fig. 2. Violin plots showing estimated trends in bird populations (proportional annual change) in the NWFP region before (1968–1993) and after (1994–2015) the NWFP for species associated with (*A*) early-seral ecosystems, (*B*) both early-seral and older forests, and (*C*) older forests. Each pair of linked symbols represents a species (posterior distributions estimated at mean ± 1 SD proportion of each ownership category and mean proportion of each other category) with the pre-NWFP period on the left. Against our predictions, trends of older-forest–associated birds on federal land were more negative post-NWFP (*C*). PI, private industrial; PNI, private nonindustrial.

than the NWFP region as a whole, changes in temperature across the routes closely tracked regional changes (*SI Appendix*, Fig. S7).

Alternatively, bird declines could be caused by regionally patchy habitat declines in locations where populations are at their greatest abundance. Therefore, even though vegetation may not be changing much overall, it could be changing dramatically in particular ecoregions—a pattern for which we found evidence (Fig. 3 and *SI Appendix*, Fig. S8). Declines in early-seral ecosystems were most evident in the Coast Range and Cascades (Fig. 3*A*). Declines in older forests were more consistent across most ecoregions (Fig. 3*B*). Early-seral–associated bird species concentrated in the Coast Range or Cascades declined more strongly than those that were spread more evenly across ecoregions (*SI Appendix*, Fig. S9). Declines in structural components of complex early-seral ecosystems—such as loss of large (live and dead) trees through salvage logging and suppression of understory vegetation with herbicides—could also have reduced habitat suitability for some species without changing the overall area of early-seral vegetation (31, 32).

One possibility that might explain continued declines in older-forest–associated bird species following the NWFP is the "extinction debt" hypothesis under which there are substantial temporal lags between initial habitat loss and fragmentation and the full population-level impact of these processes (33). In support of this hypothesis, most older-forest–associated species declined more strongly in landscapes where forest had already been substantially reduced and fragmented at the start of our study (i.e., where thresholds may have been exceeded) (*SI Appendix*, Table S1). On the other hand, bird populations in landscapes with high amounts of remaining older forest appear buffered to some extent from the effects of forest loss.

Impacts and Limitations of the NWFP. The Northwest Forest Plan is one of the most iconic and ambitious initiatives worldwide to conserve species associated with temperate old-growth forest. In the absence of the NWFP, most older forests on federal land were expected to be lost by around 2050 (22). The NWFP has at least slowed rates of older forest loss in contrast to a scenario with no such plan. We expected that over two decades this effort would have a positive, or at least initially neutral, effect on populations of species associated with older forests, but a negative influence on species associated with diverse early-seral ecosystems. Instead, we found evidence that birds associated with older forests have declined since (although not, we stress, because of) the introduction of the NWFP. Surprisingly, these declines have accelerated, especially on federal land. While it was anticipated within the NWFP that the benefits for older forests could take 50–100 y to develop (many of the lands conserved under the NWFP had been logged in the preceding 30 y), it was expected that losses of older forests on federal lands would

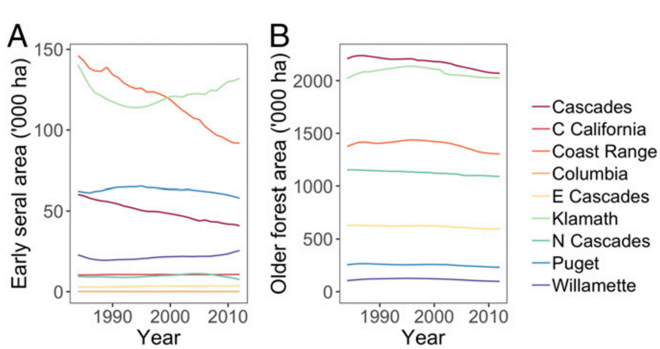

Fig. 3. Area of (*A*) diverse early-seral ecosystems and (*B*) older forests by ecoregion within the NWFP region from 1984 to 2012. Declines in diverse early-seral ecosystems were highly variable across ecoregions, while those of older forests were more consistent.

slow (22). While logging of older forests has stopped, the benefits of the NWFP for birds associated with older forests have yet to manifest themselves.

As we expected, the abundance of species associated with diverse early-seral ecosystems or older forests was related to the amount of each of those vegetation types on BBS routes, indicating that, even at coarse resolutions (40-km routes), the BBS can be used to detect population responses to habitat change. Across the NWFP region as a whole, early-seral ecosystems declined from the 1980s to the present. However, the area of diverse early-seral ecosystems has stabilized on federal and private nonindustrial land but has continued to decline on private industrial land. Most declines in diverse early-seral ecosystems were concentrated in two large ecoregions, the Coast Range and Cascades, suggesting that efforts to increase the availability of early-seral habitat could be justified in those regions.

Our most striking finding was that—in contrast to our expectations based on the broad-scale policy changes of the NWFP—we did not find a deceleration in the rate of decline of species associated with older forests. Nor did we find a deceleration in the rate of loss of older forests on federal land, despite improved protection for such forests under the NWFP; older forests on both federal and private industrial lands continue to decline. Importantly, some ongoing decline in older forest was expected under the NWFP due to wildfire, thinning, and regeneration harvests, and to a lesser extent insect damage and other causes, with forest succession too slow to compensate for losses during the early period of NWFP implementation (22).

In contrast to our expectation that the cessation of clearcutting on federal lands might have negatively affected the creation of early-seral ecosystems, the area of diverse early-seral ecosystems on federal land remained more or less constant. Increases in areas of large, high-severity wildfires appear to have compensated for any decline in early-seral ecosystems created through harvest (22, 29). The ownership class with the largest share of diverse early-seral ecosystems was private nonindustrial land, where forest management is less intense, and here, the area of these ecosystems may even have increased slightly since the early 1990s. On private industrial land, however, diverse early-seral ecosystems have continued to decline. We hypothesize that this is because of intensive management practices that convert hardwoods and shrubby areas to conifers, suppress hardwoods in plantations, and accelerate canopy closure (26, 27, 34). These lands are also located on the most productive sites where conifer tree canopies close relatively quickly.

Declines in species associated with early-seral ecosystems may also be explained by factors unrelated to forest management, such as climate change or changes in habitat in the passage or wintering grounds of migratory species (35). This can be excluded as a primary explanation for species declines because both migrant and resident birds are in decline (*SI Appendix*, Table S2) and because of the strong link in our analysis between breeding habitat availability and bird numbers (*SI Appendix*, Fig. S5). Climate change affects some species, but its impacts can be moderated by habitat availability (36). Thus, while these various factors may also influence bird populations, they should be considered as additional rather than alternative explanations.

Declines in early-seral and older forest vegetation types and associated birds are of conservation concern because they are probably below their respective ranges in historical variability (a criterion used to assess conservation needs under the 2012 Forest Service planning rule). The historical extent of old-growth conifer forest in the Pacific Northwest has fallen from around 65% of the land area before European colonization to less than 20% (37). In the Oregon Coast Range, specifically, fire simulations for the past 3,000 y found that old growth ranged mostly between 25 and 75% (38); the current area of well-developed old-growth forest is as little as 2% (39). Swanson (40) estimated that 5–20% of the Pacific Northwest would have been under early-seral ecosystems at any one time in the recent past.

SUSTAINABILITY SCIENCE

Reversing population declines of early-seral and older-forest–associated birds will require managers to consider interactions between fires, forest types, and forest management. Projections of vegetation change and fire in the Pacific Northwest point to increased prevalence of wildfire and expansion of conditions suitable for hardwoods (41). These changes could create more habitat for species associated with early-seral ecosystems (42) and suggest that active management [including ecological forestry (15)] may be less needed where these processes occur. However, federal managers will likely continue to use fire suppression to protect human structures and dense, moist old-growth forests. Fire suppression can limit opportunities for natural development of early-seral vegetation. Hard choices may increasingly have to be made between permitting this natural process to occur and reducing fire risk to remaining stands of moist older forests (43), especially as fires become more frequent.

Since Holling (1) introduced the term "adaptive management" in 1978, the term has been commonly used in forest management, but rarely applied (2). Reasons for this likely include the decades that it takes forests to respond to silvicultural treatments and lags between vegetation responses and species population trajectories. Our results highlight that even extreme policy measures implemented over broad spatial scales—such as the cessation of clearcutting on 10 million ha of federal forestlands—may not have the expected outcomes, even after two decades. While the NWFP did reduce one of the threats to the Northern Spotted Owl, Marbled Murrelet *Brachyramphus marmoratus*, and other birds associated with older forests, other threats—likely including high-severity fire, postfire salvage logging, sustained clearcutting on private land, and invasive species—have prevented these species' recovery (44, 45).

Our results call into question ecological arguments for the broadscale creation of complex early-seral ecosystems via forest management. Given that older forests—particularly old-growth forests of moist regions of the Pacific Northwest—can take centuries to develop (46) and that populations of associated species continue to decline, it would appear that the priority for conservation and restoration continues to be older forests (12, 47). In the context of increasing wildfires, any shortfall in complex early-seral ecosystems might be best achieved by reducing salvage logging (31, 32). The case for increasing the area of complex early-seral ecosystems is strongest in the Coast Range and Cascades (*SI Appendix*, Fig. S8). Any such efforts, we suggest, should be done using landscape-scale approaches, considering the entire mosaic of vegetation and disturbance regimes, which do not compromise goals for older forests (e.g., by focusing restoration on existing plantations) (12). Adaptive management including multitaxa monitoring and experiments will also be critical given our lack of ecological knowledge and experience in restoring this ecosystem. The long time lags between treatments and ecological responses in forests will require that such programs be conducted over the long term.

Materials and Methods

Forest Data. From https://lemma.forestry.oregonstate.edu/data/structure-maps, we obtained Gradient Nearest Neighbor (GNN) map products showing annual modeled estimates of vegetation structure from 1984 to 2012. The GNN method combines vegetation data from Forest Inventory Analysis plots across the region with Landsat Thematic Mapper imagery and other environmental data to predict forest structure and composition at 30-m pixel resolution (20). As GNN is model-based, it is prone to some classification error. GNN data are not available before 1984 due to nonexistence of Landsat TM. However, our data do include the period 1984–1988, when timber harvest on federal land peaked (48). We defined "diverse early-seral ecosystems" as having a quadratic mean diameter of less than 10 cm in hardwood or mixed stands (≥20% basal area of hardwoods); this metric has been shown to be biologically meaningful to early-seral–associated birds at the landscape scale (14). However, because standing and fallen dead wood are not detectable in Landsat images, we cannot claim to have quantified structurally complex early-seral ecosystems (sensu 13). We also identified conifer-dominated early-seral ecosystems ("young-growth conifer") with <20% hardwoods. We defined older forest using the regionalized Old Growth Structure Index (OGSI) after Spies et al. (49). The index is based on the abundance of large live trees, snags, and downed wood, and diversity of tree sizes. We used the broadest definition of older forests (OGSI 80), intended to identify stands of at least 80 y with the structural attributes of old growth (22). In some regions with high growth rates (e.g., the Coast Range) these structural conditions may be achieved in forests younger than 80 y of age. OGSI 80 may be less effective at detecting older forests kept relatively open by frequent fire.

Land Ownership Data. We assembled a map of land ownership for the NWFP region (for data sources, see *SI Appendix*, Table S3; for shapefile data, see dx.doi.org/10.17632/k5nj539vc2.1). We classified land as federal, private industrial, private nonindustrial, and other. The "other" category included state and tribal lands. For the NWFP region, we used a 2002 outline from the Regional Ecosystem Office (https://www.fs.fed.us/r6/reo/library/maps.html). To calculate ownership and forest composition, we measured their coverage within a 400-m buffer of each BBS route and used the proportion covered by each land ownership in our analyses. The bird data from BBS are measured at the scale of entire 39.4-km routes, so we could not attribute observations completely to specific forest and ownership categories.

Bird Data. We obtained BBS count data for all selected bird species (*SI Appendix*, Table S2) for all survey routes that wholly or partially overlapped the NWFP region. The BBS is a long-term, large-scale monitoring program initiated in 1966 to track the status and trends of North American bird populations. Each BBS survey route is 24.5 mi (39.4 km) long, with stops at 0.5-mi (800-m) intervals. At each roadside stop, a 3-min point count is conducted. During the count, every bird seen or heard within a 0.25-mi (400-m) radius is recorded. Surveys are typically carried out in June and take about 5 h to complete (https://www.pwrc.usgs.gov/bbs/about/).

Thinning, Clearcutting, and Fire Data. We obtained data on forest management treatments in national forests from the US Forest Service and on Bureau of Land Management (BLM) land from the BLM website (Dataset S1). We obtained annual data on canopy disturbance from LandTrendR (landtrendr.forestry.oregonstate.edu) and on fire occurrence from the Wildland Fire Management Research, Development, and Application Program (https://wfdss.usgs.gov/wfdss/WFDSS_Data_Downloads.shtml).

Modeling Approach. We modeled regional bird trends across the NWFP region from the BBS data using a hierarchical log-linear model in a Bayesian framework. Our approach was based directly on that developed by Sauer and Link (50): an overdispersed Poisson regression on the annual counts of a species on each route. This regression has a term for year, the coefficient for which can be used to infer trend in bird numbers over time (i.e., change in count per year). This modeling framework addresses a number of well-known limitations of the BBS data: (*i*) observers are unequal in their ability to count birds, (*ii*) observers change among years on routes and are better at detecting birds after their first year of surveying, and (*iii*) there is nonrandom annual variation across routes. Sauer and Link (50) detail how the model was formulated to account for these issues. This model also scales route-level trends into a regional trend, while appropriately propagating uncertainty from the route to the regional level. As a result, this model robustly quantifies regional trends and the associated uncertainty in those trends by accounting for route-level trends and their associated uncertainty. To test our hypotheses, we modified the Sauer and Link (50) model in a number of ways (see the next three sections of *Materials and Methods*) and fitted these models to data from each bird species separately (*SI Appendix*).

Bird Population Trends in Relation to Ownership. To examine how bird population trajectories changed in relation to ownership patterns, we compared trends in the period up to the implementation of the NWFP (pre-NWFP: 1968–1993) and the period after (post-NWFP: 1994–2015). To compare these trends, we modified the Sauer and Link (50) model, such that the trend was fitted as a segmented regression model, which allows for a quantification of the change in a trend after some intervention: here, implementation of the NWFP (51). To assess how any changes in trends varied on routes with differing ownership, we modeled route-level trends before and after the NWFP as a function of the proportion of each route composed of each ownership type in a hierarchical framework (52). This approach allows routes in landscapes composed of different ownership types to have different trends and gives a quantitative measure of how ownership influences these trends. For each species, we report trends estimated for a hypothetical route with the mean +1 SD proportion of each focal ownership and mean proportions of each nonfocal ownership (*SI Appendix*, Fig. S10 and Table S4).

Bird Population Trends in Relation to Changes in Forest Composition. We analyzed the relationships between bird abundance and the proportions of early-seral ecosystems and older-forest vegetation per route in each year. We included annual measures of the proportion of each route composed of each vegetation type as a covariate on the annual counts for the period with covariate data (1984–2012). We specified this model such that the route-level effects of forest composition (i.e., either early-seral ecosystems or older forest) were integrated into a regional effect, while propagating route-level uncertainty to the regional level. This model tests whether more of these vegetation types on a route in a year equated to more birds counted in that year and scales any effects to the regional scale, while accounting for route-level variance (*SI Appendix*, Tables S5 and S6).

Effects of Habitat Loss Moderated by Habitat Amount. We tested whether proportional changes in bird numbers were greater when there was less or more habitat at a route scale by including both initial habitat amount (in 1984) and loss in our modeling framework. To conduct this test, we again modified the Sauer and Link (50) model. We modeled annual counts as a function of the annual proportion of each route composed of each species-relevant habitat (older forest, early-seral ecosystem, or both), as previously, but further modeled the effect of annual measures of habitat as a function of the initial amount of habitat on the route (*SI Appendix*, Fig. S11 and Table S1). This formulation directly tests the hypothesis that effects of habitat loss are contingent on the amount of habitat at the outset of the study on each route; under the extinction debt hypothesis, landscapes with low amounts of habitat initially should experience the greatest effects of contemporary forest loss.

ACKNOWLEDGMENTS. We thank Cheryl Friesen (US Forest Service) for support; Raymond Davis (US Forest Service), Katherine Morrison (Oregon Department of Forestry), Luke Rogers (University of Washington), and Mark Rosenberg (California Department of Forestry and Fire Protection) for spatial data; Kenneth Ruzicka (BLM) for information on policies regarding early-seral habitat; and the volunteers and technicians who generated the data used. This work was funded by the US Forest Service (Grant 14-JV-11261975-060) and the US Department of Agriculture (Awards AFRI-2009-426 04457, AFRI 2011-68005-30416, AFRI-2015-67019-23178). We acknowledge US National Science Foundation Long Term Ecological Research Program at the H. J. Andrews Experimental Forest (Grant DEB-0823380).

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