1-7-2019

The past and future roles of competition and habitat in the range-wide occupancy dynamics of Northern Spotted Owls

Charles B. Yackulic
Southwest Biological Science Center, cyackulic@usgs.gov

Larissa L. Bailey
Colorado State University

Katie M. Dugger
Oregon State University

Raymond J. Davis
Forestry Sciences Laboratory

Alan B. Franklin
USDA APHIS National Wildlife Research Center

See next page for additional authors

Authors
Charles B. Yackulic, Larissa L. Bailey, Katie M. Dugger, Raymond J. Davis, Alan B. Franklin, Eric D. Forsman, Steven H. Ackers, Lawrence S. Andrews, Lowell V. Diller, Scott A. Gremel, Keith A. Hamm, Dale R. Herter, J. Mark Higley, Rob B. Horn, Christopher McCafferty, Janice A. Reid, Jeremy T. Rockweit, and Stan G. Sovern

Communication

Ecological Applications, 29(3), 2019, e01861

The past and future roles of competition and habitat in the range-wide occupancy dynamics of Northern Spotted Owls

Charles B. Yackulic,[1,13] Larissa L. Bailey,[2] Katie M. Dugger,[3] Raymond J. Davis,[4] Alan B. Franklin,[5] Eric D. Forsman,[4] Steven H. Ackers,[6] Lawrence S. Andrews,[6] Lowell V. Diller,[7] Scott A. Gremel,[8] Keith A. Hamm,[7] Dale R. Herter,[9] J. Mark Higley,[10] Rob B. Horn,[11] Christopher McCafferty,[6] Janice A. Reid,[12] Jeremy T. Rockweit,[2] and Stan G. Sovern[6]

[1]*U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, Arizona 86001 USA*
[2]*Department of Fish, Wildlife, and Conservation Biology, Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523 USA*
[3]*U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA*
[4]*USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Corvallis, Oregon 97331 USA*
[5]*USDA APHIS National Wildlife Research Center, Fort Collins, Colorado 80521 USA*
[6]*Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA*
[7]*Green Diamond Resource Company, Korbel, California 95550 USA*
[8]*USDI National Park Service, Olympic National Park, Port Angeles, Washington 98362 USA*
[9]*Raedeke Associates, Seattle, Washington 98133 USA*
[10]*Hoopa Tribal Forestry, Hoopa, California 95546 USA*
[11]*USDI Bureau of Land Management, Roseburg District Office, Roseburg, Oregon 97471 USA*
[12]*USDA Forest Service, Pacific Northwest Research Station, Roseburg Field Station, Roseburg, Oregon 97471 USA*

Citation: Yackulic, C. B., L. L. Bailey, K. M. Dugger, R. J. Davis, A. B. Franklin, E. D. Forsman, S. H. Ackers, L. S. Andrews, L. V. Diller, S. A. Gremel, K. A. Hamm, D. R. Herter, J. M. Higley, R. B. Horn, C. McCafferty, J. A. Reid, J. T. Rockweit, and S. G. Sovern. 2019. The past and future roles of competition and habitat in the range-wide occupancy dynamics of Northern Spotted Owls. Ecological Applications 29(3):e01861. 10.1002/eap.1861

Abstract. Slow ecological processes challenge conservation. Short-term variability can obscure the importance of slower processes that may ultimately determine the state of a system. Furthermore, management actions with slow responses can be hard to justify. One response to slow processes is to explicitly concentrate analysis on state dynamics. Here, we focus on identifying drivers of Northern Spotted Owl (*Strix occidentalis caurina*) territorial occupancy dynamics across 11 study areas spanning their geographic range and forecasting response to potential management actions. Competition with Barred Owls (*Strix varia*) has increased Spotted Owl territory extinction probabilities across all study areas and driven recent declines in Spotted Owl populations. Without management intervention, the Northern Spotted Owl subspecies will be extirpated from parts of its current range within decades. In the short term, Barred Owl removal can be effective. Over longer time spans, however, maintaining or improving habitat conditions can help promote the persistence of northern spotted owl populations. In most study areas, habitat effects on expected Northern Spotted Owl territorial occupancy are actually greater than the effects of competition from Barred Owls. This study suggests how intensive management actions (removal of a competitor) with rapid results can complement a slower management action (i.e., promoting forest succession).

Key words: competitive exclusion; ecological forecasting; geographic range dynamics; late-successional habitat; old growth forest; temporal scaling.

Introduction

Many ecological processes relevant to landscape-scale conservation and management are slow to develop and are not immediately apparent. These processes can

Manuscript received 29 August 2018; revised 17 December 2018; accepted 7 January 2019. Corresponding Editor: Carolyn H. Sieg.
[13] E-mail: cyackulic@usgs.gov

manifest themselves over decades to millennia and involve both loss and recovery of species. Slow processes of loss include extinction debts in fragmented landscapes (Tilman et al. 1994, Jones et al. 2018), exclusion of native species by invading species (Gilbert and Levine 2013, Yackulic 2017), and population declines in response to ongoing climate change (Peery et al. 2012). Slow processes of recovery include the recovery of late-successional habitats degraded by humans (Aide et al. 1996) and the range expansion of tree species limited by dispersal (Svenning and Skov 2007), with implications for animal species that depend on these plant communities (Yackulic and Ginsberg 2016). Slow processes create challenges for conservation efforts as short-term drivers of trends may be more obvious than forces acting over longer time periods. Furthermore, the optimal management strategy may involve staggering different management actions over time. Slow rates of change necessitate a focus on the processes driving loss or recovery (e.g., extinction and colonization) and what they imply for future states (e.g., extent and frequency of occurrence), in addition to the current state of the system (Yackulic et al. 2015).

Here, we show how processes of colonization and extinction can be analyzed to elucidate the relative importance of slower and faster processes and forecast future occupancy under different management scenarios. While our approach is general, we focus our analysis on the past and potential future drivers of the population dynamics of Northern Spotted Owls (*Strix occidentalis caurina*; hereafter NSO) in the Pacific Northwest region of the United States of America. NSO populations have been declining for over three decades, with initial declines driven primarily by habitat loss (Lande 1988). Older forest, the preferred habitat of NSO throughout most of their geographic range, was harvested from the late 19th century through the late 20th century, when declines in NSO populations led to the listing of the species as "threatened" under the U.S. Endangered Species Act in 1990 and the development of the Northwest Forest Plan in 1994 (Davis et al. 2017). Since 1994, the Northwest Forest Plan has significantly lessened the rate of habitat loss on federal lands from timber harvesting, but a recent increase in large, high-severity wildfires has led to reduced NSO survival and significant habitat losses in some regions (Davis et al. 2016, Rockweit et al. 2017). Even without further loss, recruitment of old forest was expected to take many decades (Lint et al. 1999) and declines in NSO were expected as populations equilibrated with past habitat loss (Thomas et al. 1993). Nonetheless, the degree and ubiquity of ongoing declines in NSO populations (Fig. 1) have outpaced forecasts linked solely to habitat loss and there is now strong evidence linking recent declines to competition with invading Barred Owls (*Strix varia*; hereafter BO; Yackulic et al. 2014, Dugger et al. 2016).

While there is some debate regarding the changes that allowed BO to expand their distribution westward into Washington and British Columbia (Livezey 2009b), it is clear that BO began to invade the northern portion of the NSO geographic range about 50 years ago and were found throughout the NSO range in low numbers when the Northwest Forest Plan was first implemented (Livezey 2009a). Over the last decade, BO has continued to spread to new areas and increase in local abundances once they are present (Fig. 1; Yackulic et al. 2012, Rossman et al. 2016, Zipkin et al. 2017). Removal of BO was an effective management action in one study area at the leading edge of the invasion, halting declines in NSO territorial occupancy (Diller et al. 2016); however, it is unclear whether BO removal will be as effective in areas with different forest conditions, or where BO are more established.

In this paper, we quantify the relative importance of habitat and BO competition in past and future NSO territorial occupancy dynamics. We rely on long-term studies of NSO populations at eleven study areas spanning the United States portion of the NSO historic geographic range. We begin by estimating current trends in NSO habitat covariates and territorial colonization and extinction rates for BO and NSO. We then quantify the influences of habitat and competition with BO on expected NSO territory occupancy. Lastly, we forecast future interactions between BO and NSO under current conditions and under scenarios with various levels of BO removal or changes in habitat condition.

Methods

Territorial colonization and extinction probabilities for NSO and BO

NSO and BO data were previously analyzed by Dugger et al. (2016) using two-species occupancy models, however that study was focused on NSO demography and did not present BO vital rates or consider the implications of the joint dynamics of the two owl species. In both studies, the spatial unit of the analysis (hereafter the "site") is NSO territories that were delineated by generating Thiessen polygons based on annual NSO activity centers (see Dugger et al. 2016). Surveys focused on identifying NSO breeding pairs, and thus, occupancy for this species was defined in terms of pairs. In a few instances, surveyors were unable to confirm a mate and these detections of unpaired individuals were treated as non-detections. For BO, exact assessments through follow-up surveys were usually not made, so we defined occupancy to include both paired and unpaired individuals. In 10 of 11 study areas, we analyzed data from 1995 to 2013, while in one study area (Green Diamond), only data from 1998 to 2013 were available for analysis. We base inferences for each study area on the model with the lowest Akaike information criterion corrected for sample size (AIC_c; Burnham and Anderson 1998). For more details on two-species occupancy modeling, see Appendix S1.

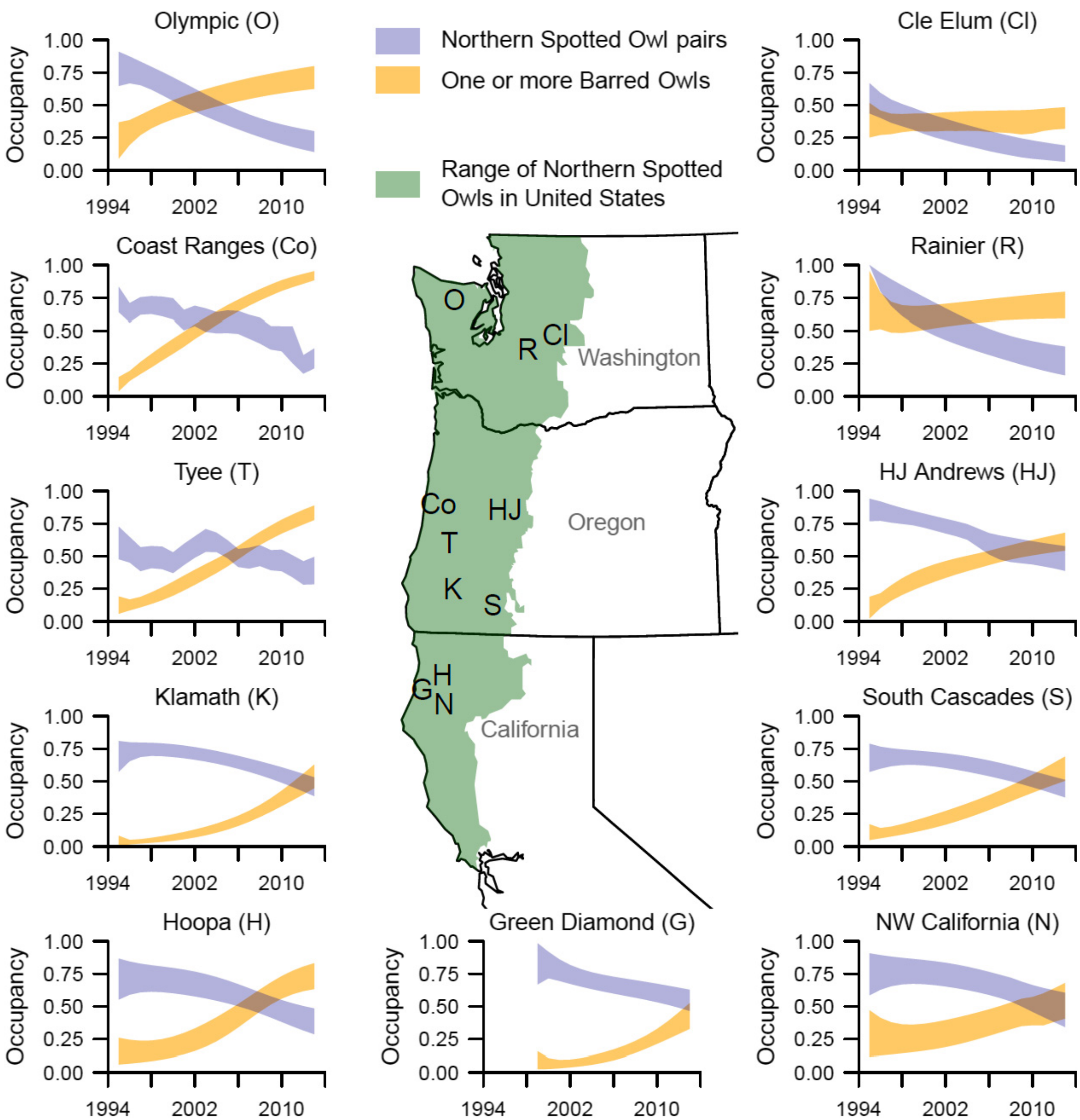

FIG. 1. Trends in occupancy probabilities of Northern Spotted Owl (NSO) and Barred Owl (BO) in different parts of the Northern Spotted Owls' geographic range. The center map shows the placement of the 11 study areas relative to state boundaries and the geographic range of the NSO in the United States. The historic range of NSO extended into Canada; however, very few NSO remain in Canada. Graphs around the map show the proportion of NSO territories that were occupied by NSO pairs (purple) or BO (orange) in each study area (code letter in parentheses) over time. Estimates given for territories with the average habitat conditions for the focal study area and the width of these lines correspond to 95% confidence intervals.

NSO habitat

To determine the degree to which habitat conditions varied among territories vs. through time, we partitioned sources of variation (i.e., spatial, temporal, and residual variation) in five habitat covariates (see Appendix S2: Table S1 for an explanation of habitat covariates) considered drivers of NSO and BO colonization and extinction rates. We first standardized the covariates based on the mean and standard deviation of each covariate in each study area. We then fit generalized linear mixed effect models for each habitat covariate and study area separately with site and year as random effects.

Competitive and habitat effects based on 2012–2013 vital rates

To calculate the effects of habitat and competition on expected NSO occupancy in each study area, we first calculated expected NSO occupancy for each territory both with and without the effects of competition with Barred Owl. To calculate expected NSO occupancy with competition, we determined the eigenvectors associated with the territory-specific transition matrices, $\phi_{i,\text{last}}$, for each territory *i*, derived from the last interval (2012–2013) of the study. We chose the last interval to account for slight changes in habitat covariates over time and trends in vital rates that were not attributed to competition or our chosen habitat covariates. We then summed the eigenvectors corresponding to the two occupied NSO states to obtain expected NSO occupancy (see Miller 2012 for general approach and R code for details specific to our application). To calculate expected NSO occupancy without competition for each territory, we modified $\phi_{i,\text{last}}$ by setting all interspecific interaction terms to zero before calculating the associated eigenvectors.

Within each study area, we sorted sites by their expected NSO occupancy without competition and chose the sites in the 97.5%, 50% and 2.5% quantiles to represent the better, average, and worse habitat conditions, respectively. We defined the effect of habitat within each study area as the difference in expected NSO occupancy without competition between sites with better and worse habitat conditions. We defined the effect of competition within a study area as the difference in the expected NSO occupancy with and without competition for the territory with average habitat conditions. We chose this approach to defining the habitat and competition effects (as opposed to comparing effect sizes) because we were trying to synthesize the impacts of up to five habitat covariates on as many as four different vital rates and compare it to the effects of competition that may be on different vital rates. As such, our approach provides a more synthetic comparison. In addition, the different habitat covariates were on different scales and are measures of relative quality within each study area, not absolute quality across study areas. Last, while our competition effect is based on a comparison with and without competition, definition of the habitat effect was somewhat arbitrary, and we could imagine another researcher defining better and worse based on either more (e.g., maximum, minimum) or fewer (e.g., 90%, 10%) quantiles. To ensure that this decision did not fundamentally alter our results, we repeated our analysis with these alternative definitions and report these results in Appendix S2.

Forecasting NSO probabilities of persistence

Using parameters derived from Dugger et al. (2016) and Diller et al. (2016), we simulated the joint occupancy dynamics of NSO and BO for 50 yr under a variety of scenarios, running 100 simulations for each scenario. Once the simulated occupancy for NSO fell to zero within a study area that study area was considered extirpated for that simulation. We began by examining a baseline scenario in which habitat was based on current values and did not change over time, and BO removal did not occur. This baseline scenario was used to determine the sensitivity of the results to uncertainty in estimated parameters by comparing this baseline scenario to scenarios in which NSO territory extinction rates were either increased or decreased by 25%. We then examined how the probability of NSO persisting 50 yr responded to (1) variation in BO removal intensity, from no removals to the removal intensity reported in Diller et al. (2016), and (2) changes in habitat condition covering the range of habitat conditions currently present in each study area (see Appendix S1 for more details). All analyses occurred in R (version 3.3.2) and data and code required to run our model are available from the USGS ScienceBase-Catalog (Yackulic 2019; see *Data Availability*).

Results

Recent range-wide declines in NSO occupancy have been driven primarily by competition with increasing BO populations. Competition increased NSO extinction probabilities in all study areas (Appendix S2: Fig. S1). As BO occupancy rates have increased over time (Fig. 1), the impact of BO on NSO has also increased. Across all 11 study areas, BO also has elevated territory extinction probabilities in co-occupied territories. Territory colonization probabilities for NSO were lowered in five study areas when BO was already present; however, there was not a consistent effect of NSO presence of BO colonization probabilities.

Despite the overwhelming influence of BO on recent NSO trends, the habitat effect is comparable in magnitude to the effect of competition (Fig. 2) and this qualitative result is insensitive to our approach to defining the habitat effect (Appendix S2: Fig. S2). The similar magnitude of habitat and competitive effects on NSO occupancy is obscured in trend analyses because over the study period (1995–2013) habitat covariates varied primarily in space (from territory to territory, Appendix S2: Table S1) but not through time in our study areas (except for disturbances, gains in habitat were not detected over the relatively short duration of the study as it takes many decades for habitat conditions to improve). Although we defined habitat and competitive effects as independent, there is an additional interaction because of the overlapping habitat preferences of BO and NSO. Specifically, effects of Barred Owl competition on expected NSO occupancy are greatest in territories with better habitat conditions (Appendix S2: Fig. S3).

We used forecasts to partition the importance of habitat and competition for long-term NSO persistence. In every study area, some combination of increase in habitat condition and BO removal led to <95% probability that NSO would persist for 50 or more years (Fig. 3). In most study areas, declines in habitat condition will necessitate increased investment in BO removal to promote NSO persistence. In the absence of increasing

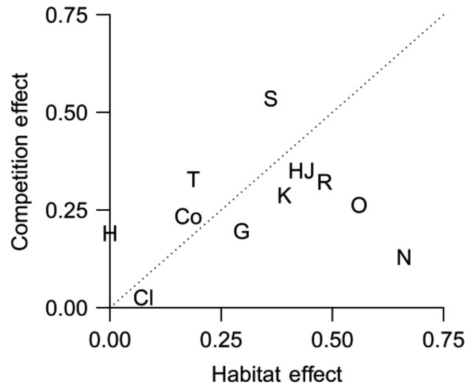

Fig. 2. Comparison of the effects of competition and habitat on expected NSO occupancy in 11 study areas. The habitat effect is the difference in expected occupancy (in the absence of competition) between sites with better and worse habitat conditions and reflects both the strength of habitat effects and the amount of variation in habitat condition within the study area. The competition effect is the difference in expected occupancy for a site with average habitat conditions when BO is present or absent. Letters follow the codes identified in Fig. 1. The dotted line represents equal effects of habitat and competition. Symbols above the dotted line represent study areas where competition effects are greater than habitat effects, whereas symbols below the line are study areas where habitat effects are greater than competition effects.

habitat conditions or BO removal, baseline forecasts suggest that NSO will be competitively excluded from many study areas within decades (Appendix S2: Fig. S4). These forecasts of time to extinction were relatively insensitive to either 25% increases or decreases in NSO extinction probabilities.

Discussion

Analysis of territorial occupancy dynamics strongly suggests that recent declines in NSO territory occupancy were driven by increasing BO prevalence. NSO territory extinction rates are higher in the presence of BO in all study areas and BO has been stable or increasing in all study areas (Fig. 1; Appendix S2: Fig. S1). Consequently, NSO is likely to be extirpated from many parts of their current range within a few decades without some form of BO removal (Fig. 3). BO removals have been shown to be an effective management tool in one study area (Diller et al. 2016) and are being tested in other parts of the NSO range (Wiens et al. 2018). Probabilities of NSO persisting for 50 years under current habitat conditions without BO removal are <5% in three study areas, 5–50% in three study areas, and above 95% in only two study areas.

At the same time, maintaining or improving habitat condition could be an important factor in promoting persistence of NSO populations over longer time spans and could allow managers to be less reliant on BO removals in the future (Fig. 3). Variation in NSO colonization and extinction probabilities due to habitat conditions currently manifests primarily in terms of spatial variation in these rates, and the occupancy patterns implied by these rates. In many study areas, this spatial variation was greater than the observed temporal variation due to competition over the 18-yr study period (Fig. 2). To the extent that current spatial variation is related to the potential for habitat improvement over coming decades, changes in habitat could play a more important role in future NSO population trends. Whereas BO removals can stabilize NSO populations and competitive exclusion may take a few decades, forest regeneration can take 50 or more years. Nonetheless, habitat recovery could eventually lessen the need for intensive management actions such as Barred Owl removal. If, on the other hand, managers allow habitat conditions to decline they may have to rely more on BO removal, and in some study areas, persistence of NSO is predicted to become infeasible.

The potential for habitat recovery varies substantially throughout the NSO geographic range and requires further study. In the short term, we expect the impact of BO on NSO to increase, particularly in more southern parts of their range where BO is currently increasing rapidly (Fig. 1). Interestingly, the study areas in the southern part of the range may also show more potential for habitat improvement over shorter time periods as NSO appears to be less strictly reliant on late-successional forest in these areas. Instead, NSO in many southern study areas benefit demographically from a mix of forest successional stages that create edges with patches of older forest (Franklin et al. 2000).

The outlook for NSO is best in study areas found in the middle of the NSO geographic range (e.g., Tyee and H. J. Andrews). Current conditions in these study areas suggest a >95% probability of persistence over the next half century. However, if densities of BO within NSO territories continue to increase (Rossman et al. 2016) and effects of BO competition on NSO occupancy dynamics intensify in response, then our forecasted persistence probabilities may be overly optimistic. Future analyses of NSO and BO occupancy dynamics should consider testing whether the intensity of BO effects on NSO vital rates is stable or increasing. In more coastal study areas in Oregon, BO densities are still increasing (Zipkin et al. 2017) and BO removals have often led to rapid BO recolonization (Wiens et al. 2018).

In the Northern parts of the NSO range, there is less potential for rapid habitat improvement, BO have been established for longest and NSO have declined substantially. A removal experiment over the last three years in the Cle Elum study area has significantly increased BO extinction probabilities; however, there has not been an associated increase in NSO occupancy (Wiens et al. 2018). It is likely that NSO responses to BO removal will be slower, and require more intense BO removals to elicit a response, in areas where both the territorial and floater populations of NSO have declined leading to lower territory colonization probabilities.

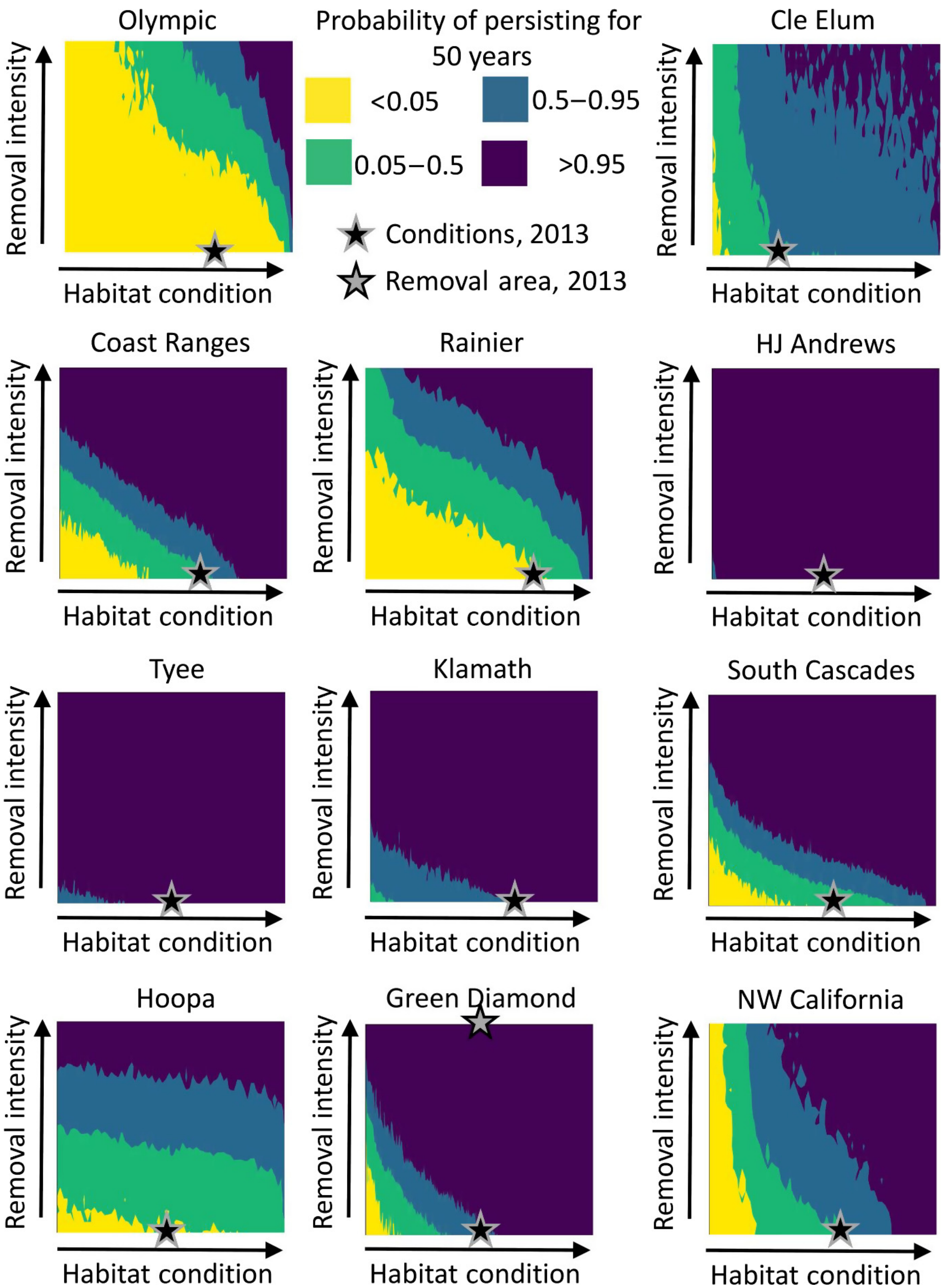
Olympic
Probability of persisting for 50 years
<0.05
0.5–0.95
0.05–0.5
>0.95
Conditions, 2013
Removal area, 2013
Cle Elum
Coast Ranges
Rainier
HJ Andrews
Tyee
Klamath
South Cascades
Hoopa
Green Diamond
NW California
Removal intensity
Habitat condition

Fig. 3. The probability that NSO persists for 50 years across various study areas as a function of BO removal intensity and habitat conditions within each study area. Allowing habitat to regenerate has the effect of slowly moving a study area to the right from its current conditions, while habitat loss will move a study area to the left. For each study area, we predict the probability that NSO persists for 50 years or more under various management scenarios consisting of different levels of habitat modification and BO removal. We simulated habitat differences by running scenarios in which all sites within a study area were given the vital rates derived from the habitat within a single site and then iterating through all sites with a study area (x-axis). We also varied the level of Barred Owl removal from zero to the intensity implied by a comparison of pre- and post-treatment Barred Owl extinction probabilities estimated in Diller et al. (2016; y-axis). Sites were then sorted based on the predicted persistence for a particular site's vital rates when Barred Owl removal was set to zero and compared to a set of simulations based on 2012 habitat conditions (including variability between sites) to determine where current habitat conditions fell along the gradient of habitat conditions implied by individual site vital rates. For each combination of habitat condition and removal intensity, we ran 100 simulations and report the percentage of simulations in which NSO persisted for more than 50 years. Stars indicate the conditions most similar to the conditions in 2013, with filled stars indicating areas without current BO removal efforts and the empty star indicating the BO removal area within the Green Diamond Study area.

Our approach assumes that current spatial variation in habitat conditions within study areas is related to the potential for habitat recovery within different study areas: an assumption that is not strictly accurate. In some areas, our approach may underestimate the potential for habitat recovery. We identified sites with better and worse habitat conditions relative to all other patches in a study area, but continued forest recovery may yield better habitats conditions than anything currently present in a study area. In other areas, conditions defined as "better" within a particular study area may be unattainable throughout the study area (e.g., if sites with worse habitat conditions are in valley bottoms and sites with better habitat conditions are in uplands, geologic time scales would be necessary to change conditions). For example, in some study areas (e.g., Olympic and Rainier), there is little history of habitat loss and, as a result, little room for habitat recovery. Future work could provide better forecasts for specific study areas by focusing on dynamic simulations of the multiple processes that affect habitat conditions for NSO. These simulations could incorporate expected changes in habitat conditions over time resulting from both forest regeneration and potential for forest fires of different intensities. As habitat characteristics can affect microclimates and the likelihood of fire, there are potentially many important site-specific feedbacks that require more research.

While we have outlined ways in which our analysis could be improved by adding complexity, the simplicity of our approach may also make it useful in situations where less data are available. Colonization and extinction probabilities can often be estimated with reasonable accuracy and precision with a few years of occupancy data and if there is sufficient spatial and temporal variation in potential drivers within the dataset, ecologists may be able to make inferences about both slower and faster ecological processes that may determine future occupancy states of the system. Eigenvalue analyses have not been frequently applied to multistate occupancy models, such as the two-species model examined here; however, they provide a useful tool for distilling how variation in multiple process parameters affect the distribution of state variables. In this specific case study, eigenvalue analysis illustrated the effects of habitat conditions and competition on expected NSO territorial occupancy.

Recent NSO declines were driven primarily by competition with increasing BO populations (Fig. 1), but this does not mean that BO removals alone are sufficient to attain long-term NSO persistence. In addition, removals may not benefit other species that depend on older forest if retention and restoration of habitat does not continue to be a management priority (but see Holm et al. 2016). The availability of high-quality NSO habitat is a necessary condition for BO removals to succeed, and the results of this analysis suggest that habitat recovery could reduce future need for removals. Nonetheless, regeneration of older forest is a relatively slow process occurring over many decades and is threatened by a variety of factors including large, high-severity forest wildfires in some parts of the NSO geographic range (Rockweit et al. 2017). Therefore, BO removals remain an important management action to promote NSO persistence over shorter time scales. More broadly, this case study suggests how intensive management actions with fast response rates (e.g., BO removals) can complement more lasting solutions (habitat recovery) that occur at slower rates.

Acknowledgements

Studies on federal lands were primarily funded by the USDA Forest Service, USDI Bureau of Land Management, and USDI National Park Service. Studies on nonfederal lands were funded by Green Diamond Resource Company, Plum Creek Timber Company, Louisiana Pacific Lumber Company, Hancock Forest Management, and the Bureau of Indian Affairs through the Hoopa Tribe. Funding for the 2014 NSO Meta-analysis workshop was provided by the USDA Forest Service and USDI Bureau of Land Management. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Aide, T. M., J. K. Zimmerman, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica 28:537–548.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Davis, R. J., B. Hollen, J. Hobson, J. E. Gower and D. Keenum. 2016. Northwest Forest Plan—the first 20 years (1994-2013): status and trends of northern spotted owl habitats. General Technical Report PNW-GTR-929. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Davis, R. J., A. N. Gray, J. B. Kim, and W. B. Cohen. 2017. Patterns of change across the forested landscape. Pages 91–101 *in* D. H. Olson and B. Van Horne, editors. People, forests, and change: lessons from the Pacific Northwest. Island Press/Center for Resource Economics, Washington, D.C., USA.

Diller, L. V., K. A. Hamm, D. A. Early, D. W. Lamphear, K. M. Dugger, C. B. Yackulic, C. J. Schwarz, P. C. Carlson, and T. L. McDonald. 2016. Demographic response of northern spotted owls to barred owl removal. Journal of Wildlife Management 80:691–707.

Dugger, K. M., et al. 2016. The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. Condor 118:57–116.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539–590.

Gilbert, B., and J. M. Levine. 2013. Plant invasions and extinction debts. Proceedings of the National Academy of Sciences of USA 110:1744–1749.

Holm, S. R., B. R. Noon, J. D. Wiens, and W. J. Ripple. 2016. Potential trophic cascades triggered by the barred owl range expansion. Wildlife Society Bulletin 40:615–624.

Jones, G. M., J. J. Keane, R. J. Gutiérrez, and M. Z. Peery. 2018. Declining old-forest species as a legacy of large trees lost. Diversity and Distributions 24:341–351.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia 75:601–607.

Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy and E. Starkey. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest Forest Plan. General Technical Report PNW-GTR-440. U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Livezey, K. B. 2009*a*. Range expansion of barred owls, part i: chronology and distribution. American Midland Naturalist 161:49–56.

Livezey, K. B. 2009*b*. Range expansion of barred owls, part ii: facilitating ecological changes. American Midland Naturalist 161:323–349.

Miller, D. A. W. 2012. General methods for sensitivity analysis of equilibrium dynamics in patch occupancy models. Ecology 93:1204–1213.

Peery, M. Z., R. J. Gutiérrez, R. Kirby, O. E. LeDee, and W. LaHaye. 2012. Climate change and spotted owls: potentially contrasting responses in the Southwestern United States. Global Change Biology 18:865–880.

Rockweit, J. T., A. B. Franklin, and P. C. Carlson. 2017. Differential impacts of wildfire on the population dynamics of an old-forest species. Ecology 98:1574–1582.

Rossman, S., C. B. Yackulic, S. P. Saunders, J. Reid, R. Davis, and E. F. Zipkin. 2016. Dynamic N-occupancy models: estimating demographic rates and local abundance from detection-nondetection data. Ecology 97:3300–3307.

Svenning, J.-C., and F. Skov. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10:453–460.

Thomas, J. W., M. G. Raphael, R. Anthony, E. Forsman, A. Gunderson, R. Holthausen, B. Marcot, G. Reeves, J. Sedell and D. Solis. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team (FEMAT). Forest Service, Washington, D.C., USA.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65.

Wiens, J. D., K. M. Dugger, D. B. Lesmeister, K. E. Dilione and D. C. Simon. 2018. Effects of experimental removal of Barred Owls on population demography of Northern Spotted Owls in Washington and Oregon—2017 progress report: U.S. Geological Survey Open-File. Report 2018-1086. Reston, Virginia.

Yackulic, C. B. 2017. Competitive exclusion over broad spatial extents is a slow process: evidence and implications for species distribution modeling. Ecography 40:305–313.

Yackulic, C. B. 2019. Northern spotted owl data and analysis models. U.S. Geological Survey Data Release. https://doi.org/10.5066/p9o0iirh

Yackulic, C. B., and J. R. Ginsberg. 2016. The scaling of geographic ranges: implications for species distribution models. Landscape Ecology 31:1195–1208.

Yackulic, C. B., J. Reid, R. Davis, J. E. Hines, J. D. Nichols, and E. Forsman. 2012. Neighborhood and habitat effects on vital rates: expansion of the Barred Owl in the Oregon Coast Ranges. Ecology 93:1953–1966.

Yackulic, C. B., J. Reid, J. D. Nichols, J. E. Hines, R. Davis, and E. Forsman. 2014. The roles of competition and habitat in the dynamics of populations and species distributions. Ecology 95:265–279.

Yackulic, C. B., J. D. Nichols, J. Reid, and R. Der. 2015. To predict the niche, model colonization and extinction. Ecology 96:16–23.

Zipkin, E. F., S. Rossman, C. B. Yackulic, J. D. Wiens, J. T. Thorson, R. J. Davis, and E. H. C. Grant. 2017. Integrating count and detection–nondetection data to model population dynamics. Ecology 98:1640–1650.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1861/full

Data Availability

Data are available on Science Base: https://doi.org/10.5066/p9o0iirh

Communication