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Research Article

Occupancy Patterns in a Reintroduced Fisher Population during Reestablishment

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ABSTRACT Monitoring population performance in the years following species reintroductions is key to assessing population restoration success and evaluating assumptions made in planning species restoration programs. From 2008–2010 we translocated 90 fishers (*Pekania pennanti*) from British Columbia, Canada, to Washington's Olympic Peninsula, USA, providing the opportunity to evaluate modeling assumptions used to identify the most suitable reintroduction areas in Washington and enhance understanding of fisher habitat associations in the late-successional forest ecosystems in the coastal Pacific Northwest. From 2013–2016, we deployed 788 motion-sensing cameras and hair (DNA)-snaring devices distributed among 263 24-km^2 primary sampling units across the Olympic Peninsula. Our objectives were to determine whether occupancy patterns of the reestablishing population supported assumptions of the initial habitat assessment models, whether the population had expanded or shifted in distribution since the initial reintroductions, compare physical habitat attributes among land-management designations, and determine whether the founding fishers had successfully reproduced. We predicted that site occupancy by fishers would be associated with landscapes characterized by high proportional coverage of dense forest canopies and medium-sized and large trees, a diversity of stand structural classes, and area near the administrative boundary separating wilderness from more intensively managed forest lands. We detected fishers across designated wilderness, federal lands outside of wilderness, and other land designations in proportion to land availability on the Peninsula. We found negligible support for predictions that occupancy by fishers was associated with percent forest cover, tree-size class, or structural class diversity. Rather, occupancy was strongly associated with lands near the wilderness boundary on both sides. We speculate that the boundary between wilderness and more intensively managed forest lands provided fishers with the most suitable prey in proximity to contiguous expanses of low- to mid-elevation late-successional forests that provided optimal resting, denning, and security values. Occupancy patterns shifted toward the west and south along a precipitation gradient during the study, indicating that population distribution had not yet stabilized 5–8 years following translocation. Genetic results indicated that ≥2 generations of fishers have been produced on the Peninsula. Annual occupancy rates across the Peninsula (0.08–0.24) were lower than in other previously studied and established fisher populations, indicating that not all habitat was fully occupied or that initial estimates of the extent of habitat was overestimated. The strong selection fishers exhibited for wilderness edge and weak selection against extensive forested wilderness areas suggested that habitat managers should strive for maintaining a suitable interspersion of required forest structures and biotic habitat components, such as prey resource availability. © 2019 The Wildlife Society.

KEY WORDS fisher, noninvasive genetic sampling, occupancy, Olympic Peninsula, *Pekania pennanti*, reintroduction, translocation.

Species translocation, the transportation and release of animals to reestablish or augment wild populations, has become a mainstay of efforts to conserve and restore imperiled or sensitive wildlife species throughout the world (Griffin et al. 1989, Seddon et al. 2007). Humans have translocated wild animals for conservation purposes for many decades, but until recently most of these efforts took place with limited planning and post-release monitoring

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(Seddon et al. 2007). A recent emphasis on scientific reporting of translocation successes and failures has greatly enhanced our understanding of species reintroductions (translocations to reestablish a population within a portion of its historical range) and the utility of this conservation tool (Griffin et al. 1989, Wolf et al. 1996, Armstrong and Seddon 2008, Powell et al. 2012).

Habitat provides the foundation for a successful species reintroduction (Griffin et al. 1989, Miller et al. 1999, Armstrong and Seddon 2008). For a translocation to be successful, the selected environment must contain suitable sites for reproduction and rearing of young, security from predators, protection from thermal extremes, and adequate food and water. Often, however, the requisite understanding of critical components of a species' habitat and multidimensional niche are poorly understood or lacking, particularly for extirpated wildlife populations. In such cases, key components of a species' habitat must be inferred using models of species-habitat associations developed in regions that may differ from the proposed reintroduction area in landscape and environmental contexts. Thus, examining assumptions made in selecting suitable reintroduction areas and refining our understanding of post-release occupancy patterns in reintroduced populations are important for enhancing future reintroduction successes.

The fisher (*Pekania pennanti*), a medium-sized member of the mustelid family, is among the most frequently and successfully translocated carnivore species in North America (Lewis et al. 2012). Fishers were extirpated from much of the northern United States and southern Canada during the mid-1900s, including Washington, USA, as a result of widespread over-trapping, incidental mortality associated with wolf (*Canis lupus*) and cougar (*Puma concolor*) control campaigns, and loss or fragmentation of habitats (Lewis and Zielinski 1996, Lewis et al. 2012). At least 20 known successful translocations have facilitated the expansion of the fisher's range in North America from its most contracted extent in the mid-1900s (43% of the historical range) to the present (68% of the historical range; Lewis et al. 2012). Despite this range expansion, fishers remain endangered in Washington. The West Coast Distinct Population Segment (DPS) of fishers, which ranges from British Columbia, Canada, south through the Cascade, Klamath, and Sierra Nevada Ranges in Washington, Oregon, and California, USA, remains the focus of ongoing debate and litigation over whether the DPS warrants federal protection under the Endangered Species Act in all or part of its range (U.S. Fish and Wildlife Service 2019).

From 2008 to 2010, the Washington Department of Fish and Wildlife and the National Park Service translocated 90 fishers from British Columbia to Washington's Olympic Peninsula to enhance the species' population in Washington and throughout the West Coast DPS. There were no previous studies of the ecological relationships and habitat associations of fishers in Washington prior to their extirpation (Lewis and Hayes 2004). Consequently, the most suitable reintroduction areas were deduced from studies of fisher resource selection patterns conducted primarily in northern Idaho, USA (Jones and Garton 1994), interior British Columbia (Weir 1995, Weir and Harestad 2003), and California (Buck 1982, Zielinski et al. 2004*a*). Collectively, these and more recent studies indicated that fishers typically selected home ranges encompassing a variety of forest communities and stand structural characteristics, but generally home ranges contained a large proportion of mid-to-late-seral forests (Lofroth et al. 2010, Raley et al. 2012). Mature forests provide fishers with critically important denning structures in tree cavities, security and escape cover from predators, a diversity of available prey in environments where fishers are effective predators, suitable microsites for thermoregulation, and dense forest canopies that intercept snow and reduce energetic costs of winter travel in areas and periods of high snowfall (Lofroth et al. 2010, Raley et al. 2012). Based on these considerations, the most suitable reintroduction areas for fishers in Washington were defined as areas below approximately 1,200 m in elevation where forested stands containing dense overstory canopies (>70 crown closure) and large trees (>50 cm in quadratic mean diameter [QMD]) dominated the landscape, and where such stands were suitably connected by areas of medium-sized trees (25–50 cm QMD; Lewis and Hayes 2004). By this definition, the Olympic Peninsula contained the largest expanse of fisher habitat in Washington owing largely to the extensive wilderness areas contained within Olympic National Park and Olympic National Forest.

Reintroduction of fishers to the Olympic Peninsula provided opportunities to evaluate assumptions of fisher habitat suitability modeling and to build an understanding of fisher habitat associations in coniferous forest ecosystems of the coastal Pacific Northwest. Our goal was to determine if fishers were successfully reestablished on the Peninsula and to assess population distribution patterns 5–8 years after the reintroduction process began. Our first objective was to determine environmental correlates of fisher occupancy using noninvasive camera surveys. We predicted that fishers would occupy primarily dense coniferous forest canopies (>70% canopy closure) comprised of mid-sized (25–50 cm QMD) to large (>50 cm QMD) trees, the foundational assumptions of the habitat suitability model (Lewis and Hayes 2004). Further, we predicted that occupancy would be greatest in landscapes containing a high diversity of stand structural characteristics, including areas near wilderness boundaries because proximity to this land-management edge likely enhanced landscape and resource diversity. Our second objective was to determine whether the population had expanded or shifted in distribution since the initial reintroductions. Because multiple generations may be required for reintroduced populations to express optimum resource selection patterns (Lewis et al. 2016, Parsons et al. 2019), we predicted that patterns of occupancy would differ among years of this study and from locations where founding fishers initially established home ranges (Lewis et al. 2016). To assess spatial shifts in distribution, we examined annual occupancy patterns in relation to elevation and the precipitation gradient that increases from the dry northeast

to the wet southwestern quadrants of the Peninsula. Our third objective was to compare landscape composition among federal wilderness areas, other federal lands that did not contain wilderness, and other lands (i.e., state, private, or tribal lands) to better understand how fisher distribution relates to historical land-use patterns. We predicted that federally protected wilderness areas would contain the greatest proportion of late-seral forest characteristics and use by fishers. Our last objective was to determine whether the founding population of translocated fishers had successfully reproduced based on genetic samples collected at camera stations. We considered evidence of 2 generations of fishers produced following reintroduction as indication of successful reproduction.

STUDY AREA

We surveyed fisher presence from 2013–2016 throughout the 9,324-km^2 Olympic Peninsula in northwestern Washington at elevations ranging from sea level to about 1,435 m, which corresponded approximately with timberline and the upper elevation used by previously radio-tracked translocated fishers (Lewis et al. 2016). The primary study area encompassed lands north of the southern United States Forest Service (USFS) boundary, excluding the small peninsula extending east from the eastern USFS boundary (Fig. 1). Inferences regarding occupancy were limited to the primary study area, although we conducted a limited number of opportunistic surveys to the south and east of the primary area to detect population expansion.

Climate was maritime, characterized by relatively dry, warm summers and wet, cool winters. Precipitation ranged from 200–500 cm annually over most of the western and southern Peninsula, where moist Pacific storms intercepted the Olympic Mountains, to approximately 40 cm in the northeastern corner of the Peninsula in the mountain's rain shadow (Gavin and Brubaker 2015). Most precipitation occurred from October through March, falling primarily as rain at elevations <300 m, and as snow at elevations above approximately 900 m.

Olympic National Park and Olympic National Forest encompass the central mountainous core of the Olympic Peninsula (Fig. 1). Additionally, a separate narrow strip (<10 km wide) of Olympic National Park extends approximately 70 km along the Pacific coast. Ninety-five percent of

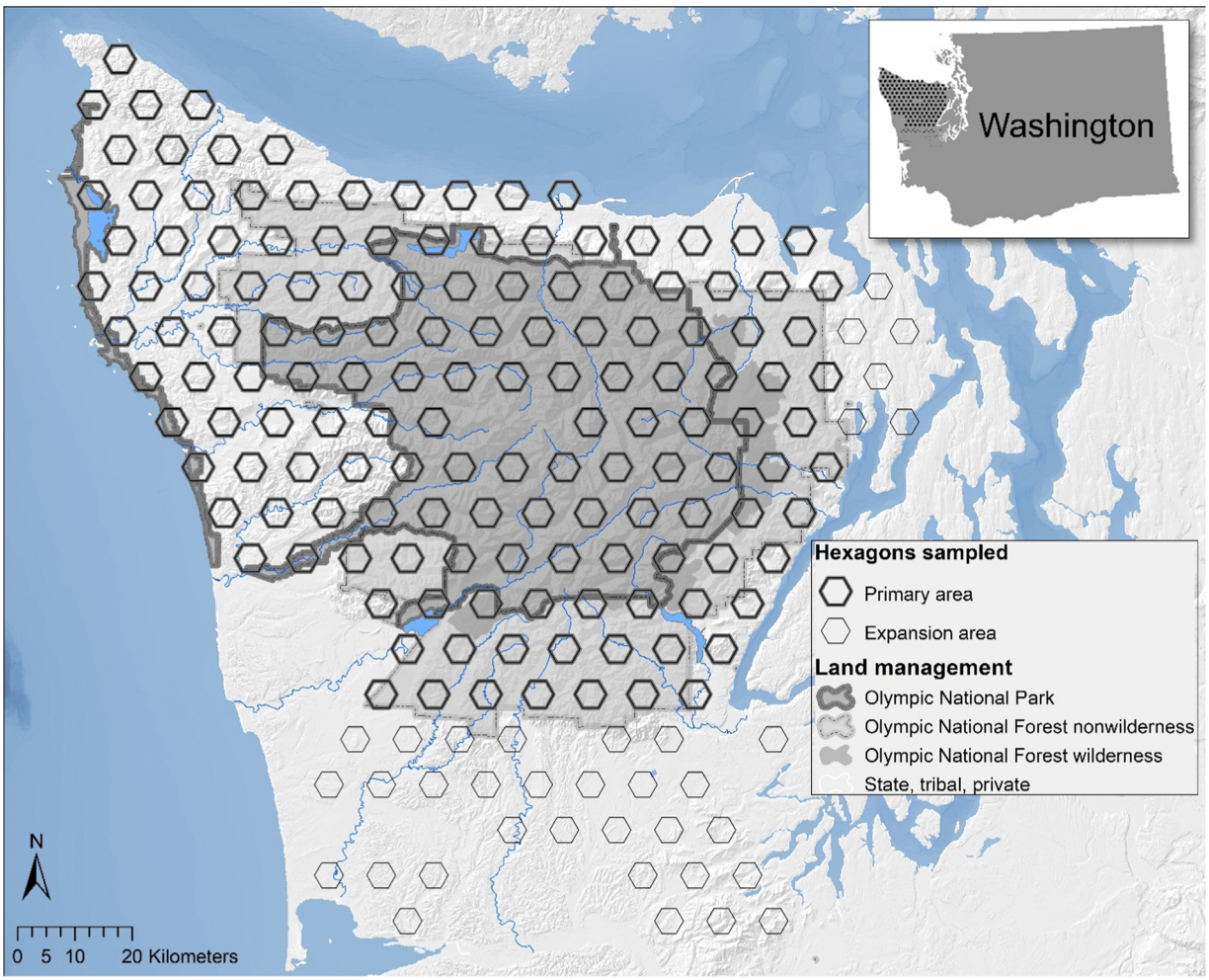

Figure 1. Location of study area and sampling hexes in the primary study area (used for occupancy analysis) and expansion areas (used to detect population expansion south and east of Olympic National Forest boundaries) relative to land-management designations on the Olympic Peninsula in northwestern Washington, USA, 2013–2016.

Olympic National Park and 14% of Olympic National Forest are congressionally designated as wilderness areas managed to protect and preserve ancient forest ecosystems and natural processes in the coastal Pacific Northwest region. Although most wilderness areas in mountain ecosystems encompass primarily high elevations, Olympic National Park encompassed forested wilderness ranging from sea level to timberline (Fig. 1), thus providing a unique opportunity to study fisher associations with wilderness characteristics independent of confounding elevation effects.

Outside of designated wilderness areas, 65% of Olympic National Forest was managed as Late-Successional Reserve under the Northwest Forest Plan (Moeur et al. 2005). These reserves, many of which were previously logged, have been managed since 1994 with the objective of restoring functional late-successional forest ecosystems. The remaining 21% of land area in the Olympic National Forest was designated for multiple uses including experimental forest management.

Nonfederal lands in the study area were managed for multiple uses by the state, private landowners, and several Native American tribes, with a focus on integrated timber production and fish and wildlife habitat management. The majority of state, private, and tribal lands have been clearcut logged since the 1940s and, today, they reflect a mosaic of regenerating, and variously thinned and harvested second-growth forests. Timber rotations averaged approximately 40–60 years between successive cuttings on productive sites and average tree sizes in regenerating stands were often <50 cm in diameter at breast height (DBH). The marked contrast in vegetation conditions between federally protected wilderness areas and state, private, and tribally owned forest lands presented a broad spectrum of vegetation and landscape characteristics available as potential habitat for fishers.

Climax forest associations reflected the joint expression of elevation, temperature, and precipitation (Henderson et al. 1989). Temperate rain forest communities, dominated by Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) prevailed at low elevations on the western coast and on glacial and alluvial terraces of the west-flowing rivers (Franklin and Dyrness 1988). Temperate rainforests of the Olympic Peninsula are renowned for the large size and productivity of overstory trees, complex multilayered canopy structure, and an abundance of standing dead snags and downed logs (Franklin and Dyrness 1988, Van Pelt et al. 2006). Western hemlock and Douglas-fir (*Pseudotsuga menziessii*) dominated low- to mid-elevation forests (below ~1,000 m), giving rise to greater prevalence of Pacific silver fir (*Abies amabilis*) at mid-elevations (~900–1,200 m), and mountain hemlock (*T. mertensiana*) and subalpine fir (*A. lasiocarpa*) at higher elevations (>1,200 m; Henderson et al. 1989). In addition to reintroduced fishers, the study area was inhabited by a carnivore community including black bears (*Ursus americanus*), mountain lions, bobcats (*Lynx rufus*), coyotes (*Canis latrans*), river otters (*Lontra canadensis*), Pacific martens (*Martes caurina*), western spotted skunks (*Spilogale gracilis*), long-tailed weasels (*Mustela frenata*), and ermine (*Mustela erminea*).

METHODS

Field Sampling and Detections

We monitored fisher detections from 2013–2016 at noninvasive sampling stations distributed across a Peninsula-wide grid of 24-km^2 hexagonal cells (i.e., hexes; Fig. 1). We sampled every other hex to enhance independence among sampling units. Of 157 hexes in the resulting sample, we deleted 14 because of access issues or because the hex center exceeded 1,425 m in elevation.

We attempted to survey each hex twice with a 2-year interval between surveys. To maintain spatial balance in sampling effort across the Peninsula, we selected annual panels of sample hexes using a generalized random tessellation stratified sampling scheme (Stevens and Olsen 2004). For logistical efficiencies in wilderness areas, we sampled hexes in clusters of 2–4 hexes that were relatively close to one another. This approach minimized travel costs while maintaining randomness and spatial balance in the sample.

We surveyed from late May to early November each year. We established 3 sampling stations in each hex, each preferably >1 km apart (minimally 800 m apart) within forested stands containing trees >20 cm DBH within safely accessible portions of each hex (slopes <38 degrees). Each station contained a motion-sensing camera (Bushnell Trophy Cam HD, Overland Park, KS, USA) and a hair-snaring device to collect DNA samples. We baited survey stations with raw chicken affixed to a tree 3–5 m from the camera tree. The hair-snaring device was a triangular plastic box (i.e., cubby) placed at the base of the bait tree (Schwartz et al. 2006, Fig. S1, available online in Supporting Information). We baited cubbies with a chicken drumstick and attached 6 gun brushes to the inside walls, 3 near each entrance. Both the tree-mounted bait and cubby devices were within the camera's field of view for detecting fishers. We applied a long-distance olfactory lure to the bait tree (Caven's Gusto, Minnesota Trapline Products, Pennock MN, USA) and protected the olfactory lure from rain with a plastic rain shield. We visited each station 3 times, with 14-day intervals between visits, resulting in 6 weeks of sampling in each hex. During each visit, field crews collected photographic images from the cameras and hair-snaring brushes that contained animal hairs. Crew members stored hair-bearing brushes in individual tubes containing silica desiccant if multiple fishers were detected on camera, or combined them in a larger tube if only one fisher was detected. Our surveys did not harm fishers or materially alter their behavior; hence, the National Park Service judged our study exempt from animal care and use review when the project was initiated as was generally accepted for observational studies at that time (Sikes et al. 2011).

Laboratory Analyses

We extracted genomic DNA from hair samples using the QIAGEN Dneasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) according to manufacturer's instructions for

tissue as modified for hair samples (Mills et al. 2000). We identified species by amplifying and sequencing about 360 base pairs (bp) using 16 S rRNA universal primers (Hoelzel and Green 1992). Reaction volumes of 30 μl contained 50–100 ng DNA, 1× reaction buffer (Life Technologies, Grand Island, NY, USA), 2.5 mM MgCl2, 200 μM each dNTP, 1 μM each primer, and 1 U Amplitaq Gold polymerase (Life Technologies). The PCR program was 94°C for 5 minutes; 34 cycles of 94°C for 1 minute, 55°C for 1 minute, and 72°C for 1 minute 30 seconds; and 72°C for 5 minutes. We determined the quality and quantity of template DNA by 1.6% agarose gel electrophoresis. We purified PCR products using ExoSap-IT (Thermo Fisher, Waltham, MA, USA) according to manufacturer's instructions. Eurofins Genomics (Louisville, KY, USA) sequenced reactions using standard Sanger sequencing protocols. We viewed and aligned DNA sequence data with Sequencher (Gene Codes Corp. Ann Arbor, MI, USA) and compared sequences to reference sequences from known species.

We genotyped fishers from hair samples based on 17 microsatellite loci used in previous mustelid studies: MpP0059, Mp0144, Mp0175, Mp0197, Mp0200, Mp0247 (Jordan et al. 2007), Ma1, Gg4 (Davis and Strobeck 1998), Mer022, Mvis020, Mvis072 (Fleming et al. 1999), Ggu101, Ggu216, Ggu234 (Duffy et al. 1998), Lut604, Lut733 (Dallas and Piertney 1998), and Pv9 (Allen et al. 1995). The reaction volume (10 μl) contained 1.0 μL DNA, 1× reaction buffer (Applied Biosystems, Foster City, CA, USA), 2.0 mM MgCl2, 200 μM of each dNTP, 1 μM reverse primer, 1 μM dye-labeled forward primer, 1.5 mg/ml BSA, and 1 U Taq polymerase (Applied Biosystems). The PCR profile was 94°C for 5 minutes then 45 cycles of 94°C for 1 minute, 55°C for 1 minute, and 72°C for 30 seconds. We amplified DNA from hair samples using the multi-tube approach (Eggert et al. 2003, Schwartz et al. 2007). We visualized the resulting products on a LI-COR DNA analyzer (LI-COR Biotechnology, Lincoln, NE, USA). We error checked using program Dropout (McKelvey and Schwartz 2005), GenAlEx (Peakall and Smouse 2012), and Micro-checker (Van Oosterhout et al. 2004). We determined sex of successfully genotyped fishers using the Y-linked marker DBY-3 (Hedmark et al. 2004). We determined recaptures and new individuals using Dropout (McKelvey and Schwartz 2005). We evaluated new individuals (descendants) for paternal and maternal relationships using exclusion conducted by hand and subsequently using the program CERVUS 3.0 using the strict (95%) confidence criteria to assess those relationships (https://cervus.software.informer.com/3.0/, accessed 14 May 2019).

Modeling Fisher Detection and Occupancy

We quantified precipitation, elevation, relative cover of land designations and forest structural classes, diversity of vegetation structural classes, and distance to federal wilderness boundary as covariates hypothesized to affect fisher occupancy. We computed mean precipitation at the primary sampling units as the mean of the 30-year (1981–2010) precipitation normals assessed at each of the 3 camera sampling stations (data from PRISM Climate Group, http://prism.oregonstate.edu/normals/, accessed 6 Sep 2018). We determined elevations at sampling stations using the United States Geological Survey National Elevation Dataset (https://catalog.data.gov/dataset/usgs-national-elevation-dataset-ned, accessed 20 Sep 2019).

We assessed the composition and diversity of selected land cover classes within 1,262-m-radius buffers inscribed around each sampling station. Our goal was to select a biologically meaningful buffer size that represented the areal extent likely to be traversed by a fisher within a 6-week sampling interval. The combined buffer area around 3 sampling stations within a hex (10–15 km^2) corresponded roughly with the average size of 50% utilization distributions of female core areas in the study area (Lewis et al. 2016).

We identified land-management designations within buffers as wilderness (combining all of Olympic National Park with USFS designated wilderness), federal lands not managed as wilderness, and other (state, private, and tribal lands combined). The 3 designations reflected the gradient of resource protection that existed on the Peninsula. Because the proportions of land areas summed to 1 and, consequently, were correlated, we examined associations only between occupancy and percent wilderness. Further, we measured the mean distance of sampling stations within each hex from the nearest boundary separating wilderness from other land designations. We included this measurement based on our previous observation that many translocated fishers established home ranges in proximity to both mature forests and managed forest landscapes (Lewis et al. 2016). The metric is easily measured and has the advantage of being independent of measurement scale while providing information on the spatial extent of potential edge effects.

We assessed proportional coverage within these buffers of the forest structural classes used to identify potential fisher reintroduction areas in Washington (Lewis and Hayes 2004). We examined the influence of percent of station buffers composed of medium-sized and large trees (>40% canopy cover and trees >25 cm QMD), and dense forest overstories (>70% canopy closure) on fisher occupancy patterns. We also examined the influence of forest structural class diversity within the station buffers (Simpson 1949), based on the proportions of pixels in open forest (<40% cover), and within forested stands (>40% cover) comprised of primarily small (<25 cm QMD), medium (25–50 cm QMD), and large (>50 cm QMD) trees. We characterized forest structural characteristics based on 2012 data from the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) project of the USFS and Oregon State University (https://lemma.forestry.oregonstate.edu/data, accessed 8 May 2019).

We used single-season occupancy models to estimate the probability of occurrence of fishers within sample hexes while accounting for imperfect detection and environmental covariate effects (MacKenzie et al. 2002). We considered each hex-by-year combination to be a distinct site, and fit single-season occupancy models with year effects, allowing us to focus on temporal and spatial patterns of fisher occupancy across the Peninsula. These models assume that occupancy status of each site is independent and conditional

on the environmental covariates present in the model. Because fisher detections were limited, we were not able to examine colonization and extinction dynamics over time.

We used fisher detections from cameras and DNA identifications in $i = 1, \ldots, 263$ year and hex combinations (i.e., sites) during $j = 1, 2, 3$ visits. We aggregated detections from paired camera and DNA data within sampling stations for this analysis because both the camera and DNA boxes were collocated. The camera was the principal detection device, although on rare occasions (3 of 68 detections) we identified fishers from DNA alone when cameras failed. We coded a detection of a fisher at any 1 of the 3 stations in a hex on a given visit as present for that site-visit combination.

We modeled detections of fishers at site i in visit j as $y_{ij} \sim Bernoulli(z_i \times p_{ij})$. Here, z_i was the latent (true) occupancy state, which indicated if site i was occupied ($z_i = 1$) or not ($z_i = 0$), and p_{ij} was the site and visit-specific detection probability, $Pr(y_{ij} = 1 \mid z_i = 1)$. We then modeled true occurrence as $z_i \sim Bernoulli(\Psi_i)$, where Ψ_i was the site-specific probability of occurrence, $Pr(z_i = 1)$. We used logit-linear models to examine the effects of covariates on detection and occupancy probabilities, where $logit(p_{ij}) = x_{ij}'\boldsymbol{\alpha}$ and $logit(\Psi_{ij}) = x_i'\boldsymbol{\beta}$. Here, x_{ij}' represented a vector of covariates that varied by site and/or survey, and $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$ were regression coefficients. We examined the following covariate effects on fisher detection probabilities: survey year, ordinal date of the station visit (including both linear and quadratic terms, and an interaction with year), proportion of the sample interval that bait was present, and percent wilderness. We included linear and quadratic terms for date in all of our models to account for nonlinear seasonal effects. We averaged the bait variable across the 3 stations in each hex. Bait was occasionally removed from a station by black bears, ravens (*Corvus corax*), or other wildlife, so this measure indicated station effectiveness. In the event that fishers removed available bait when they visited a site between camera checks, we recorded bait as available for 100% of the survey interval. We included percent wilderness in our detection probability models to test whether detection probability differed between protected versus more intensively managed forest landscapes, which could potentially reflect effects of differences in food availability or other habitat qualities. We then looked at additive effects of all other variables, singly and in combination, for 32 detection models (Table S1, available online in Supporting Information).

We modeled occupancy probability as functions of the geographic, landscape, and habitat variables described above and survey year, which we included in all models. We examined pairwise correlations among all variables to guard against including highly correlated variables within a model ($r > 0.5$), and examined habitat variables singly in all models. We examined additive and interactive effects between year and precipitation, elevation, distance to wilderness edge, percent wilderness, percent medium and large trees, percent dense canopy cover, and structural class diversity. Further, we examined models that included both year and distance to wilderness edge, and then included additive and interactive effects (with year or distance to wilderness edge) of each of the remaining variables. In total, we estimated 33 models for fisher occupancy (Table S2, available online in Supporting Information).

We first evaluated models for detection probability and held the global occupancy model constant. The global model for occupancy included effects of year, percent wilderness, distance to wilderness edge, percent medium and large trees, 30-year mean precipitation, and elevation. We did not include percent canopy cover or structural class diversity in the global model because they were correlated with percent medium and large trees ($r > 0.50$). We used model selection to choose the best model for detection probability, and used this detection model for subsequent modeling of occupancy. We used a maximum likelihood approach to model fisher detection and occupancy, using the extension package unmarked within the statistical software R (https://cran.r-project.org/web/packages/unmarked/index.html, accessed 10 May 2019). We assessed global model fit using parametric bootstrapping and calculated the overdispersion parameter, $\hat{c}$, to use in model selection and adjustment of parameter standard errors (MacKenzie and Bailey 2004). We calculated quasi-Akaike's Information Criterion (QAIC) using the R package AICcmodavg (https://cran.r-project.org/web/packages/AICcmodavg/index.html, accessed 10 May 2019), and used QAIC for model selection given $\hat{c} > 1$. To judge the relative support for individual covariate effects, we computed evidence ratios (ER) as the ratio QAIC weights for the most supported model containing a specific effect to the nested model without that effect (Burnham and Anderson 2002).

Landscape Composition of Land-Management Designations

To enhance understanding of how past forest management practices have shaped the available landscape compositions, we compared landscape composition and diversity of forest structural classes among federal wilderness areas, federal lands outside of wilderness, other land-management designations, and to sites where we detected fishers. To ensure representative characterization of landscape composition within each land designation, we included only buffers comprised of ≥95% in 1 land-management designation for this analysis. We examined differences in landscape composition among land-management designations and fisher detection sites using Kruskal-Wallis nonparametric analysis of variance (SAS Institute 2013). For compositional attributes that varied significantly among these classes overall, we further examined pair-wise differences between each of the 3 land-management classes and fisher detection sites. We used the Dwass, Steel, Critchlow-Fligner multiple comparison analysis for all pairwise comparisons, which is based on the 2-sample Wilcoxon test (Critchlow and Fligner 1991).

RESULTS

Fisher Sampling and Detections

We surveyed 788 sampling stations within the primary study area for the presence of fishers distributed among 263 year-hex combinations (sites; Table 1). We sampled

Table 1. Sampling effort, fisher detections, and generational assignments of fishers detected in the primary sampling area on the Olympic Peninsula, Washington, USA, 2013–2016.

	Sampling effort		Fisher detections				Generation[a]		
Year	Number hexes sampled	Number stations sampled	Number station-visits with detections	Number stations with detections	Number hexes with detections	Proportion hexes with detections	0	1	≥2
2013	52	156	20	13	9	0.173	4	5	0
2014	68	204	12	6	5	0.074	2	2	0
2015	75	225	15	11	7	0.093	1	2	1
2016	68	203	21	12	9	0.132	3	2	4
Totals	263	788	68	42	30	0.114	10	11	5

[a] Number of individually identified fishers each year based on DNA analysis. Some animals were detected in multiple years; other detected fishers could not be identified. Generations include generation 0 (the initial population of individuals translocated to Olympic National Park), generation 1 (offspring of the founding generation), and generation ≥2 (offspring of generation 1 and 2 parents).

143 different hexes at 3 2-week intervals, including 115 hexes that we surveyed during 2 years on a 2-year interval (i.e., 2013 and 2015, or 2014 and 2016), 27 that we surveyed during only 1 year (2015), and 2 that we surveyed during each of 3 years. Sampling stations were distributed approximately evenly among lands designated as wilderness (34%), federal lands outside of wilderness (31%), and other lands (i.e., state, private, and tribal; 35%).

We detected fishers at 42 different stations and 30 sample hexes in the primary study area (Table 1, Fig. 2). Distribution of stations where we detected fishers was indistinguishable from distribution of sampling effort among land-management categories (wilderness: 36%, federal outside of wilderness: 36%, and other lands: 29%; $\chi^2 = 0.855$, $P = 0.65$). In addition, we surveyed 12, 12, and 15 hexes in the expansion survey area each year from 2014–2016, respectively; we detected no fishers in the expansion area in 2014 and 2015 but detected 2 fishers in the expansion area in 2016 (Fig. 2).

We identified 21 individual fishers from DNA in the primary study area, including 7 of the translocated founding fishers, 9 fishers with genotypes consistent with first generation and 5 fishers with genotypes consistent with second or subsequent generations (Table 1; Table S3, available online in Supporting Information). Measures of genetic diversity for these data indicated the loci used had adequate power to distinguish individuals; we estimated the probability of identity (PI; Paetkau and Strobeck 1994) and the probability that siblings are identical (PIsib; Evett and Weir 1998) for this data as 8.81E-13 and 8.25E-06, respectively, based on measures of observed heterozygosity (0.59), expected heterozygosity (0.61), and average number of alleles per locus (5.1). Mean polymorphic information content (PIC) was 0.55 and the probability of nonexclusion was 4.7E-07. Of 21 fishers identified, only 1 male was detected in 2 adjacent hexagons, indicating general adherence to our assumption of spatial independence.

Fisher Detection Probability and Occupancy

The goodness-of-fit test for the global occupancy model indicated modest overdispersion ($\hat{c} = 1.37$). Consequently, we used this value to calculate QAIC scores for model selection, and adjusted confidence intervals accordingly for subsequent model predictions.

Model selection results for detection probability suggested considerable model uncertainty (Table 2), with 7 models <2 QAIC units from the top model. The top QAIC-ranked model included percent wilderness and year × date^2 interaction, and the linear and quadratic effects of date included in all models. Based on model-averaged coefficient estimates, detection probability tended to be higher in wilderness than non-wilderness areas ($\beta = 0.66 \pm 0.34$ [SE]; Table S1). The relationship between detection probability and date differed among years: detection was greater in the middle of the sampling season (summer) than at the start (spring) or end (fall) of the season in 2013 and 2015, but this pattern was less evident in 2014 and 2016 (Fig. S2, available online in Supporting Information). The per-survey detection probability averaged 0.59 ± 0.06 across sampling dates, indicating that the cumulative detection probability summed over 3 sample visits averaged about 0.93.

Model selection results for occupancy based on the top detection model indicated that distance from the wilderness boundary was the best predictor of occupancy, along with year and 30-year mean annual precipitation (Table 3). The distance variable was present in all models up to 99% cumulative QAIC weight. Moreover, the ER for the distance variable was 254, indicating there was over 250 times greater model support for the top model containing distance than the comparable model without distance. The model-averaged coefficient for distance to wilderness boundary indicated that occupancy decreased as distance from the wilderness boundary increased ($\beta = -1.37 \pm 0.40$; Fig. 3; Table S2). This model also indicated relatively high support for the combined effect of precipitation and precipitation × year interaction (ER = 10.6). Estimated occupancy increased with increases in mean 30-year precipitation values particularly in 2014 and 2016 compared to 2013 and to a lesser extent in 2015 (Fig. 3). The top model, which indicated fisher occupancy varied among years on the precipitation gradient, garnered over 125 times more model weight that a comparable model that considered elevation effects as an alternate explanation for geographic shifts in occupancy among years (Table S2).

There was only weak to negligible model support for the primary habitat variables that were used during planning to delineate fisher habitat on the Olympic Peninsula (Lewis and Hayes 2004). The second-ranked model in the set

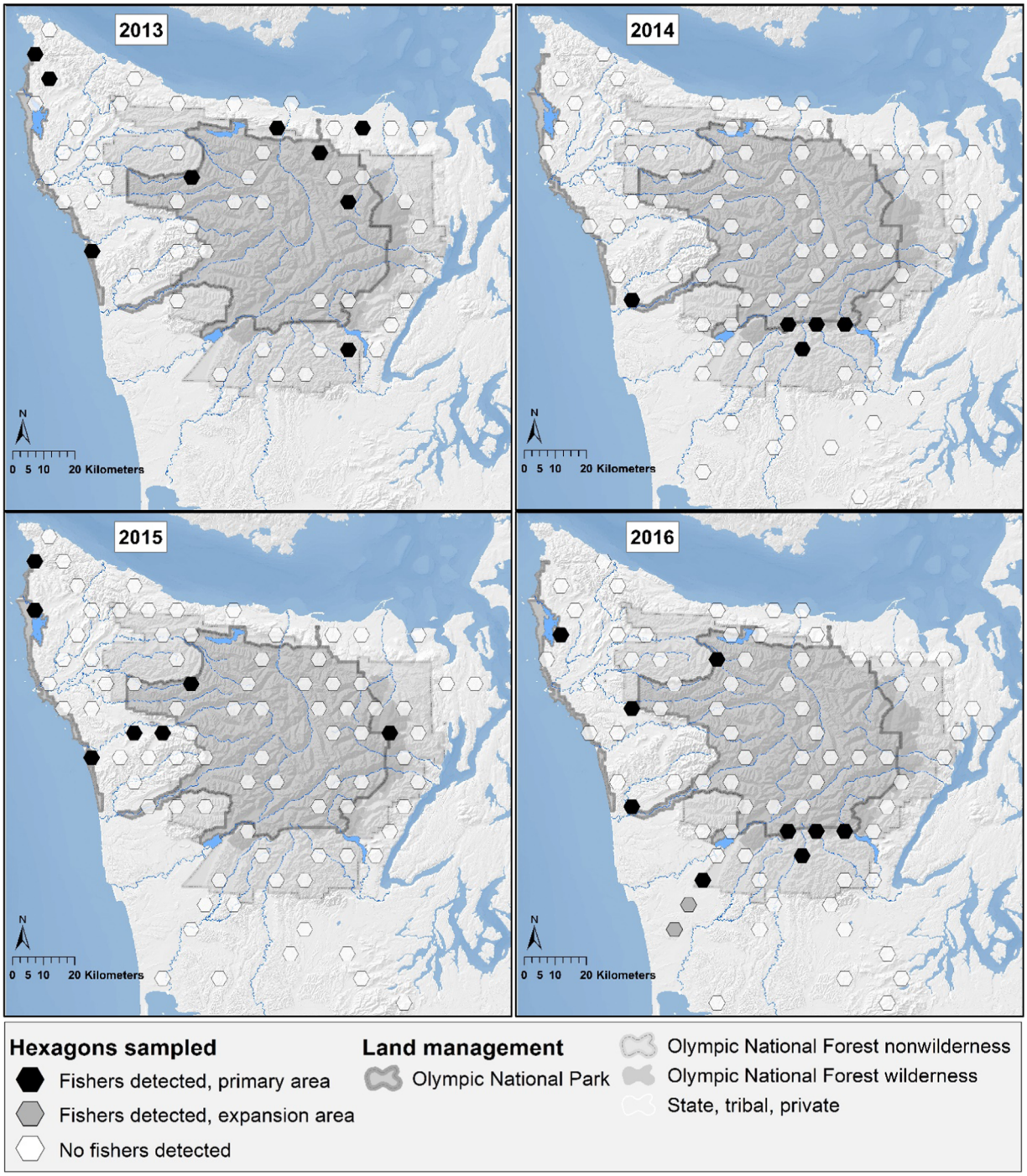

Figure 2. Sampled hexes and locations of fisher detections by survey year, Olympic Peninsula, Washington, USA, 2013–2016.

(Table 3) included a weak negative effect of percent forest wilderness on occupancy (model-averaged $\beta = -0.10 \pm 0.12$), although there was considerably less support for this effect (ER = 3.0) compared to variables in the top-ranked model (ER = 10.6–254). There was negligible model support for influences of percent medium and large trees (ER = 1.4), structural class diversity (ER = 0.8), and dense canopy cover (ER = 0.4) on fisher occupancy.

Model-averaged mean occupancy varied among years. Mean occupancy across the Peninsula was 0.24 (95% CI = 0.19–0.28) in 2013, 0.08 (0.05–0.10) in 2014, 0.12 (0.10–0.14) in 2015, and 0.14 (0.11–0.17) in 2016. Model-averaged occupancy was highest in 2013, lowest in 2014, and increased from 2014–2016. Occupancy patterns shifted from 2013 and 2014–2016 when fishers tended to use portions of the Peninsula (western and southern) where precipitation was greatest (Figs. 2 and 3).

Landscape Composition of Land-Management Designations

Landscape composition surrounding the fisher sampling stations varied among the land-management designations

Table 2. Model selection results for covariates affecting detection probability (p_{ij}) of fishers on the Olympic Peninsula, Washington, USA, 2013–2016, using a fixed global model for occupancy: Ψ_i (% wilderness + % medium and large trees + precipitation + distance + elevation + year). Models for detection probability all included ordinal date (date; both linear and quadratic effects), and then considered effects of year (yr), interaction between year and date, proportion of the sampling interval that bait was present (bait), and percent wilderness in the study site. The number of model parameters (K) and quasi-Akaike's Information Criterion (QAIC) are adjusted for overdispersion ($\hat{c} = 1.37$). Models comprising the 90% confidence set are presented.

Model	K	QAIC	ΔQAIC	QAIC weight	Cumulative model weight	Quasi log-likelihood
Date + date^2 + % wilderness + (yr × date^2)	17	215.20	0.00	0.15	0.15	−90.60
Date + date^2 + bait	14	215.72	0.52	0.12	0.27	−93.86
Date + date^2 + % wilderness	14	216.39	1.19	0.08	0.35	−94.19
Date + date^2	13	216.42	1.21	0.08	0.43	−95.21
Date + date^2 + bait + % wilderness + (yr × date^2)	18	216.43	1.23	0.08	0.52	−90.22
Date + date^2 + yr + % wilderness + (yr × date^2)	20	216.47	1.27	0.08	0.60	−88.23
Date + date^2 + bait + % wilderness	15	216.49	1.29	0.08	0.68	−93.25
Date + date^2 + yr + % wilderness	17	217.34	2.14	0.05	0.73	−91.67
Date + date^2 + bait + yr + % wilderness + (yr × date^2)	21	217.48	2.28	0.05	0.78	−87.74
Date + date^2 + bait + % wilderness + yr	18	218.15	2.95	0.03	0.81	−91.07
Date + date^2 + (yr × date)	16	218.33	3.13	0.03	0.84	−93.17
Date + date^2 + bait + (yr × date)	17	219.32	4.12	0.02	0.86	−92.66
Date + date^2 + bait + (yr × date^2)	17	219.36	4.16	0.02	0.88	−92.68
Date + date^2 + bait + yr + (yr × date^2)	20	219.88	4.68	0.01	0.90	−89.94

and where fishers were detected (Fig. 4). The proportional coverage of medium-sized and large trees was greatest in wilderness, less in federal lands not managed as wilderness, and least in other forest lands (Fig. 4A). The proportional area dominated by medium and large trees was comparable between buffers where fishers were detected and buffers sampled in federal lands not managed as wilderness. Proportional area within the dense canopy class was greater in both federal wilderness and federal lands not managed as wilderness than in other forest lands, but proportional areas of dense canopies did not differ between buffers where fishers were detected and any of the 3 land-management categories (Fig. 4B). Structural class diversity was least in wilderness, and similar among federal lands outside of wilderness, other lands, and fisher-detection sites (Fig. 4C).

DISCUSSION

The Olympic Peninsula was chosen for the first fisher reintroduction in Washington because it had the greatest extent of what was presumed to be optimal fisher habitat: large and intact expanses of low-to-mid-elevation mature coniferous forest (Lewis and Hayes 2004). Contrary to expectations, however, fisher occupancy was not associated with expansive forested wilderness that comprised the core of the reintroduction area but rather with the boundary separating wilderness from more intensively managed landscapes. Proximity of most fisher detections to the edge between wilderness and managed lands implied that neither land-use designation alone provided an optimum arrangement of life-history requisites at the scale measured, but both were important to fishers at a larger scale. We speculate that the boundary region between wilderness and more intensively managed forest lands provided fishers with the most suitable prey in proximity to late-successional forests that provided optimal resting, denning, or security values.

Preliminary analyses of fisher gastrointestinal tracts and scats collected from the Olympic Peninsula indicated that fishers preyed principally on snowshoe hares (*Lepus americanus*) followed by progressively lesser amounts of mountain beavers (*Aplodontia rufa*), northern flying squirrels (*Glaucomys sabrinus*), and an assortment of rodent and shrew species (P. J. Happe, Olympic National Park, unpublished data). We did not measure abundance or distribution of mammalian prey species, but snowshoe hares in this region are most abundant in forests dominated by dense shrubs and small and medium-sized trees (e.g., <28 cm DBH; Lewis et al. 2011, Sullivan et al. 2012). These forest characteristics were most prevalent in regenerating forests that dominated state, private, and tribal lands and some USFS areas outside of wilderness (Fig. 4A). Similarly, mountain beavers thrive among the dense brush and forest regeneration that establishes in early-seral forests following clear-cut logging practices in the coastal Pacific Northwest (Hacker and Coblentz 1993, Arjo et al. 2007), often to the point of

Table 3. Model selection results for covariates influencing occupancy of fishers on the Olympic Peninsula, Washington, USA, 2013–2016, with detection probability (p_{ii}) modeled as p_{ij} (date + date^2 + % wilderness + [year × date^2]). Occupancy covariates examined include distance to wilderness edge (distance), 30-year precipitation average (precipitation), elevation, percent wilderness, percent medium and large trees, percent closed canopy, and structural class diversity. Year (yr) was included in all occupancy models. The number of model parameters (K) and quasi-Akaike's Information Criterion (QAIC) are adjusted for overdispersion ($\hat{c} = 1.37$). Models comprising the 90% confidence set are presented.

Model	K	QAIC	ΔQAIC	QAIC weight	Cumulativemodel weight	Quasi log-likelihood
Yr + distance + precipitation + (yr × precipitation)	17	213.53	0.00	0.51	0.51	−89.77
Yr + distance + % wilderness	14	216.04	2.50	0.15	0.66	−94.02
Yr + distance + precipitation	14	216.63	3.10	0.11	0.76	−94.31
Yr + distance + % medium and large trees	14	217.66	4.13	0.06	0.83	−94.83
Yr + distance	13	218.24	4.71	0.05	0.88	−96.12
Yr + distance + elevation	14	218.69	5.16	0.04	0.91	−95.35

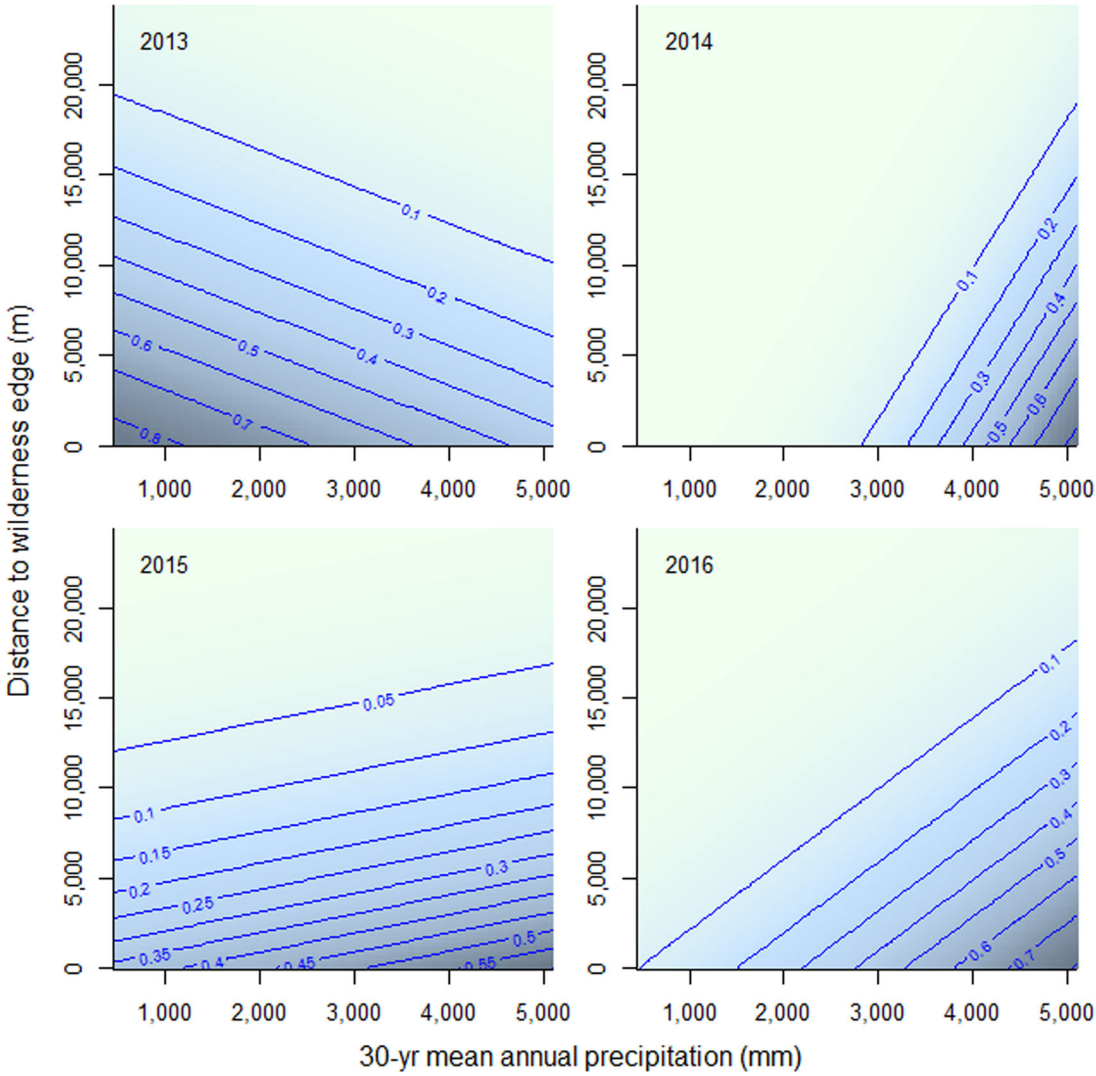

Figure 3. Fisher occupancy estimated from the top model as a function of 30-year mean annual precipitation and distance to wilderness edge, estimated for each year, Olympic Peninsula, Washington, USA, 2013–2016. Blue lines indicate mean predicted values for occupancy, where occupancy increases from light blue to dark blue.

becoming a primary pest on forest plantations (Arjo and Nolte 2006). Our field observations indicated that mountain beavers and snowshoe hares were also abundant in high-elevation subalpine parkland forests near timberline, but those sites generally existed above snowline and above the range of fishers. Other prey of fishers, notably the flying squirrel and some small-mammal species, tend to be more abundant in older stands than in young regenerating forests, particularly regenerating stands where old-forest legacies (e.g., large live and dead trees and fallen logs) have not been adequately retained (Carey 1995, 2000; Carey and Johnson 1995). We speculate based on these studies that managed forest lands outside the wilderness boundaries may have provided a greater availability of primary prey species than extensive late-successional forests within the national park and forest wilderness, but secondary prey species may be more abundant within older forests. The abundance and diversity of prey appeared to be greatest in the zone where land-use designations abutted, but additional study of prey abundance and distribution is warranted.

Living near the boundary of protected forest wilderness provided fishers with access to late-successional forest structures that are needed for resting and denning (Lofroth et al. 2010, Raley et al. 2012). Fishers select rest sites throughout the Pacific Coast region with denser overhead cover, greater volume of semi-decayed logs, and greater prevalence of large trees and snags than are available in the broader landscape (Zielinski et al. 2004*b*, Aubry et al. 2013). Within resting sites fishers use various structures, including large, deformed or deteriorating trees, snags, and logs (Lofroth et al. 2010). Moreover, cavities in large trees and snags are particularly critical resources for reproduction. Most cavities used for natal and maternal den sites are created by heartwood decay in overmature or diseased trees and made accessible to fishers through openings caused by falling branches, fire scars, wind damage, or holes made by pileated woodpeckers (*Dryocopus pileatus*; Aubry and Raley 2006, Lofroth et al. 2010, Weir et al. 2012). Although such structures are available across many land ownerships on the Olympic Peninsula as indicated by a recent study of the characteristics of pileated woodpecker

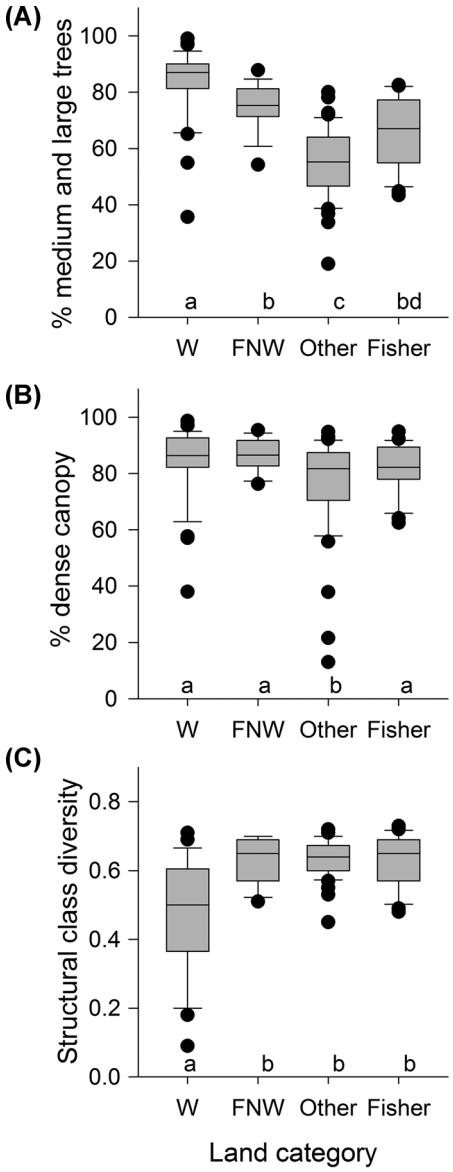

Figure 4. Percent medium and large trees (A), percent dense canopy cover (B), and structural class diversity (C) measured within 1,262-m buffers around fisher sampling stations in wilderness (W), federal lands without wilderness (FNW), state, private, or tribal lands (Other), and fisher detection sites (Fisher) on the Olympic Peninsula, Washington, USA, 2013–2016. Boxes and whisker diagrams depict the interquartile ranges (25th–75th percentiles) of each distribution as boxes, medians as horizontal lines within boxes, 10th–90th percentiles of the distribution as vertical lines, and outliers as black dots. Kruskal-Wallis chi-square scores were significant ($P < 0.01$) for A–C. Significant pairwise comparisons of medians are indicated by different lower-case letters above the *x* axes in each panel ($P \leq 0.05$).

nests (Aubry and Raley 2002), Olympic National Park and adjoining Olympic National Forest lands are renowned for their abundance of ancient trees, standing snags, and downed log structures (Franklin and Dyrness 1988, Henderson et al. 1989).

In addition, living near the boundary may also enhance security from predators. Bobcats have been identified as an important predator of fishers throughout much of their Pacific range and in Montana, USA (Roy 1991, Wengert et al. 2014, Lewis 2014). Raw camera data indicated that the bobcat was widespread throughout low elevations on the Peninsula (Happe et al. 2017). Bobcats rely heavily on hares, mountain beavers, and sciurids as prey in western Oregon and Washington (Knick et al. 1984, Witmer and deCalesta 1986, Toweill and Anthony 1988); thus, they may be drawn to similar foraging sites as fishers (Parsons et al. 2019). Predation risks on the Olympic Peninsula warrant additional study, but we hypothesize that expansive mature forests may have enhanced security values particularly for denning and resting compared to more intensively managed forest landscapes.

Our results support the general concept that fishers inhabit a variety of forest age classes and structural stages to meet their requirements for prey, thermoregulation, security, and reproduction (Lofroth et al. 2010, Raley et al. 2012). The results indicate negligible support for the effect of structural class diversity (measured within the 1,262-m buffers) on fisher occupancy, although fishers selected for stand diversity at a larger geographic scale than the buffer size used for the analysis. This is supported by our finding that occupancy probability was greatest near wilderness edges, an area that encompassed a diversity of protected and managed lands in most cases. The breadth of this landscape-scale effect may reflect the relatively large home range sizes of fishers on the Peninsula (Lewis et al. 2016), and may not be widely applicable to other regions where home range sizes are typically smaller. Our findings, however, corroborate growing evidence that the edges between managed and late-successional forests are important features of fisher habitat in densely forested coniferous ecosystems (Slauson et al. 2003, Parsons et al. 2019).

Contrary to several studies that reported forest canopy cover was a strong predictor of fisher occurrence in California (Carroll et al. 1999, Davis et al. 2007, Zielinski et al. 2010), we found negligible support for our prediction that high proportional cover of a dense forest overstory (>70% canopy closure) would be associated with fisher occupancy. Dense canopy cover forms very quickly following disturbances in mesic Pacific Northwestern forests, and does not connote presence or density of other more important structural attributes of forests such as large trees, snags, or downed logs (Sauder and Rachlow 2014). Our results support recent findings that density of forest canopy is not a sensitive predictor of fisher occurrence in areas dominated by mesic forest associations in the Pacific Northwest (Schwartz et al. 2013, Sauder and Rachlow 2014) as it is in drier regions.

Fishers were negligibly associated with the percentage of medium and large trees measured in sample-station buffers, contrary to our initial prediction and results from several other studies (Zielinski et al. 2004*a*, 2010; Davis et al. 2007; Schwartz et al. 2013; Sauder and Rachlow 2014). Differences among studies in the definitions of medium and large trees, mature forests, and mid-to-late-seral designations prevented direct comparisons to our findings. Near the northern Idaho and Montana border, fishers were positively associated with landscapes composed of >50% mature forests (25–50-m canopy height; Sauder and Rachlow 2014), or >47% large-tree stands (>38 cm DBH; Schwartz et al. 2013). In California, however, fisher home ranges were

aligned with areas containing >70% intermediate-to-large tree classes (>29 cm) or mid-to-late seral stages (Zielinski et al. 2004*a*). Although our models did not reveal a linear influence of medium-to-large tree coverage on site occupancy by fishers in western Washington, fishers selected landscapes with proportional coverage of medium and large trees similar to that reported elsewhere (interquartile range = 55–77%; Fig. 4A). We conducted our surveys in an area where spatial coverage of stands dominated by medium and large trees commonly exceeded 80–90% (Fig. 4A), indicating that landscapes overwhelmingly dominated by late-successional forests may not be optimal for fisher establishment.

The shift in fisher distribution we observed during this study confirmed predictions that naïve animals translocated to a novel environment may require multiple generations to optimize resource selection patterns (Raley et al. 2012, Lewis et al. 2016, Parsons et al. 2019). The distribution of fisher detections in 2013 aligned closely with the distribution of radio-collared fishers reported from the years immediately following translocation (Lewis et al. 2016), but subsequent annual sampling revealed occupancy patterns shifting towards the south and west along a gradient of increasing precipitation. There are multiple plausible explanations for the geographic shift in fisher occupancy patterns we observed. Fishers may have responded to the rainfall gradient directly, which is generally associated with productivity of trees, enhanced vertical structure of overstory canopies, and complexity of forest understories (Henderson et al. 1989, Van Pelt et al. 2006), characteristics that may provide optimal hunting habitat for fishers (Buskirk and Powell 1994). Alternatively, the distribution of fishers may have responded to variation in other habitat attributes that were correlated with the northeast-southwest precipitation gradient. For example, the preferred boundaries between wilderness and more intensively managed forest lands are more extensive on the western perimeter (and wetter side) of Olympic National Park than in the northeast section of the Park. We detected several fishers along extensive boundaries that encompass the Park's coastal strip and low-elevation western river systems (Fig. 2). We found little evidence that the shift to the south and west was related to elevation changes owing, in part, to the fact that much of the southern wilderness boundary, which appeared to be increasingly occupied by fishers during this study, was comparable in elevation to many of the sites occupied by fishers in 2013. Irrespective of the cause for the shift, the change in distribution corresponded with the greater prevalence of first and second generation fishers detected (Table 1), indicating that dispersal of descendants likely contributed to the changing patterns of occupancy over time.

Our surveys demonstrated that the reintroduced Olympic Peninsula fisher population has persisted 6 years since the last fishers were released, forming at least 2 new generations. Preliminary indicators of successful population establishment include stable trends in occupancy estimates during the last 3 years of the study, preliminary evidence that fishers may have expanded out of the primary study area by the fourth survey year, and genetic evidence that the founding fishers and their offspring have reproduced and established new generations in the population. But fisher occupancy estimates remain low. Average annual estimates of occupancy on the Peninsula (range = 0.08–0.24, median 0.14), were lower than occupancy rates measured in established fisher populations inhabiting the Southern Sierra Nevada (range = 0.26–0.58; Zielinski et al. 2013) and Klamath Mountains (naïve occupancy [uncorrected for detection bias]: 0.32) of California (Davis et al. 2007), and New York, USA (0.41–0.67; Fuller et al. 2016). We conclude that either fishers have not fully occupied all available habitat on the Olympic Peninsula or that the extensive forest reserves protected within federal wilderness areas did not provide all requisite components of the fisher's habitat, including biotic components such as an abundance of prey, as readily as boundary areas between wilderness and managed forest settings. Preliminary evidence also suggests that expansive landscapes where timber extraction was the dominant land use historically may also lack required habitat elements. Although the population may continue to expand into new areas as it fills available habitat, the reestablishing fisher population selectively occupied the edge zone between 2 widely disparate land-management designations before broadly occupying either extensive low-to mid-elevation forested wilderness or lands managed historically for intensive timber production.

MANAGEMENT IMPLICATIONS

Evidence that fishers strongly selected for wilderness edges supports a growing body of evidence that maintaining an interspersion of mature forest ecosystems and younger age classes enhances fisher habitat in the mesic coastal forests of the Pacific Northwest. Although habitat managers have defined fisher habitat primarily based on mature forest characteristics in the past, our results indicate special consideration should also be given to ensuring that forest mosaics provide a variety of forest age classes and sufficient prey resources. Protecting and, where possible, fostering the development of late-seral forest characteristics interspersed throughout more intensively managed portions of the landscape outside federally reserved lands may help to improve habitats at low elevations on the Peninsula. Patterns of fisher occupancy we observed raise questions about many aspects of the spatial use patterns of fishers, predator and prey distributions, and relative fitness of fishers living across diverse landscapes in Pacific Northwestern forested ecosystems. The patterns we report are likely still in flux; additional patterns of fisher occupancy will likely emerge as future generations of reintroduced fishers continue to adapt to this unique environment and reveal additional insights for managing coastal forests in the Pacific Northwest.

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