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ARTICLE

Tree community shifts and Acorn Woodpecker population increases over three decades in a Californian oak woodland

Devin E. McMahon, Ian S. Pearse, Walter D. Koenig, and Eric L. Walters

Abstract: Forest communities change in response to shifting climate, changing land use, and species introductions, as well as the interactions of established species. We surveyed the oak (*Quercus* L. spp.) community and Acorn Woodpecker (*Melanerpes formicivorus* (Swainson, 1827)) population within 230 ha of oak forest and savanna in central coastal California in 1979 and 2013 to assess demographic changes over a timescale relevant to mature oaks. Overall, percent canopy cover increased, particularly where coast live oak (*Quercus agrifolia* Née) and California black oak (*Quercus kelloggii* Newberry) were most abundant. The density of stems of *Q. agrifolia* increased, whereas the density of stems and basal area of valley oak (*Quercus lobata* Née), a species favored by Acorn Woodpeckers, decreased. The number of Acorn Woodpeckers and woodpecker territories increased over the study period, coincident with the increase in percent canopy cover; however, these increases were not related spatially. Instead, increased acorn production associated with broad-scale canopy growth likely more than compensated for the loss of *Q. lobata*. Our findings suggest that forests in this area are becoming denser and savanna is becoming more open, which so far has supported an increase in the Acorn Woodpecker population, despite potential habitat loss if *Q. lobata* continues to decline.

Key words: animal territories, community shift, land use change, plant–animal interactions, tree demographics.

Résumé : Les communautés forestières changent en réponse aux fluctuations climatiques, aux changements dans l'utilisation du territoire et aux introductions d'espèces, de même qu'aux interactions entre espèces établies. Nous avons étudié les communautés de chênes (*Quercus* L. spp.) et les populations du pic glandivore (*Melanerpes formicivorus* (Swainson, 1827)) sur 230 ha de chênaie et de savane de la côte centrale californienne en 1979 et en 2013 dans le but d'évaluer les changements démographiques sur une période de temps appropriée pour des chênes matures. Dans l'ensemble, le pourcentage de recouvrement arborescent a augmenté, particulièrement là où le chêne de Californie (*Quercus agrifolia* Née) et le chêne noir de Californie (*Quercus kelloggii* Newberry) étaient les plus abondants. La densité de tiges de *Q. agrifolia* a augmenté, tandis que la densité de tiges et la surface terrière du chêne blanc de Californie (*Quercus lobata* Née), une espèce favorite du pic glandivore, ont diminué. Le nombre d'individus et de territoires du pic glandivore a augmenté durant la période d'étude, coïncidant avec l'augmentation du pourcentage de couvert arborescent, mais ces augmentations n'étaient pas corrélées spatialement. En fait, la production accrue de glands associée à l'augmentation à grande échelle du couvert arborescent a probablement surcompensé la perte de *Q. lobata*. Nos résultats suggèrent que les forêts de cette région se densifient tandis que les savanes deviennent plus clairsemées, ce qui jusqu'à maintenant a permis un accroissement des populations du pic glandivore, en dépit d'un déclin potentiel si la population de *Q. lobata* continue à décroître. [Traduit par la Rédaction]

Mots-clés : domaines vitaux, modifications des communautés, changement d'utilisation du territoire, interactions plante–herbivore, démographie des arbres.

Introduction

Forest and savanna communities can be rapidly altered by species introductions, changing land use patterns, and climatic shifts (van Mantgem et al. 2009; Cobb et al. 2010; McEwan et al. 2011). In some cases, these changes dramatically alter the functional composition of ecosystems (Metz et al. 2012). In many cases, however, selective pressures on individual tree and shrub species cause a shift in community composition without an obvious change to the overall physiognomy of the forest (McEwan et al. 2011). Although more subtle, these changes can still have profound effects on forest processes and biotic communities (Cobb et al. 2010, 2013), in part because many trees are foundational species that provide habitat for other organisms (Ellison et al. 2005).

California's oak-dominated (*Quercus* L. spp.) ecosystems have been shaped by a variety of human practices, including managed burning by Native Americans and ranching, agriculture, and fire suppression by Europeans and present settlers (Anderson 2006). Multicentury trends in oak abundance and distribution are not well recorded, but land conversion to pasture and agriculture have apparently restricted the ranges of oak species in comparison with the extent of suitable soil and climate (Kueppers et al. 2005). More recently, sudden oak death syndrome (caused by the oomycete *Phytophthora ramorum* (Werres, De Cock & Man in 't Veld)) along with fungal pathogens and forest pests such as the goldspotted oak borer (*Agrilus auroguttatus* Schaeffer) have resulted in substantial oak mortality in many areas (Swiecki and

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Bernhardt 2010; Coleman et al. 2011; Metz et al. 2012; Lynch et al. 2013).

Even in the absence of pathogens, the abundance of some oak species may be limited by multiple barriers to regeneration, including seedling predation and microclimate variability (Tyler et al. 2008). Multiple studies have documented apparently inadequate seedling and sapling recruitment of several oak species throughout California (Muick 1991), including studies conducted decades apart at our study site in central coastal California (Griffin 1971; Pearse et al. 2014). Recent studies indicate that oak recruitment is highly site and species specific, such that recruitment of a species may be low at some sites but sufficient at others (McLaughlin and Zavaleta 2013). Oak recruitment studies, however, generally judge oak demographic trends based on the abundance of saplings or mortality of experimental seedlings. Repeated vegetation surveys provide more direct evidence of oak community change over time (Whipple et al. 2011).

Oak community changes may have cascading effects on other organisms, as acorns are an important resource for numerous animals in oak-dominated ecosystems (Jones et al. 1998). The Acorn Woodpecker (*Melanerpes formicivorus* (Swainson, 1827)) is a conspicuous bird that consumes acorns and uses oaks (particularly valley oak, *Quercus lobata* Née) both for food storage sites (known as "granaries") and for nest sites (Koenig and Mumme 1987). These woodpeckers are cooperative breeders and live in family groups that store acorns in autumn for use as winter forage. They nest in cavities in semi-open habitat in regions in which the presence of multiple oak species reduces interannual variability in acorn availability, and local populations of Acorn Woodpeckers fluctuate in tandem with acorn crops (Koenig and Haydock 1999; Koenig et al. 2011).

The foraging behavior of Acorn Woodpeckers varies among sites with different oak species composition (Scofield et al. 2011), suggesting that the oak community composition may affect the success of Acorn Woodpecker populations. It is currently unclear, however, what effect changes in oak communities will have on these woodpecker populations over the long term. On one hand, general increases in acorn production may supply woodpeckers with additional food. Alternatively, changes in oak species composition may alter the availability of favorable semi-open habitats or of nest sites, associated with the dominance of *Q. lobata* and with the presence of large *Q. lobata* individuals.

We examined changes in a Californian oak woodland and the implications both for the oak community and for Acorn Woodpeckers by repeating a forest survey conducted 34 years previously, while maintaining a continuous monitoring program of Acorn Woodpeckers. We used the resulting data to determine whether (*i*) percent canopy and shrub cover had changed and in what pattern, (*ii*) basal area and abundance of individual oak species had changed, (*iii*) Acorn Woodpecker abundance had changed coincident with changes in oak communities, and (*iv*) large changes in the oak community were spatially correlated with Acorn Woodpecker territory establishment, and why this might be the case. In particular, we examined gross patterns of community change (shifts among grassland, dense forest, and open woodland) and the implications for Acorn Woodpeckers. These community shifts and woodpecker–oak relationships may offer insight into broader-scale changes in Californian oak-based ecosystems, including the resilience of this habitat to future changes.

Methods

Site description

The study was conducted on 230 ha within the 950 ha Hastings Natural History Reservation (HNHR) in central coastal California (36.3827°N, 121.5588°W). Vegetation includes mixed hardwood forests, primarily of coast live oak (*Quercus agrifolia* Née) and Pacific madrone (*Arbutus menziesii* Pursh), foothill woodland–savanna dominated by either blue oak (*Quercus douglasii* Hook. & Arn.) or *Q. lobata*, and perennial and annual grassland, including old-field areas. California black oak (*Quercus kelloggii* Newberry) and canyon live oak (*Quercus chrysolepis* Liebm.) are also present, mostly at higher elevations. Chamise (*Adenostoma fasciculatum* Hook. & Arn.) chaparral occurs primarily on south-facing slopes. Riparian forests include various oaks and occasional willow (*Salix* L. spp.), California sycamore (*Platanus racemosa* Nutt.), white alder (*Alnus rhombifolia* Nutt.), and bigleaf maple (*Acer macrophyllum* Pursh).

Mean annual temperature (1939–2013) is 13.4 °C, with a January mean low of 1.7 °C and a July mean high of 30.3 °C. Mean annual precipitation is 522 mm, occurring almost entirely between October and May. Most of the study area has not been grazed or actively managed since 1937 (Griffin 1990), and no substantial fire has affected the study area during the period of the study. Prior to 1937, aerial imagery and known land use patterns indicate that much of the existing forest was cleared for pasture or agriculture (White 1966). Climatic conditions in this area are highly variable from year to year and exhibited no consistent patterns in rainfall or temperature over the duration of the study, although over the longer term (1939–2013), mean annual minimum temperature recorded at HNHR headquarters increased by approximately 0.8 °C (W. Koenig, unpublished data).

Vegetation sampling

Vegetation was surveyed at HNHR in 1979 and again in 2013 using a modification of the James and Shugart (1970) method. A total of six hundred and thirteen 0.37 ha sample grid cells covering approximately 230 ha of the reservation were surveyed. Sampling centroids were established in 1979 using a 61 m grid overlay and resurveyed in 2013 based on converted GPS locations. In 1979, 0.04 ha circular plots (11.3 m radius) were surveyed at the center of each grid cell. In 2013, this same diameter was established using a Yardage Pro laser sight (Bushnell Outdoor Products, Overland Park, Kansas). In both sampling years, we recorded the diameter at breast height (DBH, measured using a DBH tape measure at 1.3 m) and the species of all trees that were >1 m in height and with a DBH that was >8 cm. From this, we calculated the basal area of each tree as $\pi(0.5\text{DBH})^2$, assuming a circular cross-section, and summed the basal area by tree species for each plot. Percent tree canopy cover and percent shrub cover were estimated to the nearest 5%. Canopy cover was assessed by noting the presence or absence of canopy cover at 20 points along a roughly north–south or east–west plot axis, following James and Shugart (1970). In 2013, the cardboard sighting tube with cross hairs described by James and Shugart was replicated by noting canopy cover at the tip of a finger pointed straight upward at arm's length. Shrub cover was estimated visually from the center of the sampling plot, as transects tended to be biased by avoidance of poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Greene).

In cases of very large numbers of trees within the sample area (generally >20 in 1979 and >70 in 2013), a half-size sample plot (8 m radius for a 0.02 ha plot) was sampled, and the number of stems and basal area were doubled for analysis. In the 1979 survey, some 0.37 ha grid cells with few trees were sampled in their entirety; these results were likewise rescaled for analysis. In a preliminary analysis, we removed all points whose sampling areas differed between 1979 and 2013; however, this did not alter the results, so all plots were retained.

Acorn Woodpecker monitoring

Acorn Woodpeckers at HNHR were color banded and monitored continuously between 1979 and 2013. Group membership was determined by approximately bimonthly censuses of territories, typically at granaries or nests (Koenig and Mumme 1987). All nestlings and adult birds were captured from nesting or roosting cavities and banded; any unbanded birds associated with each group were recorded by sex. Territorial boundaries were estimated from bimonthly censuses of birds and observations of territory defense behavior and foraging ranges, and territory occupancy in a given year was unequivocally determined by observing use or disuse of that territory's granary and (or) tree cavities (E. Walters and W. Koenig, unpublished data).

Statistical analysis

For each grid cell sampled, we calculated differences between years in percent canopy cover (Δ canopy) and percent shrub cover (Δ shrub), as well as differences in the basal area (Δ BA) and number (Δ abundance) of each tree species, as value 2013 – value 1979. Changes in canopy and shrub canopy cover are reported in percentage points, such that a change from 20% to 40% canopy cover is reported as a 20% increase. For basal area and density, percent changes refer to (value 2013 – value 1979)/value 1979, reported as a percentage.

For each cell, we defined the dominant tree species in 1979 or in 2013 as the tree species with the highest basal area in the survey plot in that year. We assessed whether changes in canopy cover varied with dominant oak species in either year using a spatially explicit generalized least squares model with an exponential correlation structure. In this model, Δ canopy was a function of the dominant oak species. The model that included the specified spatial correlation structure yielded more support than a model that did not include spatial correlation (Δ Akaike information criterion (AIC) = 39.2), so the spatially explicit analysis is presented. The model was run separately using the dominant oak species in each plot in 1979 or in 2013 as the predictor variable.

To quantify changes in each oak species and in oaks as a whole, we standardized the basal area and abundance values for each grid cell by the sample area in the corresponding year. To account for spatial autocorrelation, we performed a spatially constrained bootstrap by resampling the variable of interest (e.g., change in canopy cover or Δ BA of each oak species) at each plot location 1000 times with replacement, using only values occurring at points within 660 m of the plot. This ensured that all regions of the study area were appropriately represented in each sample. The distance of 660 m was selected based on maximum semivariance for several variables using the binned variograms in R package geoR (Ribeiro and Diggle 2001); other distances were also tried, with similar results. For each variable, we took the mean value of all the resampled data points for each of the 1000 trials and then ordered the means to create percentile confidence intervals. The standard deviation of the bootstrapped distribution of means provided the standard error of each variable; thus, unless otherwise noted, values listed are mean ± standard error (Efron 1981). We used Spearman's rank correlation (ρ) to test the relationship between Δ canopy and Δ shrub, as these data did not meet the parametric assumptions.

We also assessed whether changes in woodpecker territory occupancy were related spatially to forest change parameters (total Δ canopy, total Δ shrub, or Δ BA or Δ density of each of the five oak species). To account for annual fluctuation in territory occupancy, related primarily to the variation in the acorn crop, we analyzed changes in territory occupancy for 3-year spans at the beginning and end of the study period. We used the 50 cases in which woodpecker territories had been occupied during 1977–1979, during 2011–2013, or both and coded this as a categorical variable (territory abandoned, territory maintained, or territory newly established during the study period). Territories that were established and abandoned between 1980 and 2010 were excluded from the analysis, as were two territories established as part of a recruitment experiment. We assigned to each woodpecker territory the summed forest change parameter values from all survey plots within the territory divided by the total sample area per territory; for changes in percent canopy and shrub cover, we assigned to woodpecker territories the mean value of sample plots within the territory. We compared the model performance of multinomial models including different combinations of oak predictors with the model performance of the null model (probability of each occupancy category = mean probability for all territories) using AIC. Significance of parameter values was assessed by z tests, following UCLA Statistical Consulting Group (2014).

Table 1. Overview of vegetation and Acorn Woodpecker (*Melanerpes formicivorus*) changes in the study area between 1979 and 2013 (1977–1979 and 2011–2013 for the Acorn Woodpecker data). For the analysis of woodpecker territories, 23 territories were active during 1977–1979 and 44 territories were active during 2011–2013.

Metric	1979	2013	Mean change
Mean percent canopy cover	22.2±0.8	42.7±1.3	20.3±1.1**
Mean percent shrub cover	11.8±0.9	27.5±1.2	15.7±1.1**
Mean oak basal area ($m^2 \cdot ha^{-1}$, all species)	16.5±0.7	15.1±0.6	–1.4±0.9
Mean no. of oak stems per hectare (all species)	171.6±9.0	162.0±9.0	–10.4±8.3
Total Acorn Woodpecker abundance	48	252	—
Total no. of active territories	18	44	—

Note: All values are given as mean ± standard error. Mean change may differ from change in means due to rounding. **, $p < 0.01$.

All statistical analyses were conducted in R, version 3.0.2 (R Core Team 2014). Spatially explicit regression analyses were conducted using the gls function of the nlme package (Pinheiro et al. 2014). Multinomial models were constructed using the multinom function of the nnet package (Venables and Ripley 2002). Woodpecker territories were mapped using ArcMap (Environmental Systems Resource Institute (ESRI), 2013).

Results

Canopy cover

Canopy cover increased significantly across the area sampled ($p < 0.001$, bootstrapped estimate of mean difference) from a mean cover of 22.2% in 1979 to a mean cover of 42.7% in 2013 (Table 1; Fig. 1A). Canopy cover had increased in plots dominated in 2013 by any of the five oak species or by non-oak trees (Table 2).

Plots dominated by *Q. agrifolia* or *Q. kelloggii* in 2013 experienced the greatest increases, whereas *Q. douglasii*- and *Q. lobata*-dominated plots experienced smaller increases (generalized least squares regression; Table 2; Fig. 1). In contrast, sites dominated by *Q. agrifolia* in 1979 experienced smaller increases in canopy cover (15.6% ± 2.6%) than did plots dominated in 1979 by other tree species. The number of plots in which *Q. agrifolia* was the dominant tree species also increased between the two years, whereas the number of plots dominated by *Q. lobata* and *Q. douglasii* declined between the two years (Table 2).

Areas that were already open became more open: more plots with <5% canopy cover were recorded in 2013 (142 plots) than in 1979 (104 plots), whereas the number of plots with <10% canopy cover decreased from 169 to 153, and the distribution of canopy cover generally shifted toward greater canopy cover. In general, *Q. lobata* was associated with open areas: in 1979, grid cells dominated by *Q. lobata* had substantially less canopy cover than those dominated by any other oak species, with a spatially correlated mean canopy cover of 14.2% ± 1.0%. *Quercus lobata* dominated cells again had the lowest canopy cover in 2013, although their canopy cover was similar to that of *Q. douglasii* dominated cells.

Oak abundance and species composition

Overall, neither the total basal area of oaks nor the mean density changed significantly over the time period studied (Table 1). Of the three major oak species, only *Q. lobata* experienced a significant decrease in basal area (–0.66 ± 0.37 $m^2 \cdot ha^{-1}$, a change of

Fig. 1. (A) Percent change in canopy cover. Canopy cover in the study area generally increased between 1979 and 2013 (cool colors = increase in canopy cover). Most abundant species by basal area in (B) 1979 and (C) 2013. Each grid cell covers 0.37 ha, with data taken from a central plot of approximately 0.04 ha. "Non-tree" refers to treeless grassland and shrub habitats.

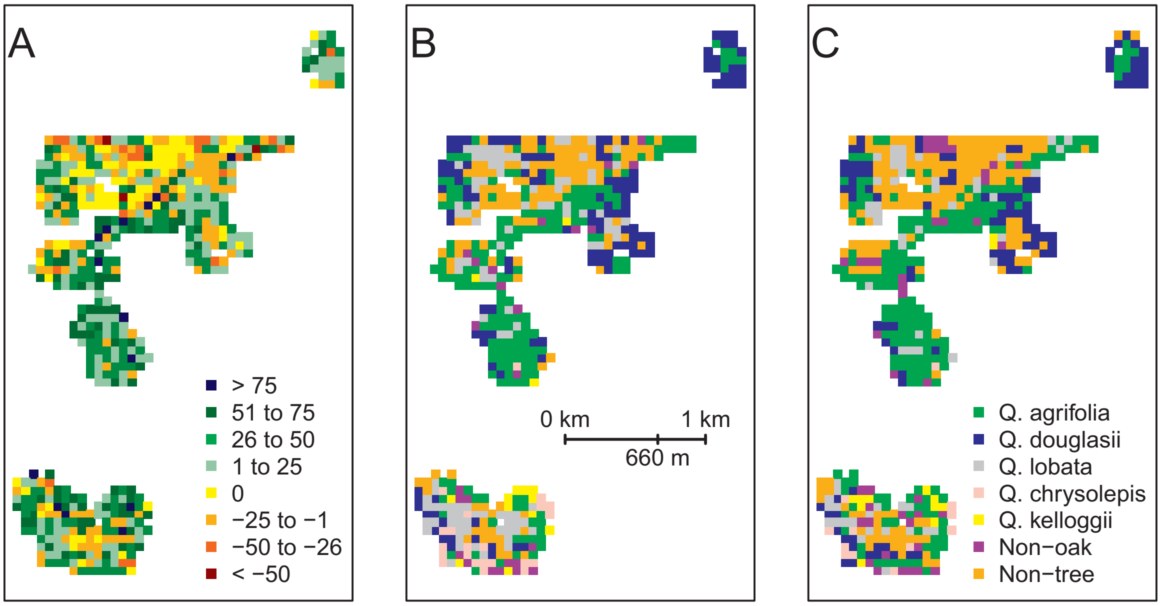
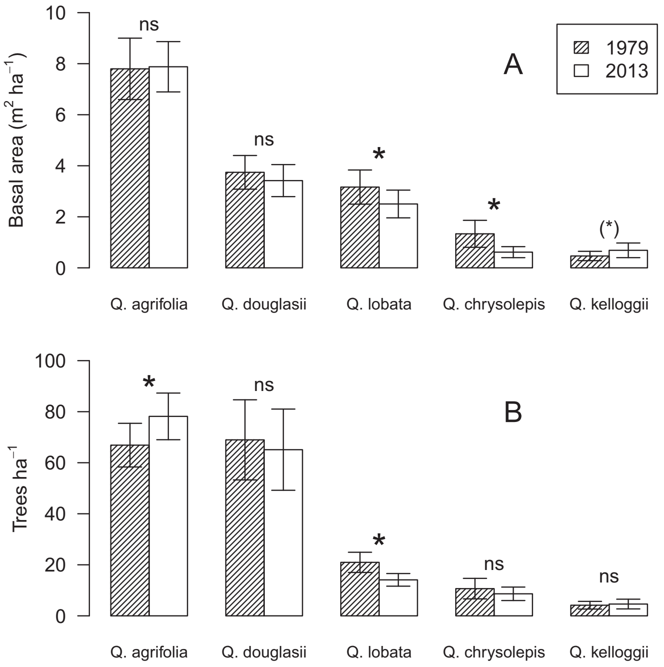


Table 2. Percent canopy change across tree species.

Dominant tree species	No. of plots	Mean tree canopy cover (%) in 2013	Tree canopy change (% cover) since 1979
2013			
Q. agrifolia	204	61.5±1.6	+33.7±1.9
Q. douglasii	107	52.1±2.0	+26.3±2.5
Q. lobata	58	49.1±3.1	+28.2±3.3
Q. chrysolepis	12	66.7±6.3	+28.4±7.1
Q. kelloggii	12	81.3±3.6	+44.3±7.3
Non-oak	43	61.9±4.1	+31.2±3.8
No trees (shrub or grassland)	174	3.2±0.8	−6.3±2.0
1979			
Q. agrifolia	193	31.5±1.4	+15.6±2.6
Q. douglasii	126	25.4±1.4	+20.8±3.0
Q. lobata	102	14.2±1.0	+25.1±3.3
Q. chrysolepis	22	40.9±4.8	+21.1±6.6
Q. kelloggii	14	32.9±3.9	+41.3±7.9
Non-oak	25	30.8±3.6	+33.7±5.8
No trees (shrub or grassland)	128	5.6±1.3	+20.5±3.0

Note: All values are given as mean ± standard error. Estimates of canopy cover change are predicted values from a spatially explicit generalized least squares model with canopy cover change (response) as a function of a plot's dominant species in 2013 or 1979. Different plots were dominated by each species between 1979 and 2013 (Fig. 1).

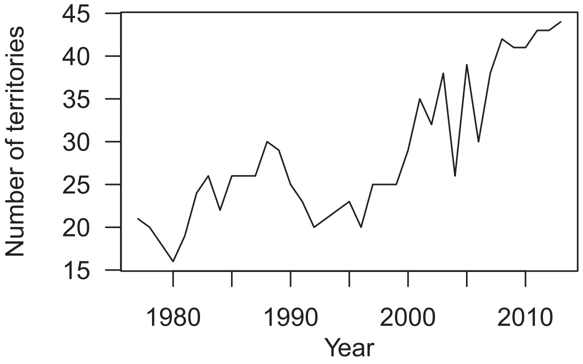
Fig. 2. (A) Change in basal area ($m^2 \cdot ha^{-1}$) by oak species: * denotes significance at the 99% confidence level; (*) denotes significance at the 90% confidence level; error bars represent two standard errors of the mean. (B) Change in number of stems ($trees \cdot ha^{-1}$) by oak species: * indicates significant change in the mean at the 95% confidence level; error bars represent two standard errors of the mean. ns, not significant.



–20.9% ± 11.7%, $p < 0.05$; Fig. 2A). Of the two less abundant oak species, the basal area of *Q. chrysolepis* decreased significantly (–0.72 ± 0.24 $m^2 \cdot ha^{-1}$, a change of –53.8% ± 17.7%, $p < 0.01$; Fig. 2A), and the basal area of *Q. kelloggii* increased with marginal significance (0.22 ± 0.13 $m^2 \cdot ha^{-1}$, a change of 47.7% ± 27.0%, $p < 0.10$). As these less abundant species were present in relatively few plots (57 for *Q. chrysolepis* and 44 for *Q. kelloggii* in 2013), these trends are informed by fewer data and are not discussed further.

In terms of stem density, *Q. lobata* experienced a significant decrease ($p < 0.01$, bootstrapped difference) from a mean of 21.0 $stems \cdot ha^{-1}$ to a mean of 14.1 $stems \cdot ha^{-1}$ (change, −6.9 ± 2.2 $stems \cdot ha^{-1}$). The number of *Q. agrifolia* stems increased significantly ($p < 0.01$) from 66.9 ha^{-1} to 78.2 ha^{-1} (change, +11.3 ± 4.6 ha^{-1}) (Fig. 2B). No significant changes were observed in *Q. douglasii*, but the number of plots containing trees of this species decreased from 212 to 166. The number of plots occupied by *Q. agrifolia* increased from 309 to 318, whereas the number of plots occupied by *Q. lobata* decreased from 213 to 160.

Fig. 3. Trends in active Acorn Woodpecker (*Melanerpes formicivorus*) territories intersecting the vegetation study area. Data on group activity were collected annually, during the nesting season. The number of active territories within the study area gradually increased between 1979 and 2013. Points represent years included in the analysis of territory occupancy.



Shrub cover

Shrub cover increased significantly between 1979 and 2013, with shrubs covering an additional 15.7% ± 1.1% of the ground, on average ($p < 0.001$, bootstrapped estimate of mean difference), from the 11.8% mean cover in 1979 (Table 1). Shrub increase was weakly but significantly correlated with canopy increase ($\rho = 0.28$, $p < 0.0001$) and was greatest in plots dominated by either *Q. agrifolia* or *Q. kelloggii* (33.9% ± 1.9% and 44.5% ± 7.4%, respectively), whereas plots without trees lost shrub cover (–6.3% ± 2.0%) (generalized least squares, $p < 0.05$).

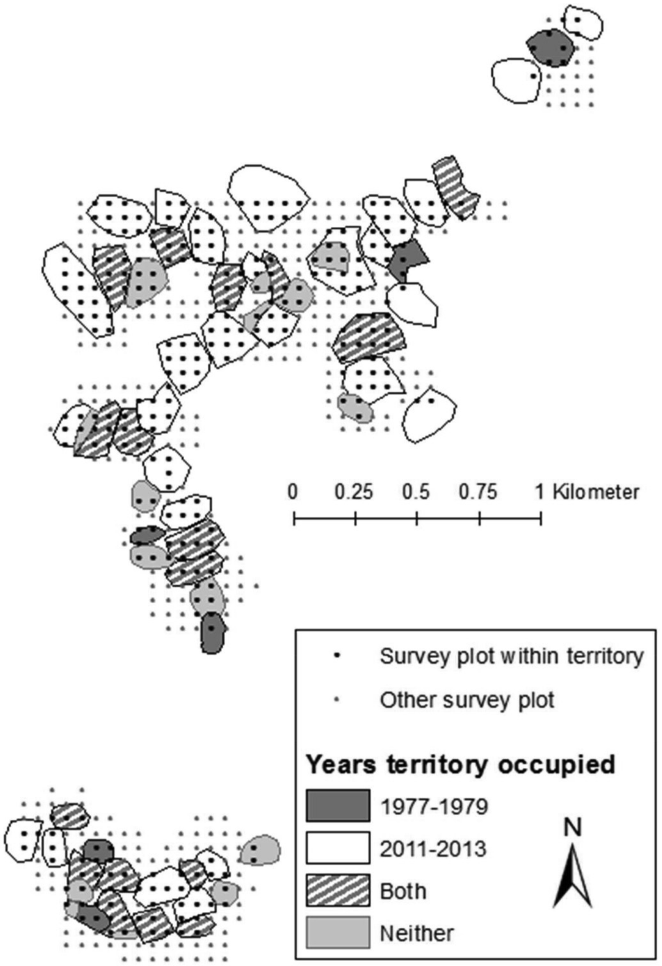
Acorn Woodpecker populations

In 1979, 18 woodpecker territories totaling 48 individuals intersected the study area, while in 2013, 44 woodpecker territories totaling 252 individuals intersected the same area, the result of a gradual increase in the woodpecker population over the study period (Table 1; Fig. 3). Between these two periods, the total number of active territories increased from 23 to 44, with 27 territories newly established, six territories abandoned, and 17 territories active during both time periods (Fig. 4).

Acorn Woodpecker populations increased concomitantly with increases in forest cover across the study area. However, we found no significant spatial correlation between occupancy of individual territories and changes in forest parameters at a given site. For the 50 territories active at the beginning and (or) end of the study, changes in canopy cover and in basal area of each of the most common oak species — *Q. agrifolia*, *Q. douglasii*, and *Q. lobata* — were not significantly associated with territory establishment or maintenance vs. territory abandonment; that is, inclusion of any or all of these terms to a model of territory occupancy did not increase the model's AIC support compared with the null model, and parameter values associated with each were not significantly different from zero. Moreover, no relationship was apparent between territory occupancy and change in shrub cover or in the density of *Q. lobata* or *Q. agrifolia*.

Nonetheless, our results suggest a negative relationship between occupancy and tree density increase. There was a nonsignificant trend toward a decreased probability of territory occupancy with a greater increase in canopy cover: for the six territories abandoned over the course of the study, three experienced a canopy cover increase of over 40%, which was true of only five territories, and none experienced a canopy cover decrease. There was also a trend toward a decreased probability of territory occupancy with an increase in the number of *Q. douglasii*. Adding both of these terms to the model of canopy cover occupancy slightly improved the model's AIC support (by 1.90 units), and the associated parameters were not significantly different from zero ($p > 0.1$). Canopy cover changes in the territories analyzed ranged from –25.0% to +46.0%, with mean ± standard deviation of 20.6% ± 16.8%.

Fig. 4. Number of active Acorn Woodpecker (*Melanerpes formicivorus*) territories in the study area increased between the time of the initial vegetation survey (1977–1979, striped or darkly shaded territories) and the second survey (2011–2013, striped or unshaded). Other territories (light shading) were occupied at other times but were not analyzed in relation to oak variables. Sixty-five territories intersected at least one survey plot (darker points), of which 50 territories (excluding those with light shading) were considered in modeling relationships between changes in oak variables and territory occupancy. The points representing the sample plots are not to scale.



Discussion

Forest change in a Californian oak woodland

Our long-term approach complements studies of regeneration and surveys of forest composition, suggesting a trend in this Californian oak ecosystem toward denser forests and more open savannas. We observed an increase in the abundance of dense-canopied *Q. agrifolia*, which can be attributed in part to its expansion in plots that were dominated by other oaks in 1979. Areas in which *Q. agrifolia* was dominant in 2013 experienced large increases in canopy cover, whereas areas in which *Q. agrifolia* was present but not dominant experienced smaller increases.

Overall, *Q. agrifolia* appears to have become a more dominant component of the oak woodland ecosystem. This trend is consistent with other studies that report increased evergreen oak abundance in California (Tyler et al. 2006), particularly at forest margins (Callaway and Davis 1998). In Sierra Nevada forests, for example, evergreen oaks are displacing deciduous species, possibly assisted by climate change, as evergreen oaks are more heat and drought tolerant (Dolanc et al. 2014). Additionally, a recent broad-scale survey of forest change over seven decades found overall decreases in total basal area and in abundance of larger trees in the central and southern coastal regions of California (McIntyre et al. 2015). Although these trends also reflected broader scale effects of drought stress and oak pathogens, they are similar to the demographic shift we observed toward young *Q. agrifolia*.

At the same time, *Q. lobata*, a tree primarily of savanna and sparser canopy habitats, declined in both stem abundance and basal area. The number of plots with <5% canopy cover (indicative of open grassland) also increased, even as the study area as a whole shifted toward higher levels of canopy cover, suggesting that loss of tree canopy is occurring primarily in areas of few trees. *Quercus douglasii*, often growing in nearly pure stands, also became more concentrated into dense patches, as it maintained statistically equivalent basal area and abundance between 1979 and 2013 while occupying substantially fewer plots in 2013. Along with canopy cover, shrub cover also increased in the study area, particularly where dense-canopied *Q. agrifolia* and *Q. kelloggii* were present. Changes in shrub cover, therefore, support the general trend toward more densely vegetated forest, whereas a gradual decline of open-grown *Q. lobata* and minimal oak re-establishment outside of forested habitat (Pearse et al. 2014) leave grassland areas more open.

Our long-term investigation provides evidence from mature trees in support of demographic trends suggested by regeneration studies. In the case of *Q. agrifolia*, increases in density and canopy cover without a corresponding increase in basal area, coupled with observations of relatively abundant *Q. agrifolia* seedlings and saplings (qualitatively in this study; quantified by Pearse et al. (2014)), suggest recruitment of young, smaller trees at our site; studies at other sites show similar trends for this species (Tyler et al. 2006). Similarly, previous work at our site demonstrated an apparent paucity of *Q. lobata* saplings in an area overlapping that of the current study (Pearse et al. 2014), a finding that was qualitatively supported by presence–absence records of seedling abundance in the sample plots of this study. Paired with even a modest death rate of mature trees (24 standing dead *Q. lobata* individuals were found within plots in 2013 compared with 13 dead *Q. douglasii* and 14 dead *Q. agrifolia* individuals), poor seedling recruitment could result in the observed decline in *Q. lobata* abundance. Previous studies have suggested that *Q. lobata* regeneration in Californian savannas may be inadequate due to seed and seedling predation and light or water limitation (Griffin 1976; Tyler et al. 2006), and our study provides direct evidence from mature trees of the decline implied by this hypothesis. Overall, our survey suggests a shift in the landscape toward more densely forested areas, more open grasslands, and less intermediate habitat dominated by sparsely canopied *Q. lobata*. Thus, additional management beyond the exclusion of grazing at our study site may be necessary to maintain *Q. lobata* and the semi-open habitat in which it thrives. Going forward, remotely sensed data could allow for the evaluation of trends in canopy density and species composition shifts, and their effects on primary production, over a broader area.

Forest change and Acorn Woodpecker populations

Shifts toward denser forests and more open grasslands may be especially apparent from the perspective of Acorn Woodpeckers. These birds frequently nest in semi-open *Q. lobata* habitats and also forage among *Q. agrifolia*, the two oak species largely driving the observed trends in oak canopy and demographic structure. For the woodpeckers, the habitat shift toward denser, *Q. agrifolia* dominated stands represents a trade-off between increased food supply due to increased density of acorn-producing foliage and decreased availability of semi-open nest sites due to the loss of *Q. lobata*. Our results suggest that this trend has so far benefited the woodpeckers in this area. We observed concomitant increases in oak canopy cover and Acorn Woodpecker numbers; however, changes in the canopy cover were not spatially associated with woodpecker territory occupancy. Based on prior work demonstrating a significant relationship between oak abundance and diversity and Acorn Woodpecker density along the Pacific coast (Koenig and Haydock 1999) and strong correlations between acorn production and woodpecker populations at our study site (Koenig et al. 2011, in press), the increasing acorn production with increasing canopy cover is likely to have been the main driver of the gradual population increases at the scale of the study area. Larger canopies are associated with more acorns in eastern U.S. hardwood forests as a result of an overall increase in the number of productive branches (Greenberg 2000). Accordingly, a general increase in productivity would provide the resources to support larger woodpecker populations but, in accordance with our results, would not necessarily predict a spatial relationship between canopy increase and woodpecker territory establishment. Instead, the general increase in canopy cover would increase acorn production within the boundaries of favorable habitat, regardless of their specific tree composition or initial canopy density. Moreover, woodpeckers nesting in relatively open areas may benefit from increased densification and acorn production at the periphery of their territories (Koenig et al. 2008).

Our data allow us to reject several alternative mechanisms by which oaks may have driven the observed increase in woodpecker numbers at the study site. The addition of new trees could have provided more nesting and granary sites, which experimental work has shown to limit territory establishment (E. Walters and W. Koenig, unpublished data). In contrast to this hypothesis, overall changes in oak abundance were not significant. Also, nesting sites of Acorn Woodpeckers are preferentially situated in *Q. lobata* (Hooge et al. 1999), which did not increase in abundance, and granaries are generally established in older, larger trees. Conversely, the death of trees could have led to expansion of the nearly open areas that woodpeckers favor for their territories. However, of the major oak species, only *Q. lobata*, which is associated with more open habitat, decreased in abundance, concomitant with a decrease in the proportion of territories with <10% canopy cover. Generally, habitat became less open, except in some cases in which trees were lost altogether. Increased productivity per unit area of canopy, rather than the observed canopy area increase, could also have provided additional food for woodpeckers, but contemporaneous acorn surveys do not suggest such increases (Koenig et al. 1994; W. Koenig and J. Knops, unpublished data).

Trends toward a decreased probability of territory establishment and an increased probability of abandonment with increased canopy cover and number of *Q. douglasii* stems suggest a possible negative effect of denser canopy on Acorn Woodpeckers. As *Q. douglasii* is often found in savanna habitats rather than in forest habitats, its increase could represent a loss of open habitat. These trends are, however, driven by a few plots (two abandoned territories experienced large gains in density of *Q. douglasii* stems, whereas one abandoned territory lost *Q. douglasii*), and thus, not enough territories were abandoned to definitively identify spatial relationships between territory occupancy and oak variables.

This lack of contrast was exacerbated by the general increase in woodpecker numbers, which resulted in many more territories established than abandoned over the study period and thus obscured the effects of oak community changes on the establishment, persistence, or abandonment of particular territories. Likewise, among-territory differences in oak community changes may have been obscured by the general oak trends across the study area, making fine-scale analysis difficult. Thus, although changes in oaks may influence the location of woodpecker territories, we focused on analysis at the scale of the entire reservation, for which oak–woodpecker relationships were more apparent.

At this broader spatial scale, widespread increases in canopy density and acorn production appear to have outweighed the loss of *Q. lobata* in allowing the establishment of new territories. If these trends continue, however, the loss of suitable granary sites may limit the increase in the woodpecker population. Future studies should consider woodpecker–canopy relationships over coarser spatial scales to determine whether landscape-level changes in productivity explain regional woodpecker population trends.

Future trends

Although annual precipitation and temperature did not change substantially over the study period at HNHR, predicted changes may exacerbate limitations on regeneration at our site and elsewhere in California. Hotter, drier summers in much of the state affect seedling establishment and stress mature trees (Kueppers et al. 2005), and recruitment may be less in drier areas (McLaughlin and Zavaleta 2013). Regional climate models predict that the suitable ranges for *Q. douglasii* and *Q. lobata* are likely to shrink, whereas limits on seed dispersal and available protected lands may prevent these species from expanding into new areas (Kueppers et al. 2005). In addition, adaptation of distinct *Q. lobata* populations to local climate conditions may further limit range shifts and amplify climatic effects on these populations (Sork et al. 2010). Increased temperature and water stress appear to already be driving decreases in total basal area and shifts in species composition throughout California (McIntyre et al. 2015). Our results suggest that over the past several decades, *Q. lobata* in particular has fared worse than other Californian oak species. Additional climate stress could further diminish *Q. lobata* populations, exacerbating the trend toward a more dichotomous landscape of denser forests and more open grasslands. Ongoing long-term observation of growth and reproduction of trees at HNHR will help elucidate oak responses to multiple stressors.

In addition, the increased dominance of *Q. agrifolia* increases ecosystem vulnerability to *P. ramorum* and *A. auroguttatus*, both of which infest *Q. agrifolia* and *Q. kelloggii*. In the case of sudden oak death, the risk of rapid change in community structure resulting from the loss of dominant species may be mitigated by the apparent recruitment of new *Q. agrifolia* saplings, as the pathogen tends to have a larger effect on older, larger trees (McPherson et al. 2010). The dry conditions of our study site may also limit the effect of *P. ramorum*, but the presence of the carrier species *Umbellularia californica* ((Hook. & Arn.) Nutt.) and the risk of insect invasion compel further monitoring of tree health in this ecosystem and in other Californian oak ecosystems.

Conclusions

Over 34 years in a central coastal Californian oak woodland, canopy cover increased, whereas total oak basal area did not change; *Q. agrifolia* became more numerous, whereas *Q. lobata* declined; and Acorn Woodpeckers increased in number and established new territories. In general, differences in vegetation density between forested and open areas increased. If woodpeckers are able to nest and roost in newly open areas and forage in denser, *Q. agrifolia*-dominated canopies, denser oak woodlands may benefit them, so long as *Q. lobata* individuals in open savanna habitats persist. However, the continued loss of *Q. lobata*, exacerbated by drought stress, could eventually limit nesting sites for the woodpeckers unless active management is able to reverse declines in *Q. lobata*. The introduction of insects and pathogens that attack *Q. agrifolia* could also reverse the observed canopy trends, emphasizing the need for forest management and wood transport regulation to control the spread of forest pests and pathogens.

Long-term surveys over relevant spatial scales are necessary to provide insight into the complex relationships between animal and plant populations. Our study provides a fine-grain perspective on forest changes in a Californian oak ecosystem. Expanding such analysis across additional sites could help to elucidate oak demographic changes in western North America and the effects on woodpeckers and other species that rely on oaks for their survival.

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