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SPATIAL CLUSTERING AND ECOLOGICAL CROWDING OF VALLEY OAK (*QUERCUS LOBATA*, NÉE) ASSOCIATED WITH SHIFTS IN RECRUITMENT ESTABLISHMENT SITES IN SOUTHERN CALIFORNIA

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Premise of research.   Valley oak (*Quercus lobata*, Née) has received much attention due to concerns about regeneration failure and, more recently, compositional and structural community changes associated with this foundation species. Changes in the structure and spatial distribution of valley oak stands, as examined in this article, are likely affecting ecological processes and interactions throughout communities where it is found.

Methodology.   We used quadrat-based methods of spatial analysis, Morisita's index of aggregation (I_M), and a derived index (I_{Mr}) to examine patterns of clustering, intensity of crowding, and changes in the probability of crowding as the definition of crowding (stems/area) is changed. Saplings, defined as stems with a diameter at breast height (dbh) greater than 1 cm and less than 10 cm (1 cm ≤ dbh < 10 cm) and adults (dbh ≥ 10 cm) were analyzed using four quadrat sizes. We mapped clusters of stems on the basis of spatial autocorrelation of dbh using Anselin's local Moran's *I* to identify the location of sapling and adult stem clusters.

Pivotal results.   Adults and saplings were clustered for all quadrat sizes, although the intensity of clustering and crowding differed among sites. Two sites had much higher intensity of clustering and crowding, and saplings were spatially segregated from adults away from open savannah habitat. At a third site, stems were less intensely clustered, and saplings did not show clustering away from adults. The intensity of sapling crowding differed among sites as the definition of crowding changed, revealing that saplings experience greater levels of crowding at two of the sites than at the third.

Conclusions.   Valley oak regeneration is spatially aggregated and ecologically crowded, indicating a shift to higher-density riparian woodland and increasingly open grassland seen at other sites and in other studies. Land change is an important driver of spatial regeneration patterns and may be playing a role here, although additional work is needed to examine the effects of possible drivers of crowding and the habitat shift. Future work should consider the ecological implications of structural and spatial changes in valley oak stands for associated species and processes.

Keywords: valley oak, *Quercus lobata*, spatial pattern, clustering, California.

Introduction

Valley oak (*Quercus lobata* Née), endemic to California, is a foundation species, composing much of the physical structure, habitat, and food resources in systems where it is found. Much research and conservation effort has focused on valley oak, *Q. lobata*, which is due in part to an apparent lack of recruitment throughout its range (Tyler et al. 2006; Zavaleta et al. 2007). Impacts on the species include stand clearing and habitat loss as natural areas have been and continue to be converted to agricultural land and residential and commercial development (Pavlik et al. 1991). Important factors found to af-

fect establishment, survival, and growth of *Q. lobata* include site, rodent herbivory, year of planting (Tyler et al. 2006), and habitat type (Pearse et al. 2014). Broader trends in landscape development and climate change have been hypothesized to drive some aspects of local stand-scale changes (McLaughlin and Zavaleta 2012; Hayes and Donnelly 2014; McMahon et al. 2015), and climate modeling efforts have suggested regional changes in the species' future distribution as the climate becomes warmer and drier (Standiford 2002; Kueppers et al. 2005; Sork et al. 2010). Several studies have observed *Q. lobata* stands shifting spatially to cooler, more mesic microclimates (McLaughlin and Zavaleta 2012; Hayes 2013) and transitioning from savannah to woodland (McMahon et al. 2015).

Valley oak, *Q. lobata*, is a deciduous oak that is both flood and drought tolerant, although seedlings and saplings are sensitive to precipitation and soil-moisture stress (Griffin 1971; Franco 1976; Tyler et al. 2002, 2006, 2008). Acorns germinate

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in the fall, and seedlings, subject to herbivory and a long dry season, often do not survive by the second year (Tyler et al. 2006; Davis et al. 2011). The sensitivity of seedlings and saplings to moisture stress seems to encourage establishment in shaded locations and along stream channels, depressions, swales, roadsides, and fence rows where moisture collects; however, *Q. lobata* adults are commonly found on hilltops and slopes, and saplings have been noted to grow larger in open habitats (Pearse et al. 2014). Acorn production varies widely among trees and from year to year (Griffin 1971; Koenig et al. 1994; Tyler et al. 2008). Although seed dispersal is primarily over short distances, resulting in clustering of seedlings around parent trees, many acorns are dispersed by birds, especially the scrub jay (*Aphelocoma californica*) and acorn woodpecker (*Melanerpes formicivorous*; Pavlik et al. 1991; Howard 1992; Tyler et al. 2006; McMahon et al. 2015). Burial greatly enhances the probability of germination and seedling establishment, because most acorns that fall on the ground will be consumed or killed by heat or desiccation (Tietje et al. 1991). Vectors for burial of *Q. lobata* acorns include scrub jays and ground squirrels, among other bird and mammal species (Grinnell 1936).

Seedlings and saplings were uncommon or absent in nearly all *Q. lobata* studies reviewed by Tyler et al. (2006), with the exception that, at one riparian forest site, seedlings and saplings were common (Knudsen 1984), and seedling density was high in some years where cattle and deer were excluded (Griffin 1976). The occurrence of seedlings and saplings also appeared to be more likely in the first and second years following a high-rainfall year and at sites farther north in the species' range (Franco 1976; Knudsen 1984). Tyler et al. (2008) found that establishment was generally associated with higher rainfall but that rainfall varied with other conditions (e.g., insect populations), which can confound the effects of rainfall alone. In two studies that associated survival with rainfall (Franco 1976; Knudsen 1984), cattle were excluded from the study sites, which may also have influenced the recruitment of saplings (Tyler et al. 2006). Zavaleta et al. (2007) found that fewer than half of the *Q. lobata* regeneration studies reported the presence of seedlings or saplings. In the one long-term study of *Q. lobata* dynamics that used aerial photography to quantify mortality and recruitment (Brown 1991), no recruitment was observed between 1938 and 1989 (Tyler et al. 2006). As a result of their review, Tyler et al. (2006) concluded that regeneration may not be sufficient to maintain *Q. lobata* stands, although they note that the conclusion is based on a few short-term studies and that more research is needed, especially documenting mortality and recruitment rates, to support their conclusion. The one example of *Q. lobata* demographic modeling, based on experimental data, indicates that population growth rates may be limited by survival and growth of seedlings and saplings once established (Davis et al. 2011).

A number of studies have examined factors likely to be important in oak recruitment, including masting, acorn predation and dispersal, effects of herbivory and browsing, climate change, habitat fragmentation, altered disturbance regimes, competition with nonnative species, changing bird and mammal populations, grazing, and land use history (Tyler et al. 2006). Several studies have documented acorn mortality caused by disease, mammals, and insect damage (Griffin 1980; Knudsen 1984; Swiecki et al. 1997). Acorn and seedling predation has been noted as a strong limiting factor for *Q. lobata* recruitment (Griffin 1971; Knudsen 1984; Callaway 1992; Tyler et al. 2002, 2008). Tyler et al. (2002, 2008) found that herbivory was among the most important factors impacting establishment, survival, and growth, with exclusion of rodents more than doubling the rate of acorn establishment in one study and nearly doubling the rate of survival into the second year after establishment. Leaf and stem damage from insects, small mammals, and browsing by cattle and deer has also been shown to reduce seedling and sapling survival (Griffin 1971, 1976; Bernhardt and Swiecki 1997; Tyler et al. 2002; Davis et al. 2011). The effects of livestock grazing on seedling and sapling recruitment are less clear, with some studies of blue oak (*Quercus douglasii*) showing negative associations between seedling presence (Standiford et al. 1997) and sapling presence (Swiecki et al. 1997), whereas another study (Muick and Bartolome 1987) found the presence or absence of cattle to have no explanatory power for predicting the presence of oak saplings (Tyler et al. 2006). Further confounding associations between grazing and recruitment, studies have found cattle may aid the growth of seedling and sapling oaks by negatively impacting nonnative grasses, which reduce seedling growth and survival through competition for soil moisture (as long as the oaks are themselves protected from cattle; Griffin 1971; Danielsen 1990; Danielsen and Halvorson 1991).

Understanding the effects of climate and climate change on *Q. lobata* recruitment is challenging because of the short duration of most studies and the wide range of annual precipitation and seasonality found across the species' range, which is likely to produce geographically different effects (Sork et al. 2010). If the climate of California continues to become warmer and drier, as has been observed and is expected to continue (Melillo et al. 2014), we should expect to see a shift of *Q. lobata* distribution from areas that have become too warm and dry to locations where temperature and moisture parameters are suitable for seedling establishment and survival (IPCC 2014; Melillo et al. 2014). Using a bioclimate model, Kueppers et al. (2005) found that a warmer and drier climate will result in a contraction of *Q. lobata* habitat area and a spatial shift to higher elevations and latitudes. McLaughlin and Zavaleta (2012) noted that bioclimate models based on climate parameters suitable for adults may not correctly predict future habitat distribution, because seedlings and saplings may have different climate tolerances than adults. Emergence and survival of *Q. lobata* seedlings is sensitive to precipitation, and competition for soil moisture can reduce seedling survival. Precipitation in the first year after acorn planting has been linked with higher rates of *Q. lobata* seedling establishment and survival, whereas dry years saw either an absence or a very low rate of establishment (Griffin 1971; Tyler et al. 2002). Using a bioclimate model parameterized to account for multiple *Q. lobata* life stages, McLaughlin and Zavaleta (2012) found that *Q. lobata* will shift with changing climate, causing an absence of recruitment in areas that are no longer cool or humid enough, but that recruitment may persist in climate microrefugia, on mesic slopes, and around areas of surface water within the species' current range. Hayes (2013) found that *Q. lobata* saplings were found primarily along riparian corridors and on mesic slopes, whereas adults were more evenly distributed across habitat types, and that the average distance to stream channels was lower for saplings than for adults at two of three *Q. lobata* stands examined.

Altered spatial patterns and changes in the structure and spatial distribution of tree communities can have implications for both biotic and abiotic components of ecosystems on scales from individual parcels to the entire globe (Jones et al. 1998; Shi and Zhang 2003; Ellison et al. 2005; Foley et al. 2005; Pielke 2005; Cobb et al. 2010, 2013; Ellis et al. 2010; McMahon et al. 2015). The composition, structure, and spatial patterns of tree communities affect the occurrence, abundance, and ecological dynamics of associated plant and animal species, natural disturbances, and biogeochemical processes of the landscape (Turner 1989; McShea and Healy 2002; Farina 2006; Chen et al. 2008; Lindenmayer 2009). Examining the spatial patterns of tree establishment sites and how they change may provide insight into either endogenous processes (e.g., clustering of saplings around parent trees) or environmental heterogeneity or environmental change (e.g., spatial variability of soil moisture or nutrients or land change that affects these variables; Ripley 1981; Dale 1999; Perry et al. 2006; Diggle 2013). In this study, we examine the spatial distribution of *Q. lobata* establishment sites to ask whether *Q. lobata* saplings are spatially clustered or experiencing ecological crowding and potential limits on density.

The structure and dynamics of *Q. lobata* stands have been related to the spread of disturbance and disease, soil development, and evapotranspiration as well as the population and community ecology of other plant species, birds, mammals, and invertebrates (Aschmann 1959; Danielsen 1990; Pavlik et al. 1991; Howard 1992; McMahon et al. 2015). Valley oak communities and their ecology have also been impacted by Native Americans and European settlers as well as by contemporary society (Aschmann 1959; Pavlik et al. 1991). Although *Q. lobata* has received much attention from researchers and conservationists due to concerns associated with climate change, habitat loss, and poor regeneration (Griffin 1971, 1976; Thomas 1987; Sork et al. 2002, 2010; Kueppers et al. 2005; Tyler et al. 2006, 2008; Zavaleta et al. 2007; Pearse et al. 2014), little is known about how spatial patterns of *Q. lobata* stands are changing at local scales (stand and landscape).

In recent studies of *Q. lobata* in the Santa Monica Mountains, sapling establishment was found to be occurring increasingly away from previous establishment sites and in microclimate refugia (McLaughlin and Zavaleta 2012) on more mesic north- and northeast-facing slopes and closer to stream channels (McLaughlin and Zavaleta 2012; Hayes 2013). Hayes (2013) found differences between sapling and adult establishment patterns among habitat classes (aspect, topographic position, and distance to streams), with saplings disproportionately occurring on mesic aspects and closer to streams than adult stems at three sites in the Santa Monica Mountains; however, at one of the three sites, sapling and adult establishment sites did not differ with regard to topographic position or distance to streams but were more evenly distributed across the site. Hayes and Donnelly (2014) suggested the differences between Paramount Ranch and the other sites could be explained by the broader landscape pattern of development in the subwatersheds upstream from each site.

In this article, we assess several hypotheses of spatial pattern among *Q. lobata* stems in the context of shifting sapling establishment to cooler mesic habitats (McLaughlin and Zavaleta 2012; Hayes 2013) and differing site conditions (Hayes and Donnelly 2014). Using the Morisita index (I_M) to measure clustering of stem locations and a local measure of Moran's I to measure spatial autocorrelation of tree size, we ask the following.

1. Are there differences among sites in clustering of *Q. lobata* sapling and adult stems? We expect that both sapling and adult stems will be clustered, given the species dispersal mechanisms and life history; however, assuming establishment sites being increasingly limited to cooler and mesic habitat, we further expect saplings to have a greater departure from random (to be more clustered) than adults. We further expect that the strength of clustering will differ among sites, because available habitat for sapling establishment also varies among sites.

2. Are saplings experiencing different levels of ecological crowding at each site? We expect that changing the definition of clustering to include greater numbers of saplings/quadrat at multiple scales will result in higher measured clustering index and greater divergence from a random distribution as more saplings are included, and we expect that clustering intensity at a given scale peaks for different numbers of stems at different sites. We consider ecological crowding to occur when the number of stems/quadrat is equal to or greater than the number of stems with the maximum clustering index.

3. Is *Q. lobata* stem diameter at breast height (dbh) spatially autocorrelated, such that saplings and adult stems are located among stems of similar or dissimilar dbh? If *Q. lobata* sapling establishment is shifting away from areas where it once occurred, we expect positive spatial autocorrelation of large dbh values (adult stems) to reveal a pattern of large stems near one another with few small stems nearby. Clusters of saplings, positive spatial autocorrelation of small dbh values, will identify a pattern of small stems near one another with few large stems nearby.

Material and Methods

Site Description

The sites examined in this study—Cheeseboro Canyon (CHE), Malibu Creek State Park (MAC), and Paramount Ranch (PAR)—are all located on the north slope and foothills of the Santa Monica Mountains National Recreation Area (fig. 1). The sites are each about 5 km apart. Two sites, CHE and MAC, are both approximately 45 ha; PAR is approximately 23 ha. The three sites have similar land use histories, including present-day use as preserves managed by the US National Park Service (CHE and PAR) and California State Parks (MAC). In the past, the sites have been used for dry-land farming, cattle grazing, and filming locations for television and film. PAR has had perhaps the most intensive land use impacts through its long history of film and television set construction and location filming, as well as an annual fair and music festival. MAC has also been used for filming, although less intensively.

All three sites are *Quercus lobata* savannah with associated nonnative grass species and coastal sage scrub (CSS) on some hillsides. The sites have similar plant and animal communities, including rodents and deer populations, as well as nonnative invasive plants. There is no cattle grazing occurring at any of the sites today, although it was most recent at CHE, ending in the 1980s (Thomas 1987). All three sites are dominated by a Mediterranean climate with cool, wet winters and hot, dry summers, although local topography can affect daily temperature ranges. Average annual precipitation is approximately 42 cm,
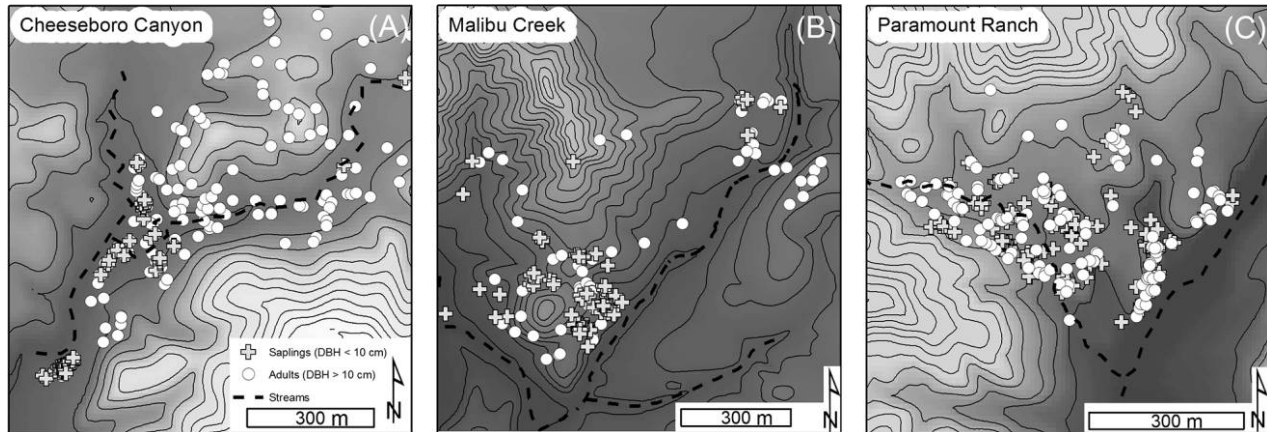
Fig. 1   Location of sapling and adult *Quercus lobata* stems at three sites, Cheeseboro Canyon (CHE; *A*), Malibu Creek (MAC; *B*), and Paramount Ranch (PAR; *C*). Adult stems (circles) can be seen to be widely distributed throughout various topographic positions at the three sites. Saplings (crosses) appear to be more restricted to the riparian corridor at CHE and to the riparian corridor and north to east aspects at MAC. Saplings at PAR appear to be widely distributed similarly to adult stems. Contour interval is 7 m; dark shading represents lower elevations. DBH = diameter at breast height.

falling primarily from November to March, with January and February being the wettest months (Arguez et al. 2010). Temperatures range from a December mean of 12.6° to a July mean of 22.2°C (Arguez et al. 2010). Summertime daily highs in the canyons can regularly approach and exceed 37°C, and morning frosts are not uncommon in winter.

Size class distributions and sapling:adult ratios of the three sites were described by Hayes (2013) and are reported here for a fuller understanding of stand structure at the study sites. The CHE and MAC stands have bimodal size class distributions with distinct cohorts of large (older) trees and small saplings, with few intermediate-sized trees. CHE has the largest individuals and the largest median dbh of 56.7 cm with an interquartile range (IQR) of 82.5 cm, indicating high variability in dbh compared with the other sites. Median dbh at MAC (10.2 cm; IQR, 22.8 cm) and PAR (9.2 cm; IQR, 44.7 cm) was much smaller and less variable. Regeneration at the sites is variable, with sapling:adult ratios of 1.13 at PAR, 0.99 at MAC, and 0.53 at CHE (Hayes 2013). Each site has a riparian component dominated by willow (*Salix* species) with occasional southern California black walnut (*Juglans californica*). The stream at CHE is intermittent depending on rainfall and seasonality. At CHE, coast live oak (*Quercus agrifolia*) occurs with *Q. lobata* and CSS, primarily purple sage (*Salvia leucophylla*) and California sage (*Artemisia californica*). Some *Q. agrifolia* woodland occurs on the north-facing slope of a prominent hill at PAR, marking the southern edge of the study area.

Methods

All *Q. lobata* stems with dbh ≥ 1 cm were located, measured with a standard dbh tape, and mapped using a Trimble GEOXH GPS; accuracy for all points was better than 30 cm. GPS coordinates in the UTM projection to the nearest whole meter were used for measurement and analysis of all spatial patterns. Stems were categorized on the basis of dbh as adults (dbh ≥ 10 cm) or saplings (1 cm ≤ dbh < 10 cm).

Maps were examined for apparent clustering of stems with respect to size and topographic position (see fig. 1). Quadrat analysis of clustering was used to evaluate departures from randomness in the observed stem patterns. Two quadrat-based approaches to stem clustering analysis were used. The first approach used Morisita's index of dispersion (I_M; Morisita 1964), which indicates how many more times likely it is that two randomly chosen points in an observed point pattern will be found in the same quadrat than if the point pattern were randomly distributed (Hurlbert 1990).

I_M (Morisita 1964) is defined as

$$I_M = \frac{\Delta_a}{\Delta_p},$$

where Δ_a is the observed probability that two randomly selected stems (without replacement) are in the same quadrat given *X* individuals and a space partitioned into *Q* quadrats, and Δ_p is equal to *1/Q*, or the expected probability of Δ_a given *X* individuals randomly distributed over *Q* quadrats following a multinomial distribution (Hurlbert 1990). If any two randomly chosen points in an observed spatial distribution have a greater probability of co-occurring in the same quadrat than the probability of two randomly chosen stems in a random spatial distribution, then the observed distribution may be thought of as departing from randomness toward clustering.

The Morisita index of aggregation and modifications of the index have been applied to examine spatial patterns and processes of seed dispersal, seed bank, and tree establishment (Houle 1994; Mosandl and Kleinert 1998; Shaukat and Sadiqi 2004; de Almeida and Galetti 2007); to compare spatial patterns of recruitment and adults (Hubbell 1979; Barros Henriques and Girnos de Sousa 1989); and to compare and rank (aggregated to uniform) the spatial distributions of species within a forest (Amaral et al. 2015). Distributions of sampling locations in environmental monitoring networks (Tuia and Kanevski 2008; Golay et al. 2014) and the spatial clustering of earthquake locations (Ouchi and Uekawa 1986; Telesca et al. 2015)

have also been analyzed using the Morisita index and derivative indices based on it.

In this study, the Morisita index was computed for adult stems, saplings, and all stems combined at each site using four quadrat sizes (100 m × 100 m, 75 m × 75 m, 50 m × 50 m, and 25 m × 25 m). Given an average crown size of 20 m in diameter (314.1 m²; Howard 1992), the 25 × 25-m quadrat size is most appropriate for assessing the occurrence of adult ecological crowding with I_M, because having more than one adult in the quadrat would exceed the available space; however, a range of grid sizes were used because of the possible effect of grid size on the measure of clustering. Given the expected rarity of *Q. lobata* regeneration, this analysis assumes that a sapling : adult ratio of 1 is high, and therefore, the same definition of clustering applies to saplings with respect to values of I_M, although, even at the 25 × 25-m quadrat size, this does not necessarily constitute ecological crowding for saplings.

Although clustering, defined as two randomly chosen stems co-occurring in the same quadrat with greater than random likelihood, may occur among saplings, it is not a very useful measure of ecologically significant crowding for saplings, because this definition potentially leaves a good deal of open space for two saplings to access resources. What is needed to identify ecologically significant crowding (i.e., statistical clustering that has ecological implications for space, water, and nutrient resources) is a measure of how the intensity of crowding increases or decreases with increasingly large numbers of stems in the quadrat, beyond a random expectation. Such a measure would allow examination of whether the probability of clustering increases for more than two stems, indicating a tendency toward spatial aggregation and little ecological pressure on space and resources at a given scale. Similarly, such a measure would indicate when aggregation beyond a certain number of stems within a quadrat approaches an ecological limitation of resources and clustering becomes less likely, indicating a threshold has been reached. An extension of I_M to multiple (i.e., >2) stems, I_{Mr}, provides such a measure.

Hurlbert (1990) defines I_{Mr} as

$$ I_{Mr} = \left[\frac{Q^{r-1}(X-r)}{X!} \right] \sum_{k=r}^{w} \frac{q_k \times k!}{(k-r)!}, $$

where Q is the number of quadrats, r is the number of stems randomly selected (without replacement) from X individuals, and

$$ \sum_{k=r}^{w} \frac{q_k \times k!}{(k-r)!} $$

is computed for all q quadrats with k (number of individuals per quadrat) $\geq r \ldots w$ (maximum k observed among Q).

To measure the presence and intensity and to identify potential thresholds in ecological crowding at the three sites, we analyzed sapling stem locations using I_{Mr} analysis. The family of indices I_{Mr} measures the degree to which the probability of finding all r individuals in the same quadrat is greater or less than it would be in a random distribution (Hurlbert 1990). Random distributions produce $I_{Mr} = 1$, clustered $I_{Mr} > 1$, and dispersed $I_{Mr} < 1$. As I_{Mr} increases, the greater the departure from randomness and the greater the intensity of clustering. We calculated I_{Mr} for all four quadrat sizes at each site for $r = 3, 4, 5, \ldots, w$.

By calculating I_{Mr} for $r = 3 \ldots w$, one can examine how I_{Mr} approaches or departs from random as r increases. The I_{Mr} approach allows examination of how the departure from random changes and identification of hypothetical threshold levels of crowding. This can reveal differences in the degree of crowding among sites and lead to further hypothesis development to explain why a crowding threshold at one site may not be reached, or perhaps exceeded, at another site. For instance, when a resource is scarce and limited to a small area, more stems may crowd together, competing to utilize that resource and resulting in increasing values of I_{Mr} as r increases, up to some threshold level of r stems—a crowding saturation point. Without a strong limiting factor and or abundant available habitat area, stems are less likely to crowd together, and we would expect lower maximum I_{Mr} values at lower values of r.

The use of I_{Mr} thus allows us to distinguish between statistical clustering and ecologically significant crowding (Hurlbert 1990). If the probability of finding two stems in the same plot results in $I_{M2} > 1$ on a 100 × 100-m quadrat grid, this is statistically "clustered" but may not be ecologically significant for the species—and this is all I_M and other clustering indices can tell us. On the other hand, if the probability of 10 randomly chosen stems being found in the same quadrat produces $I_{M10} > I_{M2}$, indicating that it is even more likely that 10 randomly chosen stems will be found in the same quadrat than that two will be found, this may be both statistically and ecologically significant. This definition of crowding would allow examining hypothetical crowding thresholds for various species, such as two stems per 25 m, 8 stems per 50 m, 17 stems per 75 m, and 31 stems per 100 m, and if I_{Mr} continued to increase for r greater than these hypothesized thresholds, it could suggest not only that stems are clustered but also that there may be factors driving an unusual intensity of stem clustering. Of course, other factors besides simple Cartesian space will affect crowding, such as availability of other resources, environmental fluxes, efficiency, and interactions with other species; this will vary among species and environments, potentially giving rise to regionally defined crowding thresholds for various species at different scales.

To check for groups of spatially segregated *Q. lobata* adults and sapling stems, a local indicator of spatial autocorrelation (LISA) statistic was used with the measured dbh values. The LISA statistic, Anselin's local Moran's I, identifies and statistically tests for spatial clusters, defined as groups of similar high or low values of an attribute, and spatial outliers, defined as high or low values among dissimilar values of an attribute (Anselin 1995). The implementation of the LISA statistic used here will assign both a measure of spatial autocorrelation and a test statistic value to each stem, so that individual stems will be displayed in the resulting maps but each stem actually represent a cluster. Shi and Zhang (2003) suggest that local indicators of spatial autocorrelation provide a useful approach when examining tree competition at both the plot and landscape scales.

Anselin's local Moran's I was calculated in ArcGIS 10.2 using the following formula:

$$ I_i = \frac{x_i - \overline{X}}{S_i^2} \sum_{j=1, j \neq i}^{n} w_{i,j}(x_j - \overline{X}), $$

where x_i is an attribute of feature i, x_j is an attribute of each neighbor j, $w_{i,j}$ is the spatial weight between features i and j, $\overline{X}$ is the mean of the attribute, and

$$S_i^2 = \frac{\sum_{j=1,\,j\neq i}^{n}\left(x_j - \overline{X}\right)^2}{n-1} - \overline{X}^2,$$

where n is the total number of features.

As implemented in ArcGIS 10.2, the resulting local Moran's I value is used along with the Z-score associated with a 95% confidence interval to categorize each feature as part of a cluster of high values, a cluster of low values, a high value outlier, a low value outlier, or not statistically significantly similar to or different from its neighbors. Further details of the calculation of Z-scores are available in ArcGIS 10.2 (ESRI 2014). In this research, a stem is designated as an adult cluster if it has a large dbh and is similar to surrounding stems. Likewise, a stem with a small dbh with similar stems nearby is designated as a sapling cluster. If all stems were of a similar size or if all stem sizes were interspersed, the LISA statistic would not be significant for any stems, and no clusters or outliers would be found. No discrete cutoff value dbh is used to designate adults versus saplings in this method, but examination of the values of stems classified as adult and sapling clusters fit well with the 10-cm threshold used in the quadrat analysis.

In the case of this research, each stem is considered a feature with an attribute value of dbh. As can be seen above, the statistic includes both the difference of the dbh of a given stem and the mean dbh of all stems as well as the sum of the weighted differences between the dbh of each stem and the mean dbh of all stems. An inverse distance weighting approach was used, such that all stems can potentially be considered neighbors of all other stems, with closer stems having a higher weight. A threshold distance, where the weight for each pair of features reaches zero, was set at the minimum distance required for every feature to have at least one neighbor. The statistic was calculated with several different threshold distances to assess the sensitivity of the results to this value, and no substantial differences in the pattern of clusters were observed.

Results

Clustering of *Quercus lobata* stems (fig. 1) is evident at all three sites, although with differing intensity at different scales and among size classes. At CHE, there was apparent segregation of saplings to the west and southwest corner of the site, along a paved two-lane road following a stream channel bordering the site; clustering of adults was less clear. At MAC, the mapped stem locations suggested clustering of both adults and saplings in a relatively small portion of the site, especially on the north- and northeast-facing hill slope adjacent to a riparian corridor. PAR appeared to have the most evenly distributed pattern of stems, yet saplings appeared to occur primarily along a hill slope on the southeast near a stream channel and through a wide, gently sloping ravine associated with an intermittent stream bottom.

I_M values indicated clustering of saplings and adults at all four quadrat sizes at all three sites (fig. 2). I_M values increased as quadrat size decreased, as might be expected for a clustered
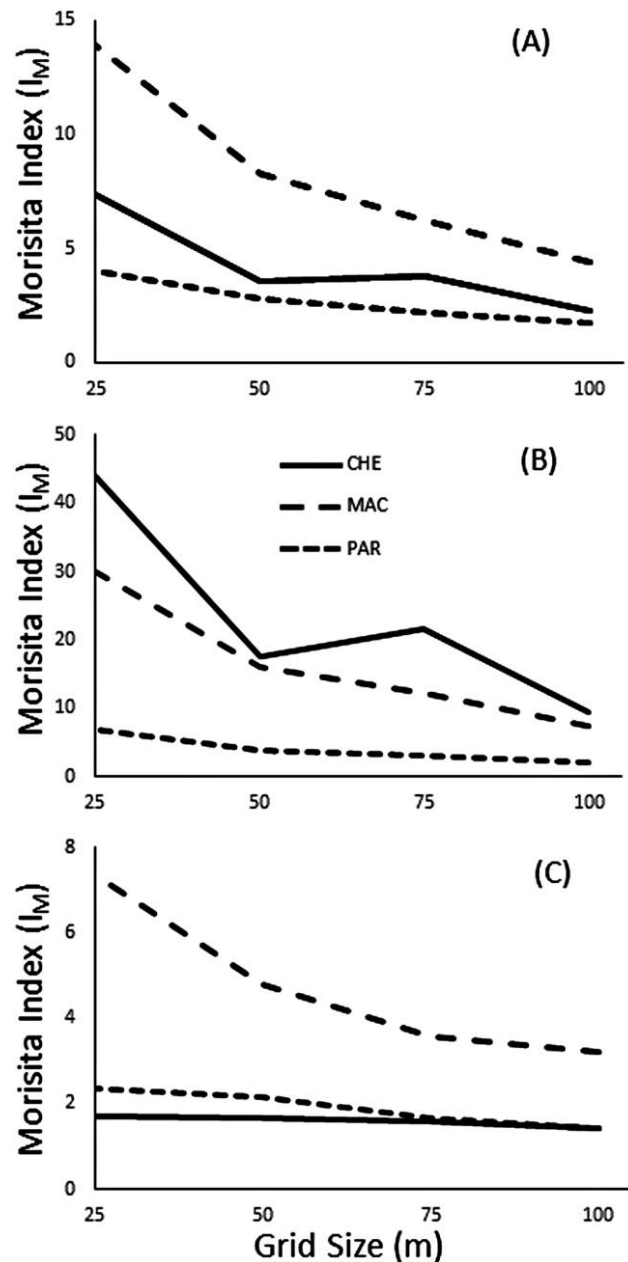
Fig. 2 Morisita index of aggregation (I_M) values for all stems (*A*), saplings (*B*), and adults (*C*) at Cheeseboro Canyon (CHE; solid line), Malibu Creek (MAC; long-dashed line), and Paramount Ranch (PAR; short-dashed line), computed using four quadrat grid sizes (100, 75, 50, and 25 m). I_M values are greater than 1, indicating clustering of stems (higher probability of two randomly chosen stems co-occurring than expected for a random distribution) for all stems and size classes and at all sites and quadrat sizes. Differences in departure from randomness toward clustering differs among sites, with MAC most intensely clustered overall, saplings most intensely clustered at CHE, and adults most intensely clustered at MAC. Note differences in I_M scale for *A*, *B*, and *C*.

pattern; however, I_M increased dramatically from 50 × 50-m to 25 × 25-m quadrats (a 75% reduction in area) at CHE and MAC and also peaked for PAR. I_M for *Q. lobata* patterns should be most ecologically relevant at the 25 × 25-m quadrat

size due to competition for space between two adult *Q. lobata* in this size area. For all stems combined, MAC showed the greatest tendency toward clustering with the highest I_M values at 25 m × 25 m. I_M at MAC was nearly twice that of CHE and nearly 3.5 times higher than at PAR. When looking at saplings alone, CHE had the greatest clustering, followed by MAC, then PAR, which had much lower I_M values than the other two sites. I_M for saplings at CHE was 1.4 times higher than at MAC and over 6 times higher than at PAR.

I_M values for adult stems increased with decreasing quadrat size as well at all sites but only slightly for CHE and PAR, whereas MAC had a considerable jump in I_M from the 50 × 50-m to 25 × 25-m quadrats. I_M values indicated the clustering of adults was much stronger at MAC than at CHE and PAR. At the 25 × 25-m quadrat size, MAC had an I_M value over three times higher than PAR and four times higher than CHE. Clustering of adults at CHE and PAR was similar for the 100- and 75-m quadrats but was stronger at PAR as quadrat size decreased.

I_{Mr} exceeded 1.0 for saplings across all sites and quadrat sizes for all values of r examined (fig. 3). I_{Mr} values for saplings were highest at CHE and lowest at PAR for nearly all values of r at all quadrat sizes. CHE and MAC I_{Mr} values were nearly

equal at the 50 × 50-m quadrat size for all r. CHE and MAC were much closer in I_{Mr} at other scales as well, compared with PAR, which consistently diverged from CHE and MAC as r increased.

The I_{Mr} curve for CHE on the 100 × 100-m grid appeared to be leveling off, indicating r_{max} (28 stems) at CHE approximates a limit for sapling clustering here; however, I_{Mr} for CHE on the 75 × 75-m grid increased further at $r_{max} = 35$ stems. This increase in r_{max} and I_{Mr} from 100 m × 100 m to 75 m × 75 m was partly real and partly a sampling artifact. Due to placement of the 75 × 75-m grid origin, one clump of saplings was grouped together in one quadrat, although this clump was split into several quadrats on the three other grids; nevertheless, there was a large number of saplings in this relatively small portion of the study area (see southwest corner of CHE study area map; fig. 1). On the 50 × 50-m and 25 × 25-m grids, I_{Mr} for CHE saplings peaked with $r_{max} = 17$ and 12, respectively; however, I_{Mr} is still rising when this limit is reached, which indicates the true crowding threshold may be higher.

I_{Mr} curves for MAC on the 100 × 100-m and 75 × 75-m grids indicated that r_{max} had exceeded or was near a crowding threshold at these scales ($r_{max} = 25$ for both grid sizes). I_{Mr}
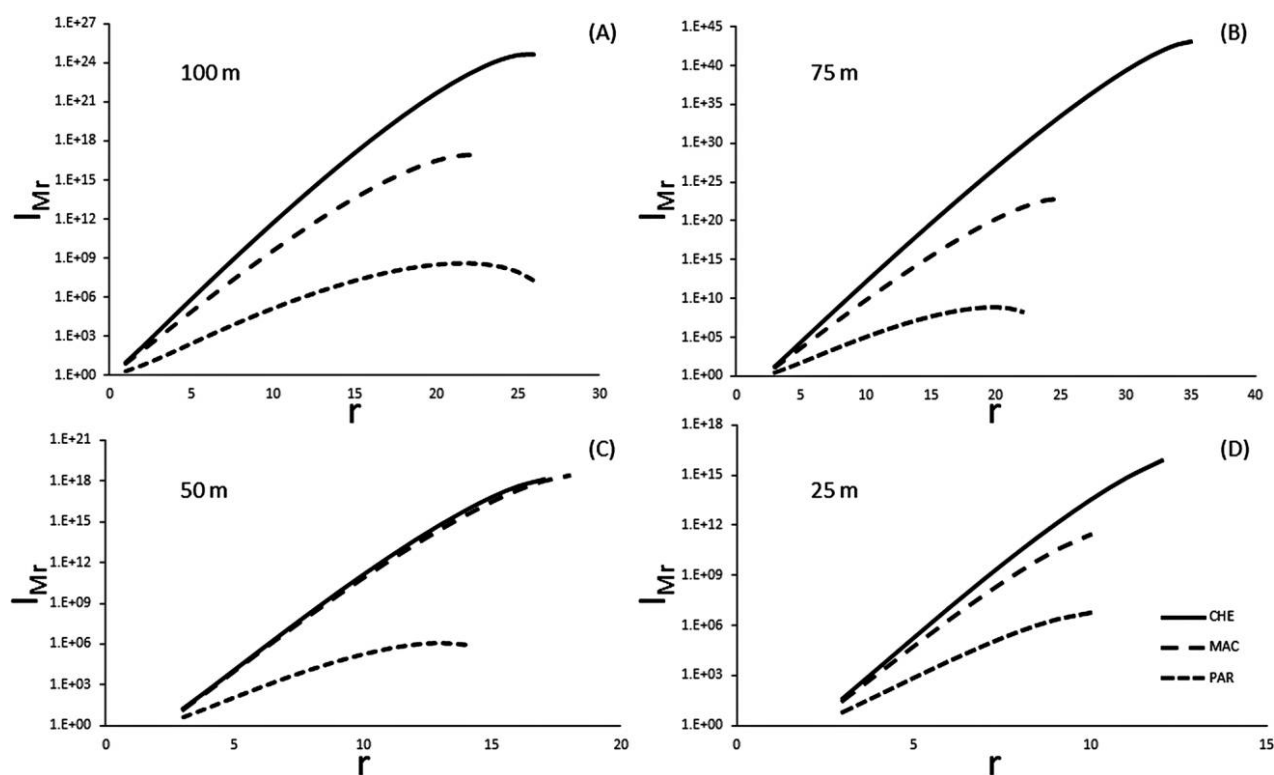
Fig. 3 Index derived from Morisita index of aggregation (I_{Mr}) values for saplings at Cheeseboro Canyon (CHE; solid line), Malibu Creek (MAC; long-dashed line), and Paramount Ranch (PAR; short-dashed line), computed using four quadrat grid sizes (25, 50, 75, and 100 m). Saplings were clustered at all sites, at all quadrat sizes. For all quadrat sizes, saplings were most intensely clustered at CHE, followed by MAC, and PAR had the lowest intensity of sapling clustering among the sites. Only on the 100-m quadrat grid (A) did sapling crowding appear to reach a threshold beyond which probability of clustering began to decrease at all three sites. At PAR, a threshold of crowding also seemed to be reached on the 75-m (B) and 50-m (C) quadrat grids as well, indicating less ecological pressure for crowding there, whereas more stems (higher r) crowding together is more likely at CHE and MAC on all quadrat grid sizes. Only on the 25-m quadrat grid, D, did saplings not reach a threshold level of crowding at any of the sites. Note different scales of I_{Mr} for A, B, C, and D.

peaked at $r = 24$ on the 100×100-m grid and decreased slightly at $r = 25$ (r_{max}), suggesting a peak in clustering intensity at this scale and I_{Mr} moving back toward random as r increases. On the 75×75-m grid, I_{Mr} peaked at $r = 25$. For the 50×50-m and 25×25-m grids, I_{Mr} was still increasing at r_{max} (18 and 10, respectively), a result similar to that found at CHE.

I_{Mr} curves for PAR indicated that sapling clustering reached a peak I_{Mr} value when $r < r_{max}$ on the 100-, 75-, and 50-m grid quadrats; I_{Mr} peaked at $r = 24, 20$, and 13 stems, respectively. Beyond these peaks, departure from randomness for greater r stems decreased but was still more probable than expected for a random distribution. Only on the 25×25-m grid was I_{Mr} still increasing at r_{max} (10), although it appeared that the slope was decreasing.

The local indicator of spatial autocorrelation was calculated using dbh values rather than the categorized sapling/adult data to identify spatial clusters and outliers on the basis of stem size. Only those stems that are part of a statistically significant cluster are shown below (fig. 4). Stems that are part of a cluster of high dbh values are labeled as a cluster of adults, and stems that are part of a cluster of low dbh values are labeled as a cluster of saplings. Because the LISA value is calculated for each feature on the basis of a comparison with the values of surrounding features, a single feature on the map actually represents a cluster of features. For this reason, the individual points in figure 4 should be interpreted generally as an area of stem clusters rather than as a point on the map.

All three sites have clusters of adult stems, whereas both CHE and MAC have clusters of sapling stems. Clusters of high or low dbh values at CHE and MAC suggest spatial segregation of adults and saplings at these two sites. At CHE, clusters of both saplings and adults are found along the riparian corridor there; however, these clusters are in different locations, along different reaches of the intermittent stream channel. Clusters of larger dbh trees are found along the east-west-running channel, which is steeper, drier, and has experienced downcutting of

the streambed, which may be causing soil moisture and groundwater loss to the stream channel. Clusters of smaller dbh trees occur along the north-south-running channel, which is also paralleled by a paved road running along the west edge of the study site. Segregation of larger and smaller stems is also apparent at MAC, although here clusters of small stems also occur along the eastern aspect of a steep hill, adjacent to the stream channel, and clusters of larger adult stems are found at higher elevations on a slope above the stream channel.

Results of the LISA analysis at PAR reveal clustering of trees with higher dbh values but not for those with lower dbh values or saplings. The absence of sapling clusters at PAR suggests a lack of spatial segregation of saplings from adults at this site. Clusters of adults occur along the riparian corridor at PAR, but there was no evidence of sapling clustering in any particular part of the study site.

Discussion

To answer our first question, we examined the I_M results of our clustering analysis, and as expected, clustering of saplings and adults as measured by I_M was present at all sites for all quadrat sizes examined (fig. 2). The relative level of sapling clustering compared with adults also fit our expectations, with saplings having greater I_M values than adults at CHE and MAC, although saplings and adults exhibited similar clustering at PAR, especially with larger quadrat sizes. Also, differences in clustering among sites were apparent. Differences in I_M tended to increase for smaller quadrats; however, the relative level of clustering among sites remained consistent across scales. Differences in clustering among sites tended to be greater for saplings, although sapling clustering at CHE and MAC was more similar at some scales than others, not showing a consistent trend with quadrat size (see fig. 2).

Results from the I_{Mr} analysis were interpreted to address our second question, and we found that the probability of finding
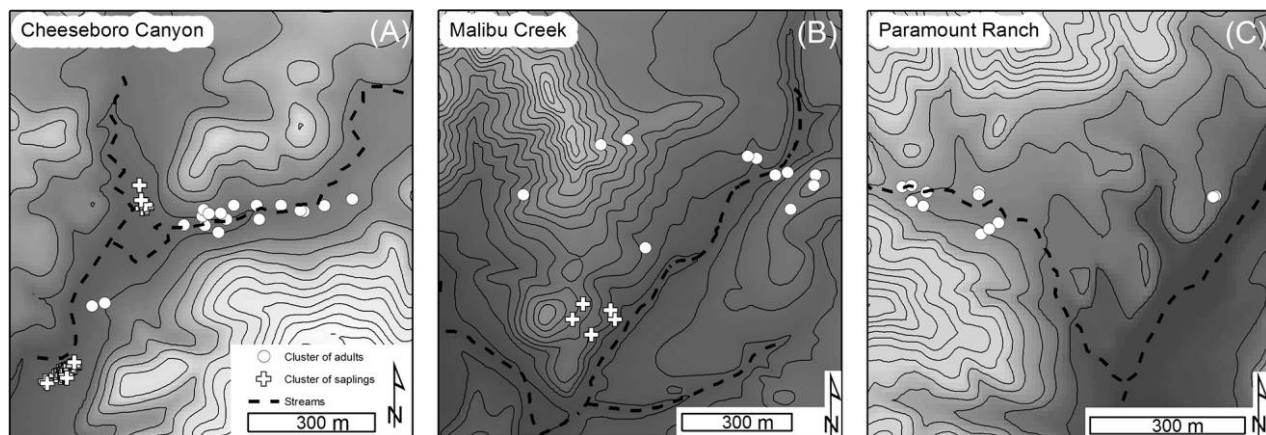
Fig. 4 Spatially segregated small stems (crosses) and large stems (circles) at Cheeseboro Canyon (CHE; *A*), Malibu Creek (MAC; *B*), and Paramount Ranch (PAR; *C*). Each symbol represents an adult stem surrounded by only other adult stems or by saplings surrounded by only other saplings. Clear segregation of small stems from large stems is apparent at CHE (*A*) and MAC (*B*). At CHE, small stems are found only along the western edge of the study area, along the riparian corridor and roadside, whereas at MAC, small stems are found grouped only along the east-facing slope of the riparian corridor. At PAR (*C*), there is evidence of spatially isolated large stems without many small stems nearby but a lack of spatially isolated groups of small stems, indicating a lack of small-stem segregation to limited areas, as seen at CHE and MAC.

all r saplings in the same quadrat was greater at our sites than for a random distribution (indicating clustering) and that I_{Mr} and the divergence from randomness (clustering intensity) continued to increase as r increased until a threshold level of clustering was reached—indicated by decreasing I_{Mr} with increasing r (fig. 3). Our expectation that clustering intensity at a given scale peaks for different numbers of stems at different sites could be tested only with the 100-m quadrat results (see fig. 3 A), because I_{Mr} was still increasing with r for some sites when other quadrat sizes were used. Our expectation of finding crowding thresholds was met for PAR, MAC, and possibly for CHE on the 100-m quadrat grid and for PAR on the 75-m and 50-m grids but not for CHE and MAC, whereas no thresholds were found when the 25-m grid was used. Clustering intensity of saplings on the 100-m quadrat grid was lowest for PAR and greatest for CHE—sapling clustering intensity at MAC was intermediate, although more similar to CHE. A crowding threshold of 24 saplings/quadrat was found for both MAC and PAR on the 100-m quadrat grid. The curve for sapling clustering intensity at CHE appeared to level off at 28 saplings/quadrat; however, 28 was also the maximum number of stems per quadrat, so we cannot tell whether I_{Mr} would have continued increasing for higher r. Sapling crowding appeared to reach threshold levels of 24 and 13 saplings/quadrat at PAR on the 75-m and 50-m grids.

To address the third research question, we employed a local indicator of spatial autocorrelation to examine spatial segregation of stems by dbh. The lack of positive spatial autocorrelation in dbh values would indicate that small and large dbh values, indicating saplings and adults, were interspersed in a pattern not significantly different than random. Statistically significant positive spatial autocorrelation was present in large dbh values, labeled as adults, in several locations at each of the three sites. These clusters can be interpreted as adult stems surrounded by other adult stems without saplings nearby and so indicate a lack of sapling establishment of *Quercus lobata* in these locations. Two of the sites, CHE and MAC, also contain statistically significant positive spatial autocorrelation in low dbh values, which indicate saplings with other nearby saplings but with few adult stems nearby. Overall, these results confirm the presence of at least some clusters, or spatially segregated groups of large and small dbh stems, that we interpret as evidence of shifting patterns of regeneration.

We interpret the stronger clustering of saplings at CHE and MAC, compared with PAR, as evidence indicating a spatial shift in establishment sites toward less common riparian corridors and northeast-facing slopes and a geographically uneven distribution of habitat within these sites, which essentially forces clustering. Although there is some evidence of this spatial shift and clustering at PAR as well, the weaker clustering and lack of spatial autocorrelation in low dbh values reinforce the suggestion by Hayes and Donnelly (2014) that PAR may have greater water availability, likely due to upstream urban runoff, providing more habitat for sapling establishment and maintaining a less intensely clustered community. By contrast, CHE and MAC have less surface water and likely have lower water tables due to groundwater withdrawal associated with household water wells (predating state water projects), decreasing the relative area of high-quality habitat with available soil moisture for sapling recruitment and groundwater for long-term survival (Hayes and Donnelly 2014).

As the climate warms and dries, and as surface water availability continues to decrease, sapling establishment will be increasingly segregated to fewer areas of optimal habitat, with smaller, more recently recruited adults clustered in the most optimal habitat. The adult population at CHE, which is the most mature of the stands and has the largest individuals, is already experiencing a decrease in crowding as fewer individuals are left in the landscape, even as saplings and adults are increasingly limited to only a narrow riparian corridor there (Hayes 2013). The loss of older, larger trees is consistent with trends of structural change seen in central and southern coast regions of California more broadly (Pearse et al. 2014; McIntyre et al. 2015), especially at CHE and MAC, where individuals are being lost from the savannah habitat without replacement. All of our analyses suggest greater or more intense clustering of saplings than of adults and may be associated with a shift from open habitats to riparian corridors and hillsides for both saplings and adults. By contrast, sapling recruitment at PAR is relatively spread out and clustering values are low in contrast with CHE and MAC (although still clustered and crowded on the basis of I_M and I_{Mr}, respectively), and a wide range of adult size classes are persisting long enough at PAR that clustering slightly exceeds levels at CHE for quadrat sizes ≥75 m × 75 m.

Quercus lobata is a foundation species in many communities where it is found, accounting for much of the biomass, physical structure, and energy and material fluxes in the system; it accordingly has complex functional relationships with many other plant and animal species and plays a role in ecosystem organization and regulation (Ellison et al 2005). Changes in the *Q. lobata* community seen at CHE and MAC, trending toward more open grasslands and denser riparian woodland, are in agreement with the findings of McMahon et al. (2015), who found such changes to be associated with changes in acorn woodpecker populations along with changes in the population structure of other oaks occupying their study sites. Changes in oak forest and savannah communities have been linked to the spread of pathogens as well as to nonnative species (Jones et al. 1998; Cobb et al. 2010), invertebrate diversity and abundance (Wetzel et al. 2016), and nutrient fluxes (Cobb et al. 2013). As *Q. lobata* becomes less common and more isolated, shifting from savannah to woodland, other parts of the ecosystem may be increasingly affected, and they are likely already experiencing changes in their ecology and function (Ellison et al. 2005; McMahon 2015).

Although PAR has relatively high establishment of saplings compared with many *Q. lobata* sites across California and appears to be exhibiting greater stability in its tree community structure, it should not necessarily be interpreted as an example of successful *Q. lobata* conservation. Conditions at PAR make this site perhaps the most precarious in terms of ecological stability and function. As the climate continues to become warmer and drier, and as urban water importation and usage patterns change, the pace and degree of effects on *Q. lobata* at PAR are unknown. Future changes at PAR in particular may be useful to shed light on how changes in the socioecological land system affect *Q. lobata* stands and their community ecology.

Additional work at these sites should focus on how changes in *Q. lobata* stand structure and spatial pattern, as well as the shift from savannah to grassland and to denser riparian wood-

land, are affecting other species and ecological processes. Acorn woodpeckers, scrub jays, and several raptors are conspicuous avian species that may be affected by changes to *Q. lobata* stands at the sites investigated here as well as other sites. The links between *Q. lobata* stand characteristics, evapotranspiration, water availability, and the local water table are also in need of additional research to better understand the resilience and sustainability of *Q. lobata* landscapes.

Acknowledgments

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