

Historical interactions are predicted to be disrupted under future climate change: The case of lace lichen and valley oak

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Funding information

National Geographic Award to VLS and SW; UCLA Life Science Funds; the Icelandic Research Fund, Grant/Award Number: 120247021; the Swiss National Foundation, Grant/Award Number: PBBEA-111207; National Natural Science Foundation of China, Grant/Award Number: 41601061; National Science Foundation, Grant/Award Number: DEB-0089445, DEB-0516529; the European Commission within FP7, Grant/Award Number: LICHENOMICS

Editor: Lyn Cook

ABSTRACT

Aim: The distributions and interactions of co-occurring species may change if their ranges shift asymmetrically in response to rapid climate change. We aim to test whether two currently interacting taxa, valley oak (*Quercus lobata*) and lace lichen (*Ramalina menziesii*), have had a long-lasting historical association and are likely to continue to associate in the future.

Location: Central western California, western United States of America

Methods: Using population genetic analyses and MAXENT software for ecological niche modelling, we estimate species' distributions during the Last Interglacial, the Last Glacial Maximum, present, and future periods. Mantel and vertex (genetic connection) tests were used to examine the spatial congruence among taxa. To compare the modelled response to climate change, we estimated migration speed between respective time periods using vector analysis.

Results: We found significant genetic congruence between valley oak and the lichen's green algal photobiont, independent of geographic isolation and habitat isolation, which is consistent with long-term association. Ecological niche models under past and future climate scenarios indicate that overlap of climatic niche sharing between valley oak and lace lichen might decrease in the future. Our models indicate that the speed of shifts in climate niches between these two taxa differed significantly in past periods from that of the present period.

Main conclusions: Our findings reveal that historical interactions between valley oak and lace lichen correlate with long-term sharing of past climate niches. However, the future association of lace lichen with valley oak may be disrupted in parts of its current distribution due to differential discordance of climate niche shifts, species' movements and generation times. This study illustrates the processes and patterns that allow long-term association during historic climate change and how they are likely to change during rapid climate change.

KEYWORDS

climate change, co-occurrence, ecological niche modelling, migration, *Quercus lobata*, *Ramalina menziesii*

1 | INTRODUCTION

Climate change is having a clear impact on the distribution of many organisms and on the species composition of numerous ecosystems (Ellis, Coppins, Dawson, & Seaward, 2007; Parmesan, 2006; Peñuelas & Filella, 2001; Root et al., 2003; Walther et al., 2002). Species can respond in only a few ways to climate change—individuals can acclimate or move locations, and populations can adapt or become extirpated (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008). The net outcome can modify the size and distribution of populations due to local extinctions and shifts in altitudinal or latitudinal range in response to warming (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008). Because individual species vary greatly in their ability to acclimate or adapt to the climate due to differences of life history traits (Aitken et al., 2008; Chen et al., 2011), these unequal rates of shifts in distribution may also disrupt the association of co-occurring species over time (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Comes & Kadereit, 1998; Hewitt et al., 2015; Overpeck, Webb, & Webb, 1992).

Historically, the species composition of plant communities changed with climate shifts (e.g., Jackson et al., 2014; Seddon, Macias-Fauria, & Willis, 2014) as new associations were formed (e.g., Webb, 1986) and old interactions have disappeared (e.g., Williams, Shuman, & Webb, 2001; Williams et al., 2013)—many due to dissimilar responses among species to climate changes. Palaeoecological studies, which have used fossil and pollen records to document the historical distribution of species, have shown that many sets of species that characterize communities today did not migrate together during postglacial range expansions (Davis, 1981). When climate change is gradual, species that benefit each other may be able to associate longer until opportunities for alternative favourable associations can emerge. In contrast, the current pace of climate change has the potential to alter interactions between species substantially but, because species responses to climate changes are variable, it will be difficult to predict future species interactions (Bertness & Ewanchuk, 2002).

The association of the epiphytic lace lichen and its phorophyte species, valley oak (*Quercus lobata*) and other oaks (*Quercus douglasii* and *Quercus agrifolia*), is conspicuous in oak-savanna and riparian oak ecosystems of California. Deciduous oak trees provide a habitat for the lichen with an open canopy in the winter that maximizes photosynthesis during the season when most of the annual rainfall, and most of the lichen annual growth, occurs (Matthes-Sears & Nash, 1986). Oaks furthermore possess a shaded canopy during the hot summer and provide early morning dew that can be absorbed by the lichen. Lace lichen provides nutritional benefits to the trees by absorption of water and nutrients and their deposition beneath the tree (Boucher & Nash, 1990; Knops, Nash, & Schlesinger, 1996). The lace lichen is a mutualistic symbiosis between a lichen-forming fungus and photosynthetic green algae (mainly *Trebouxia decolorans*, Chlorophyta).

Valley oak (Gugger, Ikegami, & Sork, 2013) and lace lichen (Sork & Werth, 2014) have had relatively stable distributions through the glacial and interglacial cycles throughout their respective ranges. Prior work using population genetic approaches suggests that lace lichen has a much greater dispersal potential (Sork & Werth, 2014; Werth & Sork, 2008) than valley oak (Grivet, Robledo-Arnuncio, Smouse, & Sork, 2009; Grivet, Smouse, & Sork, 2005; Pluess et al., 2009; Sork, Smouse, Grivet, & Scofield, 2015; Sork et al., 2010), but palaeoecological records suggest that oaks may have greater dispersal potential than indicated by genetic studies (Clark et al., 1998; Feurdean et al., 2013). The extensive latitudinal range of lace lichen (*Ramalina menziesii*), which occurs from Baja California desert ecosystems continuously through regions of western North America and Alaska, suggests a broad range of climate tolerance (Sork & Werth, 2014; Werth & Sork, 2014). In contrast, *Q. lobata* is found only in unglaciated regions of California, mostly along the foothills of the Coast Ranges and Sierra Nevada surrounding the Central Valley.

The study system of valley oak, *Q. lobata*, and the epiphytic lace lichen, *R. menziesii*, with its fungal and algal symbionts, provides a unique opportunity to study the dynamics of response to gradual and rapid climate change. Given that the two taxa share a climate niche where they currently co-occur, we might expect that they have had a long-term association in the past, which may or may not continue in the future under the current rapid rate of climate change. If oaks and lace lichen have different rates of migration in response to previous climate conditions, then their current co-occurrence may be ephemeral and a future association may be unlikely. The goals here are to estimate the patterns and processes of their historic co-occurrence and to assess whether their association will continue with predicted rapid climate warming through three specific objectives. First, we test for congruent phylogeographic patterns between lace lichen and valley oak, as evidence of parallel historical demographic responses to historical climate change. Second, we model past Last Interglacial (LIG) and Last Glacial Maximum (LGM) distributions of their climate niches to see whether a long-term association in the past could have been likely, and then model future niche distributions to see whether this association might continue with predicted climate change. Third, to understand whether migration ability is asymmetric, which could disrupt their association, we compare the inferred magnitude of response to climate change (hereafter migration speed: migration distance per year) in the two taxa from past to present and present to future.

2 | MATERIALS AND METHODS

2.1 | Sampling

Our study region includes the overlapping region of the distributions of *Q. lobata* and *R. menziesii*. For analyses of phylogeographic congruence, we used data previously collected from other studies of



Q. lobata (Gugger et al., 2013; Sork et al., 2010), *R. menziesii* (Sork & Werth, 2014; Werth & Sork, 2008), and *T. decolorans* (Werth & Sork, 2010, 2014). Within California, we excluded coastal sites where *Q. lobata* is not found and Sierra foothills localities where *R. menziesii* is not found. The final sample included 17 sites of co-occurrence (Figure 1; Supporting Information Table S1.1 in Appendix S1).

For *Q. lobata*, we included 79 individuals based on six nSSR loci (nuclear simple sequence repeats) and 48 individuals based on six cpSSR markers (chloroplast simple sequence repeats). For the lichen fungus *R. menziesii*, we included genotypes of 81 individuals, based on four unlinked nuclear genes (β -tubulin [*bet*], elongation factor 1- α [*efa*], glyceraldehyde 3-phosphate dehydrogenase [*gpd*], and an unidentified locus similar [*e*-score 5×10^{-117}] to glycine dehydrogenase [*uid*]). For the alga *T. decolorans*, we used 84 individuals genotyped for the nuclear ITS (internal transcribed spacers of nuclear ribosomal DNA) and 49 individuals genotyped for the chloroplast *rbcl* gene (ribulose-1,5-bisphosphate carboxylase oxygenase, RuBisCO). These eight molecular markers were listed in Supporting Information Table S2.1-2.8 respectively in Appendix S2. DNA sequences were aligned and edited in MEGA 5.0 (Tamura et al., 2011). Polymorphic sites of sequence data were binarized to 0 or 1 for congruence analyses.

2.2 | Phylogeographic congruence test between oak and lichen

To test the concordance among the genetic structure of *Q. lobata*, the fungus *R. menziesii*, and the photobiont *T. decolorans*, we performed a simple Mantel test, a partial Mantel test, and a spatial convergence test of similarity of vertex locations. Firstly, genetic correlations (simple Mantel test) among *Q. lobata*, the fungus *R. Menziesii*, and the photobiont *T. decolorans* were estimated based on Nei's genetic distance outputted from GENALEX 6.5 (Peakall & Smouse, 2012). To test whether genetic congruence between oak and lichen was the result of correlations controlled by shared isolation-by-distance (IBD) or isolation-by-environment (IBE), a partial Mantel test was also executed controlling for geographic distance and climatic suitability respectively. Climatic suitability was extracted from a MAXENT prediction based on current distribution (as below). IBD and IBE were also examined between genetic differences, geographic distance, and climatic differences using simple and partial Mantel tests through ZT software with 10,000 permutations (Bonnet & Peer, 2002).

Secondly, spatial convergence was estimated using Population Graphs (PopGraph), a network approach that analyses population

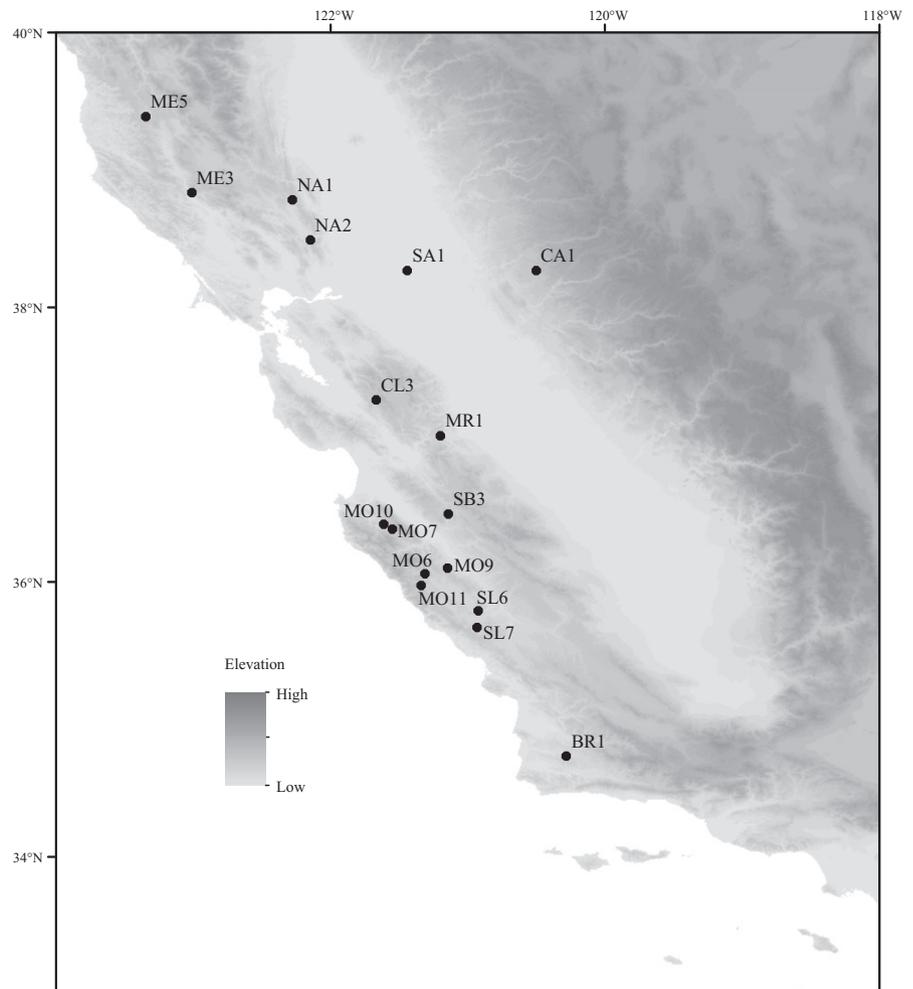


FIGURE 1 Co-occurrences and spatial location of sampling sites of valley oak and lace lichen

genetic data within a graph theoretic framework to create a network of exchanged migrants (Dyer & Nason, 2004). Because the congruence test relies on gene flow and similarity of vertex locations, PopGraph is a robust algorithm to test for the concordance between the spatial genetic variations of the co-distribution among species (Dyer, Nason, & Garrick, 2010; Widmer et al., 2012). The cumulative density function index (CDF) was used to measure “Structural Congruence”, i.e., the probability of having x number of edges in common in observed congruence graph is different from that in the expected congruence graph. Low CDF values indicate better congruence.

2.3 | Ecological niche modelling

We built ecological niche modelling (ENMs) using MaxEnt 3.4.0 (Phillips, Anderson, & Schapire, 2006) based on occurrence points for *Q. lobata* and *R. menziesii* (sources of these points were in Supporting Information Appendix S1). MaxEnt does not need absence data but requires background sampling data to build the model for evaluating model performance. Model background points are recommended to be drawn from areas where the species are well established and fill their environmental niches (Park et al., 2009; Phillips et al., 2009). We set a 500-km buffer from all occurrence points for both species and generated the model domain for this study (see Supporting Information Figure S3.1 in Appendix S3).

Climate prediction models are from WorldClim database (<http://www.worldclim.org>) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), representing 2.5 arc-minutes resolution for the LIG (c. 120–140 ka), the LGM (c. 21 ka), with present projection (1950–2000), and the future (2070) based on CMIP5 rcp85 scenario (high emission) and rcp26 scenario (low emission). Prior to modelling, we projected all climate layers (WGS84 datum) to Albers Equal Area Conic to maintain equal grid size and distance over the modelling domain, as we removed the duplicated occurrence points within a grid cell for bias correction (see below).

All ENMs were built using six variables related to temperature and precipitation. To test significance of model predictions, we tested the model's AUC (the area under the curve of receiver operating characteristic) values against a null model with random presence points (Raes & ter Steege, 2007). More details about selection of variables and running of MaxEnt are in Supporting Information Appendix S1.

To estimate niche sharing among species during each time period, we calculated the predicted overlap of niches between valley oak and lace lichen. Suitability of modelling layers was binarized using the threshold of maximum sensitivity plus specificity as this threshold produces the most accurate predictions in presence-only ENMs (Jiménez-Valverde & Lobo, 2007; Liu, Newell, & White, 2016). Niche overlap was calculated using the binarized layers with the ‘raster’ package in R (Hijmans, 2016).

2.4 | Climatic sensitivity

To compare the potential sensitivity of lichen and oak to climate change, we tested the hypothesis that the amount of migration needed in a given period of time based on the change in climate niche is less than or equal to the dispersal capacity of that species. Although we understand the dispersal of a species is restricted, due to the model limitation over geological time-scale, we assumed species could reach any location within the modelled domain. We estimated magnitude of climate change (i.e., estimated migration speed/migration distance per year) (V_M , units are m/year) based on the geographic shift in modelled suitable climates from the MaxEnt models. Here, the V_M is calculated as the time interval between two periods (years) divided by migration distance (m) within the time interval to yield the metres per year (m/year) shift in climate. Specifically, we defined 60-arcmin grid cells and calculated the geographic centroids of the modelled niche for every 60-arcmin grid cell above the threshold of maximum sensitivity plus specificity as outputted from MaxEnt. Then, we calculated the V_M between the centroids of past time and the nearest centroid of forward time (i.e., from LIG to LGM, LGM to present, and present to future). The nearest centroid is defined by the shortest distance over the earth's surface calculated with Haversine formula between given two locations. Nonparametric independent-samples Mann–Whitney–Wilcoxon tests implemented in R were used to test for differences in magnitude of climatic velocities (V_M) between taxa during the same period. V_M was compared to the “observed” migration speed (V_O) to assess whether species can track climate change through integrating with other available evidence.

For the oak and fungus *R. menziesii*, we assumed that V_O was determined by dispersal ability of seed or spore. For valley oak, the V_O has been estimated to be 350 m/generation based on empirical estimates of gene flow for this species (Dutech, Sork, Irwin, Smouse, & Davis, 2005; Grivet et al., 2005; Sork et al., 2010). V_O for valley oak is around 3.5 m/year based on a conservative mean generation time in oaks of 100 years (Gugger et al., 2013). As such information is not available for the green alga *T. decolorans* or for *R. menziesii*, we estimated the migration rate based on data from similar lichen species despite the limitation of having slightly different dispersal biology. The lichen species *Lobaria pulmonaria*, like *R. menziesii*, is epiphytic on trees and dispersed by propagules or sexual spores. A long-term study of the epiphytic lichen fungus (*L. pulmonaria*) found that the average dispersal distance was 35 m with a maximum distance of 75 m, within 9 years (Öckinger, Niklasson, & Nilsson, 2005). A field experiment suggested the maximum dispersal distance of propagules of *L. pulmonaria* from a source tree is c. 200 m within 7 days, but short dispersal distance of propagules for successful establishment of lichen thalli would also be expected, given the leptokurtic nature of dispersal (Werth et al., 2006). We treated the V_O of lichen as 35 m/year with a possible maximum of 75 m/year representing a rather conservative estimate in respect of average distance within 9 years.

3 | RESULTS

3.1 | Genetic congruence between lichen and oak

Both nSSR and cpSSR of *Q. lobata* showed congruence with *rbcL* of the algal photobiont of *R. menziesii* ($p < 0.05$) (Table 1). The Partial Mantel test suggested these significant correlations were independent from IBD and IBE ($p < 0.05$). The vertex test from PopGraph also revealed congruence between chloroplast inheritance of *Q. lobata* and chloroplast inheritance of the green algae (CDF ≈ 0.00). Moreover, genetic structure of *Q. lobata* exhibited significant IBD and IBE estimated from nSSR ($p < 0.05$). Significant IBD was revealed by simple Mantel test and partial Mantel test in the fungus ($p < 0.01$), suggesting IBD was not impacted by IBE. Significant IBD was not found for the green algae, but its genetic structure showed a slight association with climate ($0.05 < p < 0.10$). The highest degree of genetic congruence in networks was found for the chloroplast DNA of *Q. lobata* and chloroplast DNA of the green algae (Figure 2).

TABLE 1 Congruence test among oak and epiphytic lichen based on simple Mantel test (S), partial Mantel test (P), and vertex test (V). Partial Mantel test was controlled by geographic distance (geo) and climatic suitability (clim) respectively. Bold letters represent significant ($p < 0.05$) or marginally significant ($0.05 < p < 0.10$) correlations

Pairwise comparison	R_S	$R_{P(\text{geo})}$	R_P (climoak)	R_P (climlichen)	V (CDF ^a)
Oak _{nu} vs. Fungus _{nu}	-0.114	-0.024	-0.127	-0.119	0.403
Oak _{cp} vs. Fungus _{nu}	-0.014	-0.027	-0.013	-0.015	0.338
Oak _{nu} vs. Alga _{nu}	-0.190	-0.182	-0.144	-0.186	0.244
Oak _{nu} vs. Alga _{cp}	0.357*	0.342*	0.389*	0.374*	0.328
Oak _{cp} vs. Alga _{nu}	0.017	0.016	0.008	0.020	0.244
Oak _{cp} vs. Alga _{cp}	-0.177*	-0.175*	-0.180*	-0.178*	0.000
Oak _{nu} vs. geo	-0.224*	—	-0.211*	—	—
Oak _{cp} vs. geo	0.026	—	0.022	—	—
Fungus _{nu} vs. geo	0.413**	—	—	0.410**	—
Alga _{nu} vs. geo	0.058	—	—	0.071	—
Alga _{cp} vs. geo	-0.119	—	—	-0.109	—
Oak _{nu} vs. clim _{oak}	-0.259*	-0.248*	—	—	—
Oak _{cp} vs. clim _{oak}	0.046	0.044	—	—	—
Fungus _{nu} vs. clim _{lichen}	0.093	0.076	—	—	—
Alga _{nu} vs. clim _{lichen}	-0.196[#]	-0.200[#]	—	—	—
Alga _{cp} vs. clim _{lichen}	-0.205[#]	-0.200	—	—	—

“—” means no data.

^aCDF, the probability of having edges in common in observed congruence graph is different from that in expected congruence graph.

** $p < 0.01$, * $p < 0.05$, [#] $p < 0.10$.

3.2 | ENMs and climatic sensitivity

Ecological niche modellings for valley oak and lace lichen in their region of overlap performed well for present conditions (test and training AUC > 0.96 for both species). AUC values from two species are significantly higher than the null model by Wilcoxon rank sum test (null model AUC = 0.64, $p < 0.001$). The response curves from MaxEnt models showed unimodal distributions except the few parameters with low contributions suggesting that overfitting is not an issue in our results (see Supporting Information Figure S3.3 in Appendix S3). Valley oak and lace lichen likely shared climate niches to the highest degree in the western part of the California Central Valley during the LIG and present (Figure 3a,c). However, their overlapping niche ranges were estimated to have been reduced in the western California Central Valley during the LGM (Figure 3b). In the near future, a northwards migration of the overlapping ranges is visible (Figure 3d, e and see Supporting Information Figure S3.4b,c in Appendix S3). Parts of overlapping ranges in the western part of California are predicted to disappear under the high emission scenario (Figure 3e). Compared with the observed distribution of valley oak and lace lichen (Figure 1 and see Supporting Information Figure S3.1 in Appendix S3), the prediction based on current conditions (Figure 3c) likely overestimated the overlapping ranges, but such overestimation had no impact on the interpretation.

Statistical analyses suggested that *R. menziesii* had significantly higher V_M than *Q. lobata* from the LIG to the LGM (CCSM4: $V_{M,\text{oak}} = 0.17 \pm 0.07$ m/year, $V_{M,\text{lichen}} = 1.06 \pm 0.18$ m/year, $p < 0.001$; MIROC: $V_{M,\text{oak}} = 0.19 \pm 0.07$ m/year, $V_{M,\text{lichen}} = 9.22 \pm 1.22$ m/year, $p < 0.01$; Table 2) and from the LGM to present (CCSM4: $V_{M,\text{oak}} = 3.33 \pm 1.04$ m/year, $V_{M,\text{lichen}} = 1.06 \pm 0.18$ m/year, $p < 0.01$; MIROC: $V_{M,\text{oak}} = 3.91 \pm 1.07$ m/year, $V_{M,\text{lichen}} = 13.57 \pm 1.84$ m/year, $p < 0.01$; Table 2). The V_O values of both oak (3.5 m/year) and lace lichen (35 m/year) are higher than or closer to the V_M estimates from the LIG to the LGM and from the LGM to present. However, from the present to future time periods, the geographic location of the match to the niche of valley oak ($V_{M,\text{oak}} > 200$ m/year) is shifting faster than that of the lace lichen ($V_{M,\text{lichen}} > 60$ m/year) under both low-emission and high-emission models (Table 2). The V_O values of valley oak and the conservative V_O of lace lichen are both lower than the V_M from present to future, indicating valley oak and lace lichen may not keep pace with current climate change.

4 | DISCUSSION

The lace lichen and valley oak populations exhibit strong evidence of a long-term historic association in the Californian oak ecosystems of our study. Genetic markers reveal significant spatial genetic congruence between valley oak and lace lichen, which implies that they were most likely co-distributed historically. Specifically, significant congruence was found between valley oak and the lace lichen photobiont, a pattern that likely reflects the historic association of this lichen with valley oak in California, while in symbiosis with

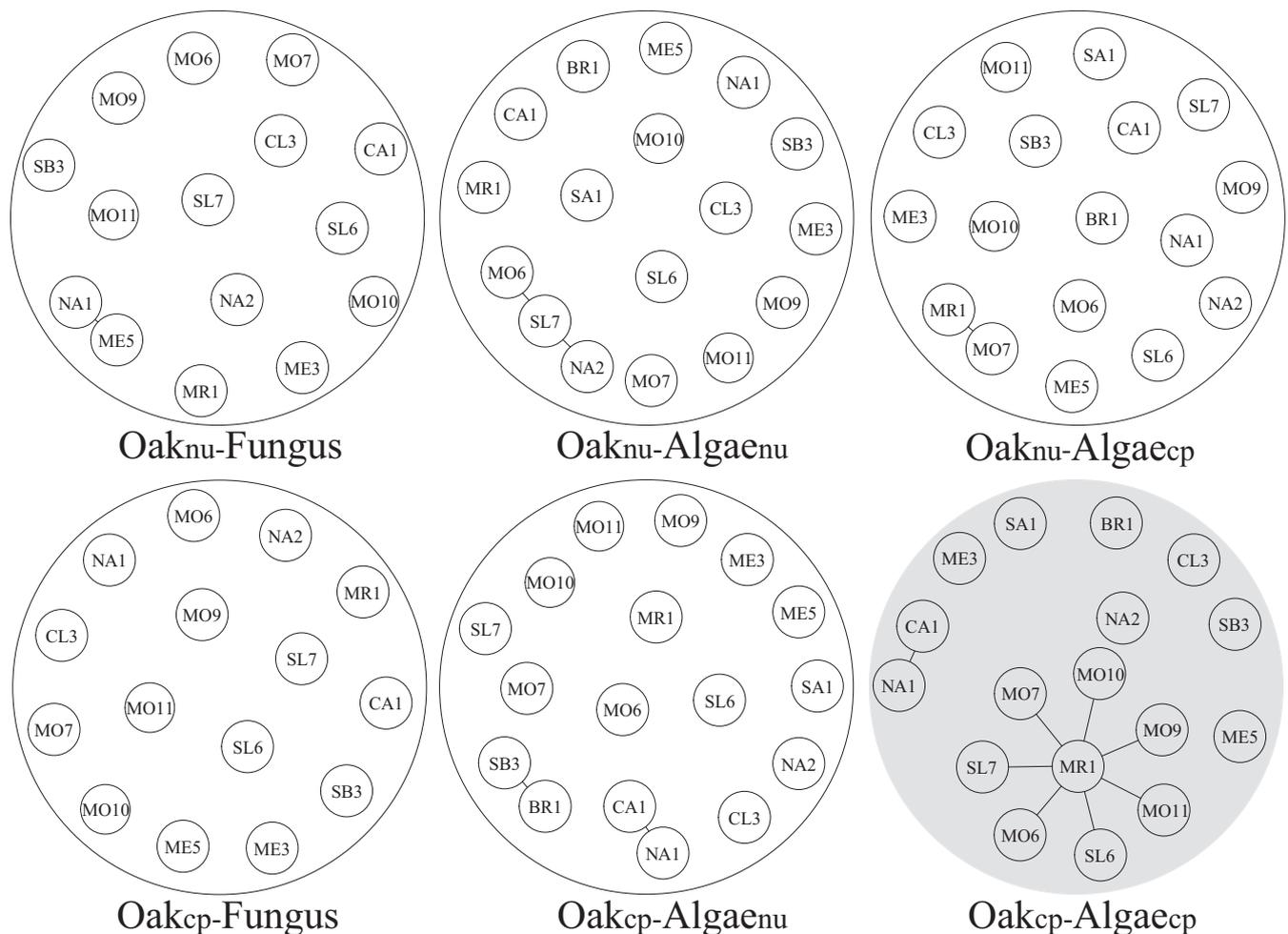


FIGURE 2 Population connectedness patterns among valley oak, fungus, and algae. These patterns were estimated from valley oak (*Quercus lobata*) nuclear (Oak_{nu}) and chloroplast genetic (Oak_{cp}) markers, fungal (*Ramalina menziesii*) nuclear genes (Fungus), and algal (*Trebouxia decolorans*) nuclear (Algae_{nu}) and chloroplast (Algae_{cp}) markers. Obvious genetic congruence (CDF in Table 1) is indicated by grey background

R. menziesii or with other species of lichen-forming fungi. In addition, ENMs indicate that valley oak and lace lichen have had overlapping climate niches in the past that could have made a long-term association possible. In contrast, these species may not retain their association in the future, due to differences in dispersal abilities and rates, differential sensitivities to climate change, and different generation times. The future asymmetry seems to be due to the more rapid rate of climate change than in the past.

4.1 | Genetic congruence

Species distribution patterns at the scale of California are likely to be shaped by natural selection, vicariance events, and isolation by distance (Lapointe & Rissler, 2005). These forces suggest that gene movement of taxa with similar dispersal ability would present similar genetic structures, but co-occurrence would also result in shared effects from other processes. For the lace lichen and valley oak, it seems that their genetic congruence reflects a long-term association

that is shaped by the movement of the oak. We found the strongest congruence between algal chloroplast and both oak markers. Because the chloroplast marker of valley oak is maternally inherited and the photobiont (*T. decolorans*) is haploid, their respective genetic markers both provide evidence of dispersal and colonization processes, which contribute to the genetically congruent patterns of the two taxa.

Genetic congruence related to dispersal and colonization was also likely to have been influenced by shared environments. We found significant isolation by environment detected in oak and algae but not in the fungal genome of *R. menziesii* (Table 1). Previously, for valley oak, we found the distribution of genetic variation to be associated with climate variables, as well as gene movement and demographic history (Gugger et al., 2013; Sork et al., 2010). For the epiphytic lichen, the fungus has a high dispersal ability mediated by meiotic ascospores (Werth & Sork, 2010) but its establishment relies on the presence of an algal photobiont, *T. decolorans* or, sometimes, *T. sp. nr. jamesii*. Because genetic congruence between algae and oak was not controlled by the differences

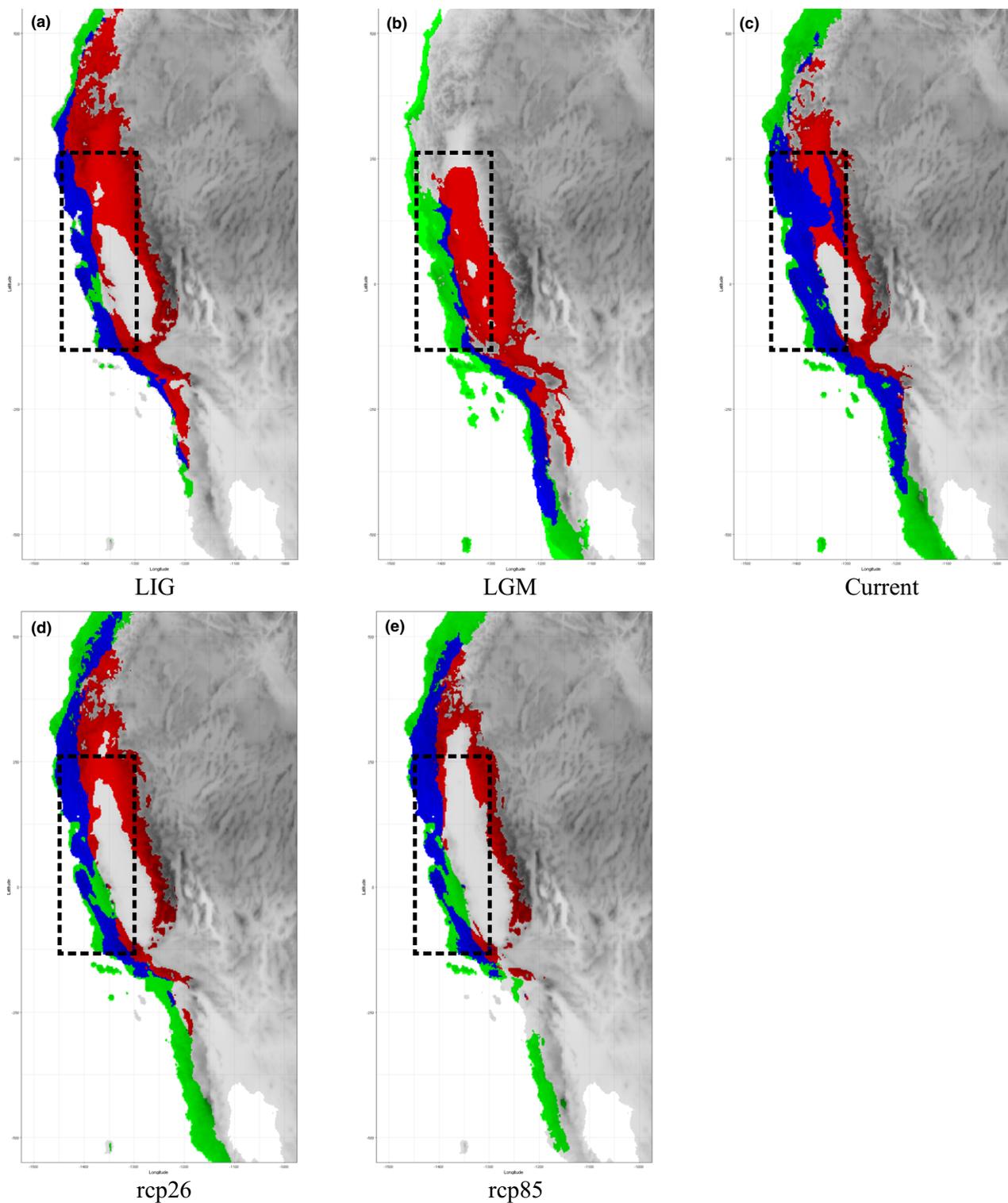


FIGURE 3 Predicted distribution ranges of lace lichen and valley oak under the Last Interglacial (LIG, (a), the Last Glacial Maximum (LGM, (b), at current (c), and in 2070 under rcp26 (d) and rcp85 (rcp85, e). Green: predicted range of lace lichen; Red: predicted range of valley oak; Blue: predicted range of co-occurrence of both species. Squares indicate overlapping range of samples. LGM, rcp26, and rcp85 based on MIROC model. Results of CCSM4 model are in Supporting Information Figure S3.4 in Appendix S3

of geography and habitat, we infer that the tight association between these taxa was influenced by the dispersal limitation of valley oak. Similar congruence was reported in plant-insect

interactions with the explanation that the demographic history of a beetle can be constrained by a limited-dispersal plant (Garrick, Nason, Fernández-Manjarrés, & Dyer, 2013).

TABLE 2 Comparisons of estimated migration speed (V_M) of oak and epiphytic lichen among different glacial periods, using two climate models (see text for description). Mean V_M (m/year) was calculated with SE. N is the number of centroids (modelled populations). The Mann–Whitney–Wilcoxon test was used to test the null hypothesis of equal migration speed

Migration models ^a	Migration time	Mean $V_M \pm SE$		Mann–Whitney–Wilcoxon test p
		Oak	Lichen	
LIG→LGM _{CCSM4}	120,000 years	0.17 ± 0.07 ($N = 37$)	1.06 ± 0.18 ($N = 64$)	***
LIG→LGM _{MIROC}		0.19 ± 0.07 ($N = 34$)	1.21 ± 0.25 ($N = 58$)	**
LGM→Present _{CCSM4}	21,000 years	3.33 ± 1.04 ($N = 49$)	9.22 ± 1.22 ($N = 103$)	**
LGM→Present _{MIROC}		3.91 ± 1.07 ($N = 49$)	13.57 ± 1.84 ($N = 103$)	**
Present→Future _{rcp26_CCSM4}	70 years	228.93 ± 86.71 ($N = 49$)	60.51 ± 29.82 ($N = 105$)	*
Present→Future _{rcp85_CCSM4}		374.18 ± 109.47 ($N = 58$)	78.64 ± 34.46 ($N = 101$)	**
Present→Future _{rcp26_MIROC}	70 years	214.86 ± 77.43 ($N = 49$)	69.07 ± 33.96 ($N = 92$)	*
Present→Future _{rcp85_MIROC}		256.7 ± 105.82 ($N = 46$)	66.19 ± 37.67 ($N = 72$)	#

^aCCSM4 (Community Climate System Model Version 4); MIROC (Model for Interdisciplinary Research On Climate).

*** $p < 0.01$, * $p < 0.05$, # $p < 0.10$.

4.2 | Historical and future niches and climatic sensitivity

Our niche modelling predicts that valley oak and lace lichen have exhibited variable co-occurrence from the LIG to present (Figure 3). The area of overlapping climate niches is predicted to have reduced in size in western central California during the LGM compared with predictions of presence at the LIG and the present. Although the spatial association between valley oak and lace lichen might have been disrupted during the LGM, genetic congruence was maintained. In response to glaciation, valley oak could have moved to the lowland of the California central valley and lace lichen could have moved to the lowland next to the coast (Figures 1 and 3 and see Supporting Information Figure S3.1 in Appendix S3). During the LGM, the climate was colder than during the LIG or at present time (Kukla et al., 2002), however, during the warmer periods, valley oak and lace lichen may have come into contact in the highland of the western ranges of the California central valley where the two taxa could share a common microclimate. Likely, because both taxa could track the climate shifts from the LIG to the LGM and from LGM to present, genetic congruence shaped by past co-occurrence could be retained to the present, despite their significant differences in migration speed V_M (Table 2).

Phylogeographic studies provide evidence that the association of the two taxa began during the late Pleistocene. Sork and Werth (2014) estimated divergence of *R. menziesii* lineages in the western central California to have occurred during the late Pleistocene (95% HPD: c. 63,000–571,000 years ago). Lineages of *Q. lobata* also diverged during the late Pleistocene (95%HPD: c. 28,000–1,622,000 years ago) (Gugger et al., 2013). Thus, establishment of co-occurrence between valley oak and lace lichen accompanied by climatic fluctuations probably occurred about c. 63,000–571,000 years ago. In addition, species niche modelling predicts sharp contraction of range overlap during the LGM, but expansion of overlap since then. This interpretation is supported by population genetic analysis that

also indicated population expansion from the LGM of *Q. lobata* (Gugger et al., 2013) and *R. menziesii* (Sork & Werth, 2014).

Future migrations of oak and lace lichen might not be synchronous. We found that estimated migration speeds ($V_{M_oak} > 200$ m/year and $V_{M_lichen} > 60$ m/year) of the two taxa based on predicted future climate shifts (Table 2) will be faster than their observed migration speeds ($V_{O_oak} > 3.5$ m/year and $V_{O_lichen} > 35$ m/year), especially for valley oak. This result could mean that the ability to acclimate to rapid climate change may not be matched by the dispersal ability to arrive at new sites. For the lichen, it depends on the estimate of V_O . If the conservative estimate of 35 m/year is correct, then the lichen will not be able to keep up with climate change. Meanwhile, valley oak must first establish from seed at a new place with similar habitat where the initial isolation of individuals in newly colonized sites may hinder future reproduction and jeopardize the survival of valley oak (Sork et al., 2002). For valley oak to keep pace with the rapid climate change, it must have a high rate of colonization. In addition, long generation time of oak (the conservative estimation is 100 years, larger than the time of rapid future climate change) (Gugger et al., 2013) and lichen (>35 years) (Scheidegger & Goward, 2002) will hamper the ability of these two taxa to adapt to future climate change in a short time.

The future of lace lichen as a species does not necessarily require valley oaks or blue oaks, given that it can be found across many ecoregions of western North America and on different phorophyte species unique to each ecoregion (Sork & Werth, 2014). However, the continued presence of lace lichen in California inland regions may require rapid evolution to a new phorophyte. In addition, climate change may threaten the distribution of *R. menziesii* for other reasons. Living and dispersing lichens need moisture in the form of winter rainfall and frequent fog (Sork & Werth, 2014). Rapid warming will likely reduce the fog frequency (a factor difficult to model and not considered in our niche models) and increase the drought climate in California (Johnstone & Dawson, 2010), and is thus likely to cause further decline in lace lichen populations.

Our study follows the general pattern that predicted response of plant species to climate change is individualistic, and the predicted time, rate, and direction of spread of species are variable (Comes & Kadereit, 1998). Nonetheless, under historic rates of climate change, interacting species could co-occur for long periods of time. Under rapid future climate change, biotic interactions and the ecological networks may likely be disrupted more quickly (Lenoir et al., 2008). In the case of valley oak and the lace lichen, we predict that rapid ongoing climate change will create differential patterns in habitat shift and migration speed, disrupting their co-occurrence in their future ranges, eventually leading to a breakup of historically developed genetic congruence.

5 | CONCLUSIONS

This study illustrates the complex ways in which the distribution of two taxa could shift as a result of rapid climate change, disrupting interactions. Integrating phylogeographic analyses with ENMs, we showed that these two historically and contemporarily co-occurring species are unlikely to co-occur in the future. The predicted rate of climate change is likely to disrupt these species' future association because it exacerbates the gap in generation time and differential dispersal abilities of the two taxa. The predicted disruption of these two taxa is probably typical of many sets of interacting species and, in each case, it will be difficult to predict its impact on the future population dynamics for the involved taxa.

ACKNOWLEDGEMENTS

The following provided highly appreciated locality information for *R. menziesii*: S Altermann, D Baltzo, M Cody, J Delgadillo, K Dillman, K Glew, T Goward, K Knudsen, J Larson, J McIntosh, B Poulsen, P Raggio, D Reynolds, P Rundel, and S Tucker. Funding was provided by a National Geographic Award to V.L.S. and S.W., postdoctoral fellowships from the Swiss National Foundation (PBBEA-111207) and the European Commission within FP7 (LICHENOMICS), and the Icelandic Research Fund (120247021) to S.W.; a UCLA Senate research award, UCLA Life Science funds, and National Science Foundation awards (DEB-0089445; DEB-0516529) to V.L.S.; the National Natural Science Foundation of China (41601061) to J.L.Z. We thank Rodney J. Dyer for his help with the program PopGraph. We acknowledge the stewardship of the Native American nations for protecting the natural resources of western North America, allowing this work to be done. We also acknowledge the University of California Natural Reserve System, and the following Field Stations: Sedgwick Reserve (UC Santa Barbara), Hastings Natural History Reservation (UC Berkeley), Angelo Coast Range Reserve (UC Berkeley), McLaughlin Natural Reserve (UC Davis), Quail Ridge Reserve (UC Davis), and Landels-Hill Big Creek Reserve (UC Santa Cruz). The following agencies granted collecting permits to us: California State Parks, Channel Islands Natl. Park, Point Reyes Natl. Seashore, and Natural Reserve System (NRS) of University of California.

CONFLICT OF INTEREST

The authors have no conflict of interest.

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BIOSKETCHES

Jian-Li Zhao's research interests focus on plant population genetics at different spatio-temporal and phylogenetic scales. Common research interests of authors include plant evolutionary biology, phylogeography, and biogeography.

Author contributions: J.L.Z and V.L.S. developed the focus, subsampled existing data sets, conducted data analysis, and prepared manuscript. V.L.S. and S.W. designed the larger project and collected samples. S.W. generated gene sequences and contributed to manuscript preparation. M.I. provided distribution models and prepared manuscript. P.F.G. collaborated on data analysis and manuscript preparation. All authors read and approved the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Zhao J-L, Werth S, Ikegami M, Guger PF, Sork VL. Historical interactions are predicted to be disrupted under future climate change: The case of lichen and valley oak. *J Biogeogr.* 2018;00:1–11. <https://doi.org/10.1111/jbi.13442>