Potential Effects of Sudden Oak Death on the Oak Woodland Bird Community of Coastal California[1]

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Abstract

Oak-dependent birds are expected to suffer severe population declines as a result of sudden oak death (SOD). We investigated how the disappearance of two highly SOD-sensitive tree species, tanoak (*Lithocarpus densiflorus*) and coast live oak (*Quercus agrifolia*), may in turn affect levels of bird species richness, diversity, and equitability in coastal oak habitats of California. Combining avian census data from Audubon Christmas Bird Counts and North American Breeding Bird Surveys with oak distributional data from the California Gap Analysis, we use the statistical relationships between bird community indices and oak species diversity and areal extent to quantify expected bird responses to SOD while assuming complete loss of *Q. agrifolia* or *L. densiflorus* and complete, partial, or no loss of oak habitat. Additionally, we combine existing *Phytophthora ramorum* locality data with estimates of temperature, precipitation, and seasonality to model the potential distribution of SOD. Results suggest that species richness, diversity, and equitability of oak-dependent birds will decline by 5 to 15 percent in areas where SOD eliminates either tanoak or coast live oak. According to the spatial disease model, these declines are expected over 10,130 km^2, or 24 percent of the combined California ranges of *Q. agrifolia* and *L. densiflorus*. Although the overall influence of SOD on the statewide avian community is likely to be modest, bird losses are predicted to be relatively great for central regions already harboring the disease and, following a slight southward expansion of *P. ramorum* into San Luis Obispo and Santa Barbara counties, within neighboring oak habitats that will potentially suffer SOD mortality in the near future.

Key words: California birds, *Phytophthora ramorum,* sudden oak death, *Quercus agrifolia, Lithocarpus densiflorus,* anthropogenic climate change

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Introduction

Sudden oak death (SOD) threatens to reduce or eliminate several species of oaks (family Fagaceae) endemic to the west coast of North America. Since its detection in 1995, SOD has caused significant mortality of coast live oak (*Quercus agrifolia*) and tanoak (*Lithocarpus densiflorus*) within primarily coastal areas of central California (Garbelotto and others 2001, Rizzo and others 2002, Swiecki and Bernhardt 2002) (*fig. 1*). The disease is caused by the fungus-like pathogen *Phytophthora ramorum* and promotes the rapid development of bleeding bark cankers and foliar pigment degeneration in mature trees, often resulting in tree death (McPherson and others 2002, Rizzo and Garbelotto 2003). Known mortality from SOD is recent and thus the wildlife impacts remain largely unknown (CalPIF 2002).

Here we develop regression models for estimating the effects of SOD on the California oak woodland bird community. Birds are particularly useful indicators since excellent survey databases are readily available for both wintering and breeding populations. The most extensive of these are the Audubon Christmas Bird Count (CBC) and North American Breeding Bird Survey (BBS), both of which have been used extensively and highly successfully to study avian distribution and abundance (Bock and Root 1981, Root 1988, Price and others 1995, Koenig 1998), as well as model the population-level effects of SOD on certain California birds (Monahan and Koenig [In press]). Our approach here estimates SOD impacts using these two independent datasets whose seasonal timing and methodologies are quite different and thus to some degree complementary.

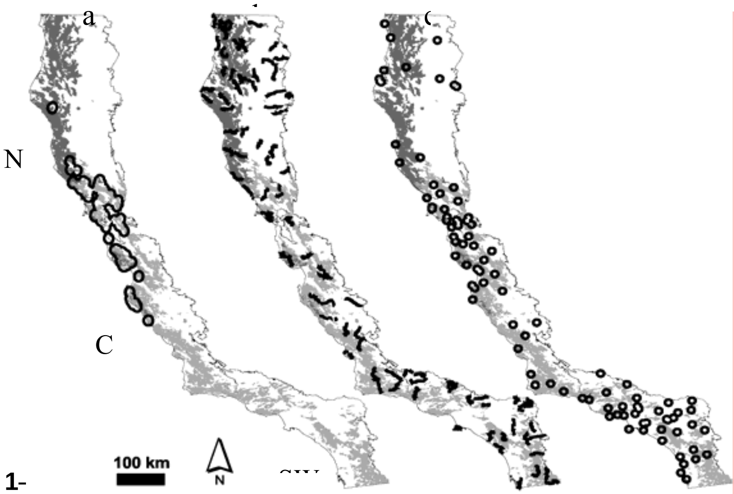

Figure 1- d locations of BBS routes (b) and CBC circles (c) used in the present study. Maps of a, b, and c as well as the California distributions of *Q. agrifolia* (light gray) and *L. densiflorus* (dark gray) are all bounded by three Jepson ecological regions (Northwestern-NW, Central Western-CW, and Southwestern-SW).

In this study we 1) use the statistical relationships between major avian community indices (species richness, diversity, and equitability) and oak species diversity and areal extent to quantify expected bird responses to SOD while assuming complete loss of *L. densiflorus* or *Q. agrifolia* and complete, partial, or no loss of associated oak habitat, 2) map the predicted bird responses in geographic space, and 3) consider their spatial associations to climatic SOD models developed using existing *P. ramorum* point occurrence data.

Methods

Data overview

In order to focus on birds most likely to be affected by the loss of oaks and avoid problems associated with habitat diversity within sites, analyses were restricted to 16 oak-affiliated year-round resident bird species: acorn woodpecker (*Melanerpes formicivorus*), Nuttall's woodpecker (*Picoides nuttallii*), black phoebe (*Sayornis nigricans*), Hutton's vireo (*Vireo huttoni*), Steller's jay (*Cyanocitta stelleri*), western scrub-jay (*Aphelocoma californica*), chestnut-backed chickadee (*Poecile rufescens*), oak titmouse (*Baeolophus inornatus*), common bushtit (*Psaltriparus minimus*), brown creeper (*Certhia americana*), western bluebird (*Sialia mexicana*), wrentit (*Chamaea fasciata*), California thrasher (*Toxostoma redivivum*), rufous-sided towhee (*Pipilo maculatus*), California towhee (*Pipilo crissalis*), and dark-eyed junco (*Junco hyemalis*). These species were chosen for their high dependence on oak habitats for survival and reproduction (Grinnell and Miller 1944, Pitelka 1951, American Ornithologists' Union 1957, Verner 1979, American Ornithologists' Union 1998, Koenig and Haydock 1999, Cicero 2000).

Three common indices were used to characterize diversity of this oak-dependent avian community. These included richness (number of species counted during the survey; maximum = 16); Shannon's diversity index $H = -\sum p_i \ln p_i$, where p_i = the proportion of the ith species; and Shannon's equitability index $E_H = H / \ln S$, where S is the total number of species found (species richness). The minimum value for H is 0 but it is otherwise unbounded; E ranges from 0 to 1 and is a measure of how evenly the numbers of the different species observed are distributed, with 0 being the most skewed (almost all individuals of one species) and 1 being most even (the same number of all species observed) (Magurran 1988, Rosenzweig 1995).

Bird distribution and abundance data were obtained from Audubon Christmas Bird Counts (CBC) (Butcher 1990) and the North American Breeding Bird Survey (BBS) (Sauer and others 2003). A single CBC involves between a few and over 100 people counting all the birds they can during a single day within the last two weeks of December within a 24 km diameter circle (total area approximately 450 km^2). Sites are usually centered on some geographic landmark and are in many cases surveyed year after year. CBC analyses utilized data from the 38 years, 1960 to 1997, inclusive. Breeding Bird Surveys consist of 3-minute censuses at a series of 50 stops, 0.8 km apart, conducted once during the breeding season along a road transect. BBS data used spanned 37 years from 1966 to 2002; we included recent survey data since only a handful of sites were associated with areas where SOD symptoms continue to develop. For each BBS or CBC site surveyed, bird community indices were calculated using only the 16 oak-associated species. For the CBC data, community measures were correlated with effort (party hours). The closest linear relationship between these measures and effort was achieved when dividing indices by the log-transformed number of party hours, thus all CBC estimates were divided by this value. For both BBS and CBC data, average values per site were then calculated by determining mean indices across all years during which a particular circle or route was surveyed.

In order to control for major habitat differences between census sites, we only considered CBC circles and BBS routes occurring within the Jepson ecological regions (Hickman 1993) bounding the complete distributions of *Q. agrifolia* or *L. densiflorus* (*fig. 1*). This effectively excluded large portions of the state devoid of either oak species. Analyses thus involved 60 CBC circles and 56 BBS routes intersected with the Northwestern (NW), Central Western (CW), and Southwestern (SW) California Jepson regions.

Distributional data for California oaks were determined from the California Gap Analysis Project (GAP) (Davis and others 1998). These data are 80 percent accurate (with 95 percent confidence) to a spatial resolution of 100 ha (in other words, 1/450 of the area encompassed by a CBC circle or 1/40 of the length of a BBS route). Target species included *Q. agrifolia*, *L. densiflorus*, and seven other major tree oaks: California black oak (*Q. kelloggii*), canyon live oak (*Q. chrysolepis*), blue oak (*Q. douglasii*), Engelmann oak (*Q. engelmannii*), Oregon white oak (*Q. garryana*), valley oak (*Q. lobata*), and interior live oak (*Q. wislizenii*). Analyses thus considered all tree species of oaks in mainland California; shrub oaks were not included.

Geographic distributions were generated separately for *Q. agrifolia* and *L. densiflorus* occurring in the absence of all other focal oaks and for all possible combinations of 1, 2, and ≥ 3 additional oak species. Geographic overlap between *Q. agrifolia* and *L. densiflorus* is relatively small (approximately 900 km^2), and thus the effect of simultaneous loss of both species in the same areas was not explored. The maximum number of target oak species found within a particular CBC circle or BBS route was used to estimate oak species diversity. The proportion of the total CBC area or length of BBS route that included any of the species of oaks as determined by the GAP distributions was used as an estimate of oak areal extent. Spearman rank correlations considered the influence of oak species diversity and areal extent on the avian community indices.

Point occurrence data for *P. ramorum* were obtained from the California Oak Mortality Task Force archive (Kelly and Tuxen 2003). Climate data used in the analyses originated from WorldClim (Hijmans and others [In press]).

Estimating the effects of SOD on birds

In all cases, we assumed a reduction in oak diversity due to SOD and equivalence of *Q. agrifolia* or *L. densiflorus* with the other tree oak species. We then used three methods characterized by slightly different assumptions to estimate how SOD might affect California oak woodland birds through elimination of *Q. agrifolia* or *L. densiflorus*, differing according to the post-SOD projections of how much oak area would be retained after the disease sweep. Since the ultimate effects of SOD on oak habitats remain unknown, selected habitat loss scenarios were designed to bracket the range of expected outcomes.

In method one (M1), oak area was assumed to decrease by the amount initially occupied by either *Q. agrifolia* or *L. densiflorus*; that is, M1 assumed that there was no small-scale habitat overlap between the target species and any other oak species. In method two (M2), oak area was assumed to decrease by the average amount of area lost when oak diversity dropped by one focal tree species, where values were determined by averaging across all CBC sites or BBS routes minus one tree oak species (including *Q. agrifolia* or *L. densiflorus*, when initial oak species diversity > 1). Finally, in method three (M3), we assumed that there would be no change in oak area, except when oak diversity was limited to a single oak species, in which case the comparison was between sites containing only *Q. agrifolia* or *L. densiflorus* and sites containing no species of oaks, but still within the appropriate Jepson regions. This last method thus assumed complete habitat overlap between *Q. agrifolia* or *L. densiflorus* and other oak species.

We regressed oak woodland bird species richness, diversity, and equitability on oak species diversity and areal extent and calculated new values for oak areal extent under post-SOD conditions, that is, when oak diversity declined by one through loss of *Q. agrifolia* or *L. densiflorus*. We used these post-SOD values for oak species diversity (in other words, one less oak species in all cases) and oak habitat in conjunction with the regression coefficients to calculate post-SOD estimates for each bird index. We then weighted these predicted changes by the areas within California that would be affected by the loss of *Q. agrifolia* or *L. densiflorus* to estimate the total changes in bird species richness, diversity, and equitability expected following a disease sweep. Thus, values presented are estimates of the overall change in avian diversity that is expected to occur within the statewide tanoak and coast live oak geographic ranges.

Predicting the geographical extent of SOD

In all cases, we assume complete elimination of either *Q. agrifolia* or *L. densiflorus*. To determine the extent to which this is realistic over large spatial scales, we developed climatic models aimed at predicting the potential geographic range of *P. ramorum* and, by extension, SOD. Optimal infection of the California bay (*Umbellularia californica*) by *P. ramorum* requires 9 to 12 hr of leaf moisture and temperatures of 18 to 22 °C (Garbelotto and others 2003). Associated climate variables used in our models consisted of 19 measures of temperature, precipitation, and seasonality: 1) annual mean temperature, 2) mean diurnal range, 3) isothermality, 4) temperature seasonality, 5) maximum temperature of the warmest month, 6) minimum temperature of the coldest month, 7) temperature annual range, 8) mean temperature of the wettest quarter, 9) mean temperature of the driest quarter, 10) mean temperature of the warmest quarter, 11) mean temperature of the coldest quarter, 12) annual precipitation, 13) precipitation of the wettest month, 14) precipitation of the driest month, 15) precipitation seasonality, 16) precipitation of the wettest quarter, 17) precipitation of the driest quarter, 18) precipitation of the warmest quarter, and 19) precipitation of the coldest quarter. Climate data were obtained at 30 s resolution (approximately 1 km^2) for 32° 30' to 42° N and 124° 30' to 114° W.

We used a simple profile-matching algorithm (BIOCLIM) (Nix 1986, Busby 1991) to project into geographic space the association between existing pathogen localities and present-day climate. Analyses used the 19 climatic attributes of 183 confirmed *P. ramorum* localities rendered spatially unique at 30 s resolution. Localities were randomly assigned to training (n = 92) and testing (n = 91) subsets for purposes of selecting a single optimal model using approximate Bayesian sampling techniques (see Monahan and Koenig [In press]); pseudo-absence testing data (n = 91) were randomly drawn from areas throughout California where *P. ramorum* is currently absent. The Bayesian analysis provided a framework for comparing among candidate models developed using prior knowledge of typical distributional attributes of BIOCLIM parameters. We decided *a priori* to maximize model sensitivity, specificity, and improvement over chance expectations (Kappa) (Fielding and Bell 1997). Uniform priors were selected to define all minimum (0-0.75 quantiles) and maximum (0.925-1.0 quantiles) model parameters (38 total). Analyses used the priors to randomly determine parameter values from the training data. Combining each new candidate BIOCLIM model with both sets of testing data, sensitivity, specificity, and Kappa were calculated along with their deviations from unity. We allowed for 20,000 iterations and used 10 percent of the ranked output data to define posterior parameter distributions for use in subsequent analyses. The posteriors effectively identify particular combinations of BIOCLIM quantiles that return "best-fit" models; posteriors may also be used to draw inferences about which climate variables most greatly influence overall accuracy.

Results

Oak variables

CBC and BBS datasets yielded comparable estimates of the effects of oak species diversity and oak areal extent on oak woodland bird species richness, diversity, and equitability (*table 1*). All oak woodland bird indices were positively correlated ($P < 0.01$) with either oak diversity or the amount of oak habitat. These results suggest that oak species diversity and areal extent are key predictors of oak woodland bird species richness, diversity, and equitability and therefore useful variables for purposes of estimating the effects of SOD.

Table 1—*Spearman rank correlations assessing the influence of oak species diversity (*N*) and oak areal extent (*A*) on oak woodland bird species richness, diversity, and equitability. Results reported for two independent bird census datasets (BBS and CBC). Sample sizes (*n*) refer to the number of BBS routes or CBC circles included in the analyses.*

	BBS[1]			CBC[1]		
Bird Index	*N*	*A*	*n*	*N*	*A*	*n*
Richness	0.620**	0.388*	56	0.659**	0.447**	60
Diversity	0.577**	0.364*	56	0.590**	0.567**	60
Equitability	0.365*	0.056	56	0.405**	0.531**	60

[1] * $P < 0.01$, ** $P < 0.001$

Effects of SOD on birds

The three regression models (M1 through M3) used to simulate the effects of SOD yielded predictably different oak woodland bird community responses. M1, which assumed the greatest loss of oak habitat due to loss of *Q. agrifolia* or *L. densiflorus,* generally predicted declines of the greatest magnitude, while M3, which assumed no loss of oak habitat except for sites containing only *Q. agrifolia* or *L. densiflorus*, yielded the smallest estimated declines (*fig. 2a*). Although M1 and M3 paint unrealistically severe (M1) and unrealistically mild (M3) pictures of the likely effects of SOD on oak distributions, the probable effects of SOD on oak areal extent are unknown, and we consider results averaged across M1 through M3 as providing the best current estimates of the effects of the disease on birds. Similarly, given *a priori* knowledge of the seasonal and methodological biases of the survey data, SOD effects are also likely best approximated by averaging across BBS and CBC data.

Using these values, results suggest that bird species richness will decline by 15.2 percent with the loss of *Q. agrifolia* and by 8.7 percent with the elimination of *L. densiflorus*. Similarly, bird species diversity is expected to decrease by 13.4 percent given complete removal of *Q. agrifolia* and 8.9 percent with the loss of *L. densiflorus*. However, the associated estimated declines in relative abundance vary greatly depending on choice of census data. Equitability as determined from BBS data essentially remained unchanged, but based on the CBC was predicted to decline by 11 percent (*Q. agrifolia*) and 10 percent (*L. densiflorus*). Hence, according to the CBC results, but not the BBS, SOD is expected to skew the oak woodland bird community towards fewer, more dominant species.

Partitioning results by the number of oak species in the sites and averaging across M1 through M3, most of the estimated declines in bird species richness, diversity, and equitability were predicted for areas where initial oak species diversity was low (*fig. 2b*). Following the loss of *Q. agrifolia*, 90 to 93 percent of the estimated weighted declines were predicted to occur in woodlands where oak diversity was limited to ≤ 2 species, and 72 to 78 percent in areas with just coast live oak. Similarly, following the loss of *L. densiflorus*, 74 to 82 percent of the estimated weighted declines were expected for areas with ≤ 2 oak species, and 48 to 72 percent in areas where initial oak species diversity was limited to tanoak.

Current geographical extent of SOD

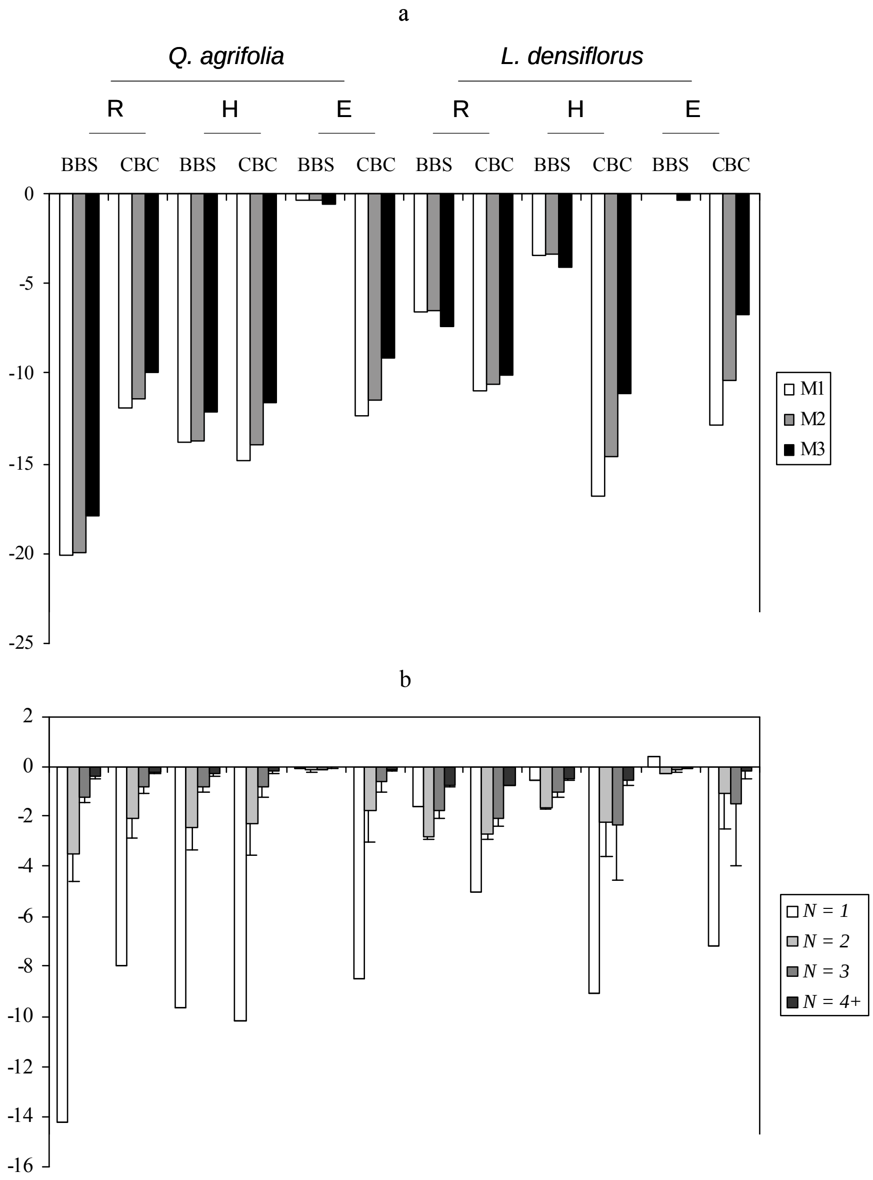

Figure 2—Estimated effects of SOD on bird species richness (R), diversity (H), and equitability (E). Results reported for separate BBS and CBC analyses involving the statewide elimination of either *Q. agrifolia* or *L. densiflorus*; results partitioned according to regression model (a) and initial oak species diversity (b, mean M1 through M3 ± SD).

The optimal SOD model was obtained using a 100 percent bounding envelope with 3-variable relaxation. Hence, minimum and maximum values for each of the 19 starting climate variables were best defined using 0 and 1 quantiles, respectively, and the final model encompassed intersections of 17 or more of these univariate climate distributions projected in geographic space. The final model was extremely accurate at predicting where *P. ramorum* currently does and does not occur (sensitivity = 0.97, specificity = 0.99). It also provided significant improvement over chance expectations (Kappa = 0.96; according to Landis and Koch [1977], models yielding Kappa values above 0.75 should be considered excellent). Qualitatively the model showed close spatial agreement with other risk models developed using different techniques (Meentemeyer and others 2004, Fowler and Magarey 2005, Guo and others 2005, Kelly and others 2005).

The optimal model identified 17,570 km^2 of coastal California as climatically suited to infection by *P. ramorum*, of which 10,130 km^2 (58 percent) intersect the statewide geographic ranges of *Q. agrifolia* and *L. densiflorus* and 5,000 km^2 (28 percent) intersect areas where *N* is limited to either *Q. agrifolia* or *L. densiflorus* (*fig. 3*). Results suggest that the disease may eventually encompass 6,175 km^2 (24 percent) of the *Q. agrifolia* distribution and 4,693 km^2 (27 percent) of *L. densiflorus*. SOD-suitable areas of special future concern include 750 km^2 of the southern CW Jepson ecological region (San Luis Obispo and Santa Barbara counties). Thus far, SOD has primarily been found in the NW and northern CW Jepson regions, while the geographically disjunct areas predicted for the southern CW region remain disease free. Re-weighting bird results obtained from M1 through M3 by the proportion of the *L. densiflorus* range encompassed by the optimal SOD model, oak woodland bird species richness is expected to decline by 8.5 percent, diversity by 9.6 percent, and equitability by 5.8 percent. Similarly, loss of *Q. agrifolia* within SOD-suitable habitats is expected to reduce bird richness by 13 percent, diversity by 11.3 percent, and equitability by 4.7 percent.

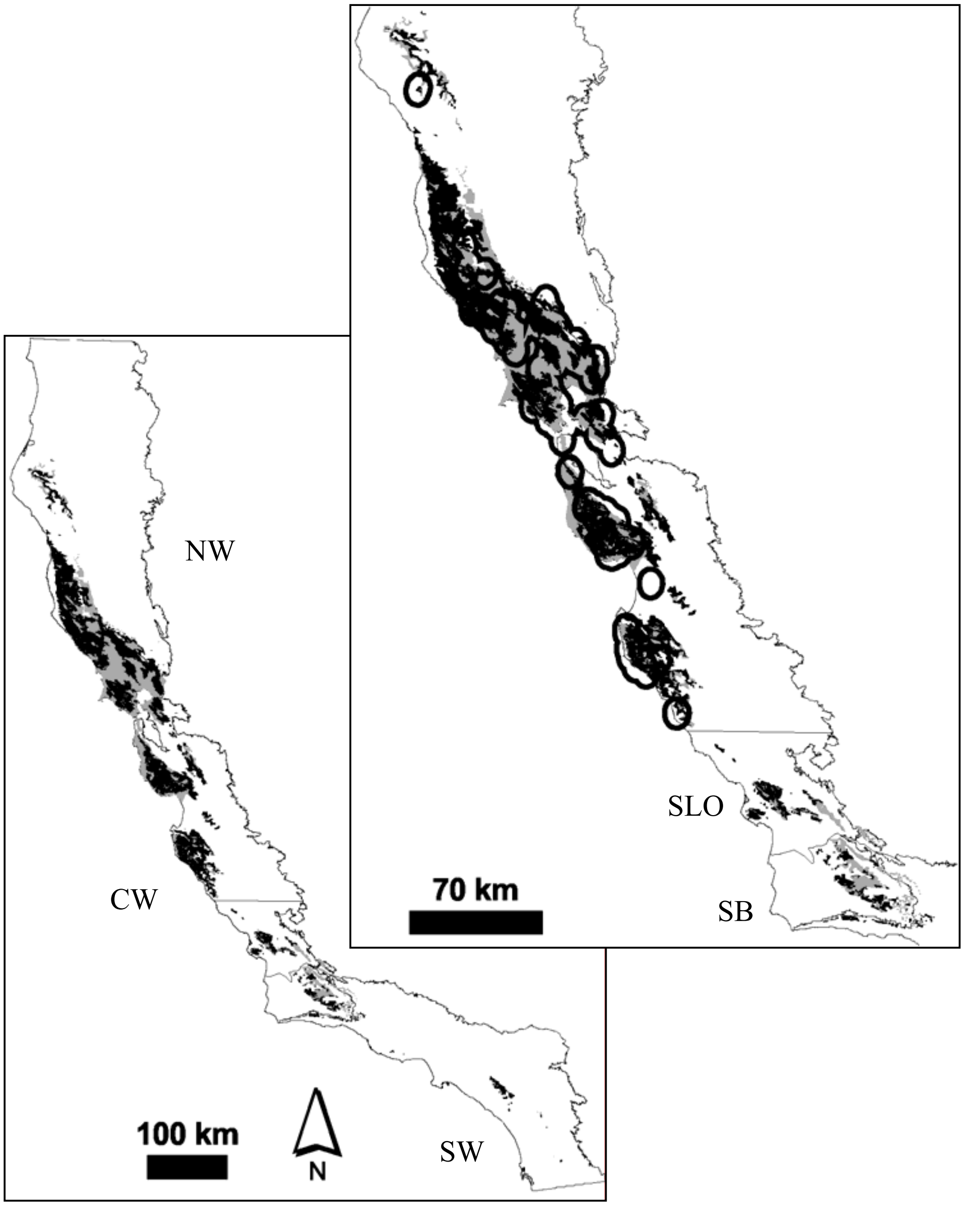

Figure 3—Current climatic SOD model (gray) and intersections with either *Q. agrifolia* or *L. densiflorus* (black). *P. ramorum* localities as of December 2004 are given by the bold polygon. Both San Luis Obispo (SLO) and Santa Barbara (SB) counties possess SOD-suitable climates.

Discussion

We used observed relationships between bird species richness, diversity, and equitability and oak species diversity and areal extent to quantify how the loss of two major tree oak species from California may impact the coastal oak woodland bird community. Three different assumptions were made concerning overlap between the SOD-sensitive oak species (*Q. agrifolia* or *L. densiflorus*) and other tree oaks, ranging from no overlap (and thus complete loss of *Q. agrifolia* or *L. densiflorus* with loss of oak area [M1]) to complete overlap (and thus no loss of oak habitat with loss of *Q. agrifolia* or *L. densiflorus* [M3]). Since the probable effects of SOD on oak areal extent are unknown, we consider results averaged across M1 through M3 as providing the best current estimates of how the disease stands to impact the avian community. Similarly, the effects of SOD are also likely best approximated by averaging results obtained from the two independent census datasets. Using these values, the statewide elimination of *Q. agrifolia* is predicted to result in 15.2 percent decline in oak woodland bird species richness, 13.4 percent decline in diversity, and 5.7 percent decline in equitability within the current range (25,282 km^2, or 6.2 percent of California's land area) of this species. Complete loss of *L. densiflorus* is expected to reduce oak woodland bird species richness by 8.7 percent, diversity by 8.9 percent, and equitability by 5 percent within its current range (17,173 km^2, or 4.2 percent of California's land area). Weighted estimates obtained for areas encompassed by the optimal SOD model were comparable.

Our post-SOD bird projections are not without precedent, for avian declines of this magnitude have been previously documented in other habitats following forest conversion. For example, the rapid loss of Appalachian Fraser fir (*Abies fraseri*) from an introduced insect (*Adelges piceae*) resulted in >50 percent population declines for six of 11 common bird species in the breeding community (Rabenold and others 1998). The establishment of chestnut blight fungus (*Cryphonectria parasitica*), which virtually exterminated the American chestnut (*Castanea dentata*) throughout much of its original range within 50 years (Anagnostakis 1987, McKeen 1995), was contemporaneous with declines in rank abundance for certain cavity nesting bird species (Haney and others 2001). Rapid loss of the American elm (*Ulmus americana*) following Dutch elm disease (*Ophiostoma ulmi*) (Karnosky 1979) was associated with pronounced population declines in mature forest bird species (Canterbury and Blockstein 1997). Furthermore, sizeable population declines are expected among at least five California bird species, including cavity nesters and mature oak woodland specialists such as acorn and Nuttall's woodpeckers, Hutton's vireo, and oak titmouse, following the SOD-induced loss of *Q. agrifolia* (Monahan and Koenig [In press]).

There are, however, several potentially mitigating factors that may lessen the ultimate impact of SOD as predicted by our models. Oak habitats rich in other tree species might allow certain insectivorous bird species to switch foraging substrates following loss of *Q. agrifolia* (Apigian and Allen-Diaz 2005). Even without this potential buffering capacity, stand-level tree mortality resulting from SOD has thus far not usually been complete (McPherson and others 2002, Rizzo and others 2002), approaching only 50 percent for *Q. agrifolia* in areas of high infection (Brown and Allen-Diaz 2005). Furthermore, if the disease locally eliminates coast live oak or tanoak, recolonization remains a possibility (Weste and others 2002). In the absence of complete elimination of *Q. agrifolia* or *L. densiflorus*, understanding changes in stand structure may be key to accurately estimating bird responses at smaller spatial scales (Winslow and Tietje 2005). Thus, the present post-SOD estimates likely represent the most extreme scenarios for oak woodland birds.

Despite uncertainty surrounding future spatiotemporal dynamics of the disease, most field and laboratory studies indicate that the ultimate influence of SOD will be to significantly reduce numbers of *Q. agrifolia* and *L. densiflorus* in California (Rizzo and Garbelotto 2003). These findings are supported by our climatic SOD model, which predicts that *P. ramorum* could expand to occupy 10,130 km^2 or 24 percent of the total statewide *Q. agrifolia* and *L. densiflorus* distributions (5,000 km^2 or 23 percent of areas where oak species diversity is limited to either *Q. agrifolia* or *L. densiflorus*). Coast live oak woodlands in San Luis Obispo and Santa Barbara counties are of special concern with respect to establishment of the disease, and future SOD projections further suggest that long-term disease sweeps may occur in Sonoma, Monterey, and San Luis Obispo counties (Monahan and Koenig [In press]). Based on our findings, current SOD management decisions aimed at lessening the ultimate impact of the disease on both oaks and birds should target these California counties and direct preventative treatments primarily towards coast live oak woodlands that are low in initial oak species diversity.

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