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Estimating the potential effects of sudden oak death on oak-dependent birds

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ABSTRACT

Sudden oak death (SOD), a disease induced by the fungus-like pathogen *Phytophthora ramorum*, threatens to seriously reduce or eliminate several oak species endemic to the west coast of North America. We investigated how the disappearance of one of these species, coast live oak (*Quercus agrifolia*), may affect populations of five resident oak-affiliated California birds – acorn woodpecker (*Melanerpes formicivorus*), Nuttall's woodpecker (*Picoides nuttallii*), Hutton's vireo (*Vireo huttoni*), western scrub-jay (*Aphelocoma californica*), and oak titmouse (*Baeolophus inornatus*) – using geocoded data from Audubon Christmas Bird Counts, North American Breeding Bird Surveys, and the California Gap Analysis. Capitalizing on observed relationships between the focal bird species and both oak species diversity and areal extent, we modeled relative bird abundance while assuming complete loss of *Q. agrifolia* and complete, partial, or no loss of oak habitat following a disease sweep. Post-SOD projections of bird populations occurring within the range of coast live oak were on average 25–68% smaller and 13–49% more variable relative to pre-SOD estimates. SOD effects were greatest for habitats with low initial oak species diversity. Climatic SOD models predicted that the disease stands to negatively impact populations of all five focal bird species throughout 20% of California's coast live oak habitats. This study provides the first spatially explicit insights into the potential effects of SOD on avian distribution and abundance. Results may be used to help prioritize conservation plans aimed at minimizing overall community level disturbances resulting from the disease.

1. Introduction

Highly virulent forest pathogens have the potential to greatly reduce or even eliminate tree species at large spatial scales. For example, within forests of the eastern United States, diseases caused by fungal pathogens introduced over the past century have significantly impacted the native American chestnut (*Castanea dentata*), American beech (*Fagus grandifolia*), and American elm (*Ulmus americana*), in some cases dramatically changing forest composition (Houston, 1975; Karnosky, 1979; Anagnostakis, 1987). Declines can be rapid

and severe, as exemplified by the reduction of the American chestnut by the chestnut blight fungus (*Cryphonectria parasitica*), which virtually exterminated the tree throughout much of its original range within 50 years (McKeen, 1995). Unfortunately, even with knowledge on how tree diseases affect canopy composition, it is often difficult to predict a priori the cascading effects on the larger community.
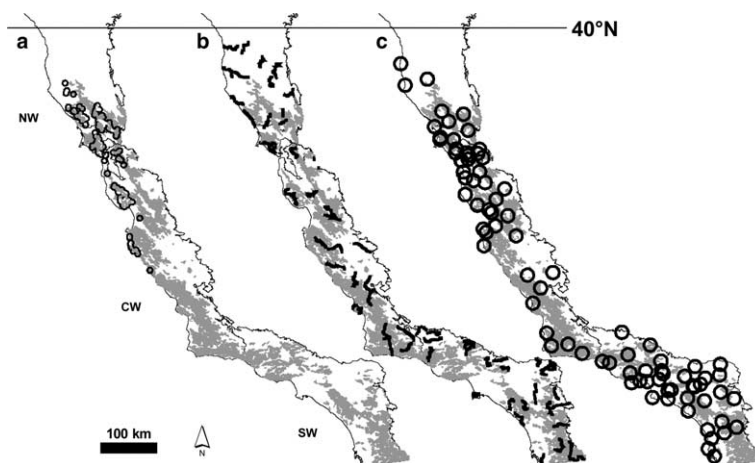
Sudden oak death (SOD) is a disease that currently threatens to reduce or eliminate several species of red oaks (family Fagaceae) endemic to the west coast of North America. Since its detection in 1995, SOD has caused significant

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Fig. 1 – Southern distribution of *P. ramorum* (a, black buffer) and locations of BBS routes (b, bold black lines) and CBC circles (c, black circles) used in the study. Three Jepson ecological regions (NW, CW, SW) bounded by 40°N encompass the entire statewide distribution of *Q. agrifolia* (gray areas).

mortality of coast live oak (*Quercus agrifolia*) within primarily coastal areas of central California (Garbelotto et al., 2001; Rizzo et al., 2002; Swiecki and Bernhardt, 2002; Garbelotto et al., 2003; Rizzo and Garbelotto, 2003) (Fig. 1(a)). The disease is triggered 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 et al., 2002; Rizzo and Garbelotto, 2003). Known mortality due to *P. ramorum* is recent, and thus the wildlife impacts are unknown (CalPIF, 2002).

State and federal wildlife agencies as well as the general public are becoming increasingly interested in knowing how SOD stands to negatively impact native species of oak-dependent vertebrates. Birds are particularly useful indicators in this regard since excellent survey databases are readily available for both wintering and breeding populations throughout North America. 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 successful to study avian distribution and abundance (Bock and Root, 1981; Root, 1988; Price et al., 1995; Koenig, 1998), as well as model the potential community-level effects of SOD on California birds (Monahan and Koenig, 2005). Our approach here estimates the population-level consequences of SOD using the two independent datasets whose seasonal timing and methodologies are quite different and thus to some degree complementary.

We use the statistical relationship between relative bird abundance and oak species diversity and oak areal extent to quantify expected avian population declines and census size fluctuations resulting from a reduction in oak diversity and either complete, partial, or no loss of oak habitat. Permanent change to coast live oak habitats is probable since *Q. agrifolia* suffers extensive SOD mortality (Rizzo and Garbelotto, 2003), and because large portions of its geographic range are expected to experience disease sweeps as *P. ramorum* continues to expand throughout California (Meentemeyer et al., 2004; Guo et al., 2005).

We focus on five bird species, acorn woodpecker (*Melanerpes formicivorus*), Nuttall's woodpecker (*Picoides nuttallii*), Hutton's vireo (*Vireo huttoni*), western scrub-jay (*Aphelocoma californica*), and oak titmouse (*Baeolophus inornatus*), chosen for their high dependence on coastal oak habitats for survival and reproduction (Grinnell and Miller, 1944; Pitelka, 1951; American Ornithologists' Union, 1957; Short, 1971; Miller and Bock, 1972; Verner, 1979; Koenig and Haydock, 1999; Cicero, 2000) (Fig. 2). While SOD clearly stands to negatively impact populations of such oak-dependent bird species, our goal here is to estimate where in California these SOD-induced losses will be greatest for both birds and coast live oak.

In this study we (1) compare post-SOD relative abundance predictions (mean and CV) for two independent bird census datasets and three different habitat loss scenarios, (2) estimate model accuracies with respect to known *P. ramorum* occurrences and climatic SOD models identifying the potential current geographical extent of the disease, and (3) consider how our findings might be further impacted by a continued *P. ramorum* range expansion coupled with anthropogenic climate change by modeling the future geographical extent of the disease in the year 2050.

2. Methods

2.1. Data overview

Bird distribution and abundance data were obtained from Audubon Christmas Bird Counts (CBC) (Butcher, 1990) and the North American Breeding Bird Survey (BBS) (Sauer et al., 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 between 1960 and 1997, inclusive. For each species x count combination, we standardized observer effort by using the log-transformed ($\log(x + 1)$) number of birds
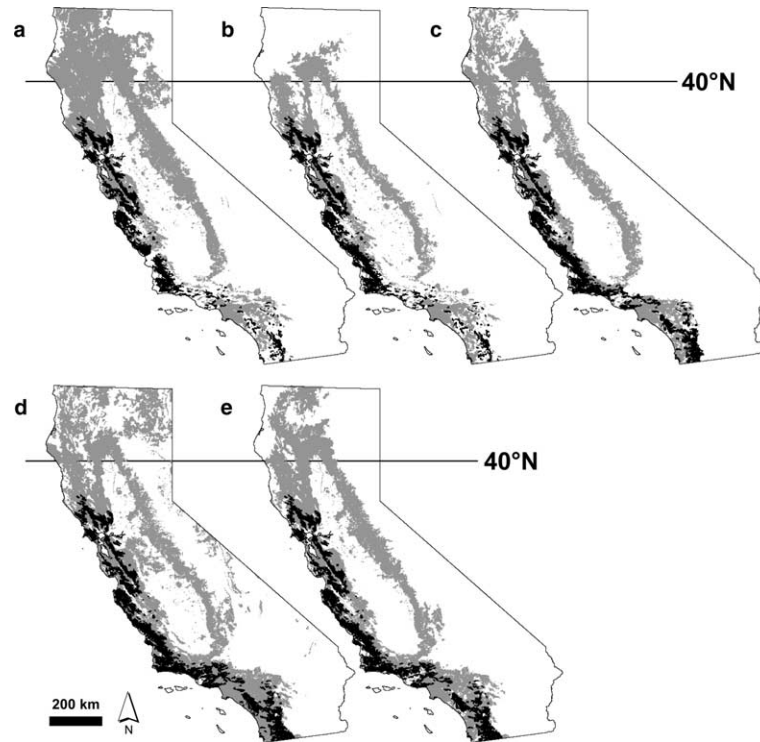
Fig. 2 – Statewide range maps of five oak-dependent bird species (gray + black areas), acorn woodpecker (a), Nuttall's woodpecker (b), Hutton's vireo (c), western scrub-jay (d), and oak titmouse (e), intersected with coast live oak habitats (black areas only). Intersections encompass 10% (acorn woodpecker) to 17% (Nuttall's woodpecker and Hutton's vireo) of the bird species' California distributions.

counted divided by the number of 'party-hours' of observation. We then determined the mean and coefficient of variation (CV; SD/mean × 100) of this value ('birds per party hour') across all years the count was performed as an estimate of overall relative abundance and variability of the species at that site. Breeding Bird Surveys consist of 3-min censuses at a series of 50 stops, 0.8 km apart, conducted once during the breeding season along a road transect. Data used spanned 37 years from 1966 to 2002; number of birds counted was log-transformed and the mean and CV across all years calculated as with the CBC data.

In an effort to control for major habitat differences among sites, we only considered CBC circles and BBS routes occurring south of 40°N and within the Jepson ecological regions (Hickman, 1993) bounding the complete distribution of *Q. agrifolia* (Fig. 1(b) and (c)). This effectively excluded large portions of the state where coast live oaks are absent. Analyses thus involved 92 CBC circles and 91 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 et al., 1998). These data are 80% accurate (with 95% confidence) to a spatial resolution of 100 ha (i.e., 1/450 of the area encompassed by a CBC circle or 1/40 of the length of a BBS route). Oak species considered included *Q. agrifolia* and the eight other major tree oaks within the study area: 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*), interior live oak (*Q. wislizenii*), and tanoak (*Lithocarpus densiflorus*). The analyses thus considered all tree species of oaks in mainland California; shrub oaks were not included.

Distributions were generated for *Q. agrifolia* occurring in the absence of all other focal oaks and for all possible combinations of 1, 2, and ⩾3 additional oak species. The maximum number of 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. We used Spearman rank correlations to estimate the influence of oak species diversity and areal extent on both the mean and coefficient of variation in relative bird abundance (Table 1).

Point occurrence data for *P. ramorum* were obtained from the California Oak Mortality Task Force archive (Kelly and Tuxen, 2003). All climate data used in the present analyses originated from WorldClim (Hijmans et al., 2004), extracted at 30 s resolution (approximately 1 km^2) for 32°30′ to 42°N and 124°30′ to 114°W.

2.2.　Estimating the effects of SOD on birds

We used three regression models characterized by slightly different assumptions to estimate how SOD might affect focal bird populations through elimination of *Q. agrifolia*. All three methods assumed a reduction in oak diversity due to SOD

Common name[a]	Scientific name[a]	Data	Mean		CV		n[c]
			Diversity	Area	Diversity	Area	
Acorn woodpecker	*Melanerpes formicivorus*	CBC	0.55***	0.71***	−0.56***	−0.61***	51
		BBS	0.13	0.42**	−0.20	−0.42**	54
Nuttall's woodpecker	*Picoides nuttallii*	CBC	0.34*	0.45***	−0.39**	−0.40**	50
		BBS	0.35*	0.31*	−0.36*	−0.23	48
Hutton's Vireo	*Vireo huttoni*	CBC	0.44**	0.19	−0.31*	−0.01	49
		BBS	0.05	0.33*	−0.09	−0.32*	47
Western Scrub-jay	*Aphelocoma californica*	CBC	0.51***	0.47***	−0.42**	−0.15	51
		BBS	0.30*	0.41***	−0.27*	−0.32*	58
Oak Titmouse	*Baeolophus inornatus*	CBC	0.62***	0.64***	−0.62***	−0.52***	51
		BBS	0.27	0.39**	−0.22	−0.40**	54

Table 1 – Spearman rank correlations assessing the influence of oak species diversity (diversity) and oak areal extent (area) on both mean and interannual variation (CV) in relative bird abundance. Spearman rank[b].

a AOU nomenclature (American Ornithologists' Union, 1998).
b *P < 0.05, **P < 0.01, ***P < 0.001.
c Sample sizes refer to the number of CBC circles or BBS routes used in Spearman correlations.

and equivalence of Q. *agrifolia* with the other tree oak species, an assumption we consider reasonable given that none of the bird species are strictly confined to coast live oak woodlands (Fig. 2). However, the methods differed according to the post-SOD projections of how much oak habitat would be retained after the disease sweep.

In method 1 (M1), oak area was assumed to decrease by the amount initially occupied by Q. *agrifolia*; that is, M1 assumed that there was no small-scale habitat overlap between Q. *agrifolia* and any other oak species. In method 2 (M2), oak habitat 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*, when initial oak species diversity >1). Finally, in method 3 (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* and sites containing no species of oaks, but still within the appropriate Jepson regions. This last method assumed complete habitat overlap between Q. *agrifolia* and other oak species.

We regressed the BBS and CBC estimates of relative bird abundance on oak species diversity and areal extent and calculated new values for oak area under each of the three habitat loss scenarios, that is, when oak diversity declined by one through loss of Q. *agrifolia*. We used these post-SOD values for oak species diversity (i.e., one less oak species in all cases) and oak habitat in conjunction with the regression coefficients to calculate post-SOD estimates of relative bird abundance. We then weighted estimated changes in relative bird abundance by the areas within California that would be affected by the loss of Q. *agrifolia* to estimate the proportion of the total population of the bird within the geographic range of coast live oak that would be lost as a consequence of SOD elimination of Q. *agrifolia* from the landscape. Finally,

we used the bird species' California GAP distributions (Fig. 2) to scale the estimated localized changes in relative abundance up to the statewide level.

2.3. Predicting the geographical extent of SOD

In all cases we assumed complete elimination of Q. *agrifolia*. 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 9-12 h of leaf moisture and temperatures of 18–22 °C (Garbelotto et al., 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, or mean of monthly (maximum temperature–minimum temperature), (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.

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 190 confirmed P. *ramorum* localities rendered spatially unique at 30 s resolution. Localities were randomly assigned to

training ($n = 95$) and testing ($n = 95$) subsets for purposes of selecting a single optimal model using approximate Bayesian sampling techniques; pseudo-absence testing data ($n = 95$) 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, the conditional probability that a given occurrence is correctly classified, and Kappa, measuring improvement over chance expectations (Fielding and Bell, 1997). True negative rates could not be computed due to lack of explicit absence data. Uniform priors were selected to define all minimum (0–7.5% quantiles) and maximum (92.5–100% 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 and Kappa were calculated along with their deviations from unity. We allowed for 20,000 iterations and used standard rejection sampling to generate posterior parameter distributions. The posteriors 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.

Regressions of *P. ramorum* climatic attributes on year of discovery (2000–2004 inclusive) were used to identify potential pathogen expansion signatures. We used coefficients from significant regressions ($P < 0.05$) to adjust minimum and maximum BIOCLIM parameter values for purposes of predicting the potential future geographical extent of *P. ramorum* following both range expansion and climate change. Existing studies suggest that future climates should at least in part influence the distribution of the disease (Rizzo et al., 2002; Garbelotto et al., 2003). Our future climate projections for the year 2050 were based on one equilibrium, CCM3 (Kiehl et al., 1998), and two transient models, ECHAM4 (Roeckner et al., 1996) and CGCM1 (Flato et al., 2000), selected for their original spatial resolutions (allowing 10 min downscaling) and in an effort to bracket regional sensitivity (average air temperature at $2 \times CO_2$; globally +1.5 to +4.5 °C). All scenarios assumed a 1% increase of CO_2 per annum (ISO92a). Models ECHAM4 and CGCM1 received both greenhouse gas and sulfate aerosol forcings. CGCM1 utilized the mean of four ensembles (model experiments with identical forcings but initiated from different points on the control run).

3. Results

3.1. Effects of SOD on relative bird abundance

The CBC and BBS datasets yielded similar estimates of the effects of oak species diversity and oak areal extent on relative bird abundance (Table 1). Mean relative abundances of all five focal bird species were positively correlated ($P < 0.05$) with either oak diversity or the amount of oak habitat. Conversely, coefficients of variation in relative bird abundance were negatively correlated ($P < 0.05$) with one or both oak variables.

The three regression models (M1 through M3) yielded predictably different estimates of how SOD stands to impact populations of oak-dependent bird species. M1, which assumed the greatest loss of oak habitat due to loss of *Q. agrifolia*, generally predicted mean population declines and CV increases of the greatest magnitude, while M3, which assumed no habitat loss except for sites containing only *Q. agrifolia*, yielded the smallest estimated changes. Although M1 and M3 paint unrealistically severe (M1) and 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 considered 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, predicted declines in abundance within the range of *Q. agrifolia* were greatest for acorn woodpecker, Nuttall's woodpecker, and oak titmouse, in all cases exceeding 50% (Fig. 3(a)). Populations of the two other species, Hutton's vireo and western scrub-jay, were each estimated to decline by 25%. Within the state as a whole, however, the estimated localized losses were modest and represented only 4% (Hutton's vireo and western scrub-jay) to 10% (oak titmouse). Mean differences between the CBC and BBS datasets were also small, ranging from just 3% (western scrub-jay) to 27% (acorn woodpecker). Similarly, mean differences among regression models were modest, ranging from 3% (Hutton's vireo) to 14% (oak titmouse).

Increases in CV of abundance were greatest for acorn woodpecker (49%) and oak titmouse (47%) (Fig. 3(b)). Responses of the other three species ranged from 13% (Hutton's vireo) to 29% (Nuttall's woodpecker). Survey differences in CV of abundance ranged from 5% (acorn and Nuttall's woodpeckers) to 43% (western scrub-jay), and only in the case of Hutton's vireo and western scrub-jay did these exceed overall average predictions. Mean differences among regression models were again small, ranging from 3% (Hutton's vireo) to 15% (acorn woodpecker).

More than 88% of the estimated bird losses were predicted to occur in woodlands where oak diversity was limited to ⩽2 species, and ⩾68% in areas with just *Q. agrifolia* (Fig. 4(a)). Similarly, with the exception of Hutton's vireo, ⩾78% of the estimated increases in CV of relative abundance were predicted to occur in regions where oak diversity was limited to ⩽2 species, and ⩾51% in areas where initial oak species diversity was limited to *Q. agrifolia* (Fig. 4(b)). Many of these habitats currently suffer from SOD (Fig. 5), suggesting that the predicted decreases in mean and increases in CV of relative bird abundance will initially occur in and adjoining known diseased areas.

3.2. Current geographical extent of SOD

Several SOD model parameters exhibited pronounced differences between the priors and posteriors generated from the approximate Bayesian analysis. In particular, minimum and maximum temperature seasonality, minimum mean temperature of the driest quarter, minimum precipitation of the driest quarter, and maximum mean temperatures of the
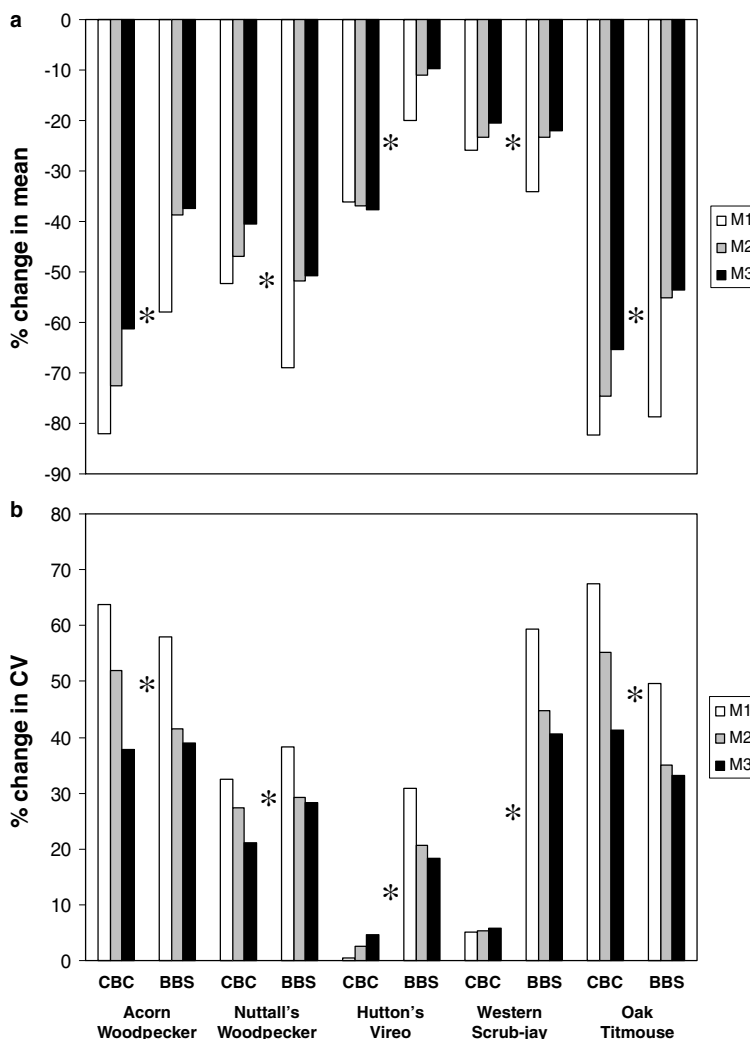
Fig. 3 – Effects of SOD on five oak-dependent bird species within the statewide range of Q. agrifolia. Results reported for three regression methods (M1–M3) summarizing % decreases in mean (a) and % increases in CV (b) of relative bird abundance. Asterisks report results averaged across all three methods and both census datasets.

warmest and coldest quarters all possessed posteriors that were markedly different from the uniform priors (Fig. 6).

The optimal SOD model was obtained using a 100% 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 100% 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 occurs (sensitivity = 0.97) and also provided significant improvement over chance expectations (Kappa = 0.96; values over 0.75 are considered 'excellent' [Landis and Koch, 1977]). Qualitatively the model showed close spatial agreement with other risk models developed using different techniques (Meentemeyer et al., 2004; Guo et al., 2005).

The optimal model identified 17,570 km² of coastal California as climatically suited to *P. ramorum* (Fig. 7(a)), including 6175 km² or 24% of the total *Q. agrifolia* range (Fig. 7(b)), and 2451 km² or 17% of habitats where oak diversity is limited to

coast live oak (Fig. 7(c)). Populations of all 5 focal bird species co-occurring in mixed coast live oak woodlands threatened by SOD cover 5107 km² or 20% of the *Q. agrifolia* range. SOD-suitable areas of special future concern include 750 km² of the southern CW Jepson region (San Luis Obispo and Santa Barbara counties).

3.3. Future geographical extent of SOD

The majority of the regressions of pathogen climate attributes on year of discovery were uninformative, suggesting that for these climate variables *P. ramorum* has reached temporary equilibrium. However, five variables were significantly correlated with year, including minimum mean temperature diurnal range, minimum min temperature of the coldest month, minimum mean temperature of the wettest quarter, maximum temperature seasonality, and maximum temperature annual range (Fig. 8). These associations are most likely attributable to a recent *P. ramorum* range expansion into colder and more seasonal environments.
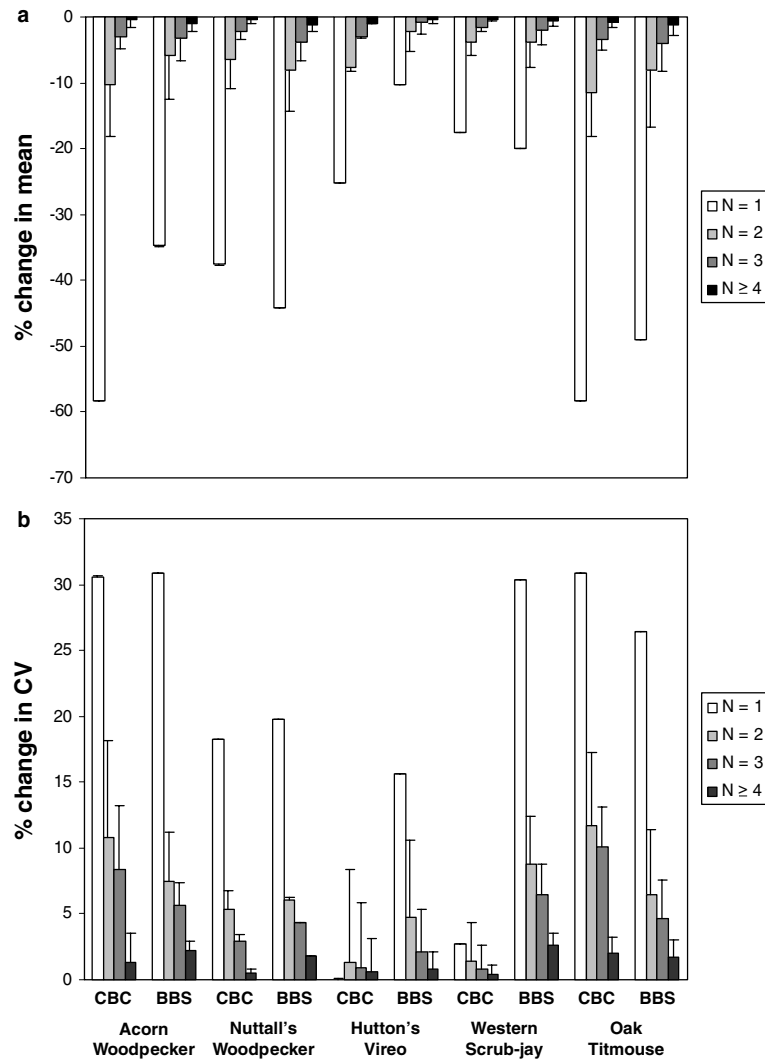
Fig. 4 – Effects of SOD on five oak-dependent bird species within the statewide range of Q. *agrifolia*. Estimated % decreases in mean (a) and % increases in CV (b) of relative bird abundance following a disease sweep. Results averaged across M1 through M3 (±1 SD) and partitioned according to initial oak species diversity (N = 1, 2, 3, or 4+).

The effects of a continued range expansion coupled with climate change are not expected to dramatically reshape the potential distribution of SOD over the next 50 years. While projections under the CCM3 model indicate possible disease sweeps throughout NW California and portions of the Sierra Nevada (largely overlapping the range of Q. *kelloggii*, another SOD-sensitive species) (Fig. 9(a)), predicted SOD distributions under the ECHAM4 and CGCM1 models are less extensive and tied predominantly to coastal areas encompassed by the current model (Fig. 9(b) and (c)). Populations of the 5 focal bird species inhabiting mixed coast live oak woodlands from Mendocino County south through Santa Barbara County are at greatest risk of suffering long-term cascading effects of SOD.

4. Discussion

We used observed relationships between relative bird abundance and oak species diversity and areal extent to estimate how the SOD-induced loss of a major tree oak species, Q. *agri-*

folia, will potentially affect populations of oak-dependent birds. Estimated effects were greatest for acorn woodpecker, Nuttall's woodpecker, and oak titmouse, whose populations throughout California's coast live oak woodlands were predicted to sustain 52–68% decreases in mean abundance and 29–49% increases in year-to-year variability as a result of SOD. Populations of the two lesser oak-dependent species, Hutton's vireo and western scrub-jay, also suffered sizeable declines. In all cases mean differences among habitat loss scenarios were small relative to overall average estimates, suggesting that model results were not particularly sensitive to uncertainty surrounding how SOD stands to threaten oak areal extent.

Avian population changes 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% population declines for several common bird species in the breeding community (Rabenold et al., 1998). Establishment of chestnut blight fungus (*C. parasitica*) was
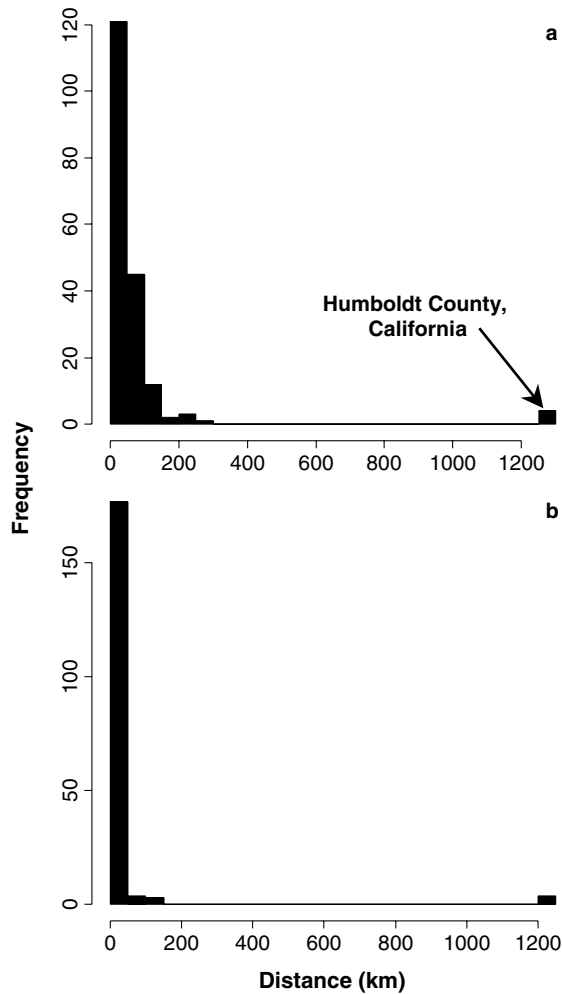
Fig. 5 – Spatial proximity of *P. ramorum* point localities relative to regions where all five focal bird species co-occur and initial oak species diversity is limited to either coast live oak (a) or ⩾1 other oak species (b).

contemporaneous with declines in rank abundance for certain cavity nesting bird species (Haney et al., 2001). Rapid loss of the American elm (*U. americana*) following Dutch elm disease (*Ophiostoma ulmi*) was associated with pronounced population declines in mature forest bird species (Canterbury and Blockstein, 1997). While in all such cases certain bird species also benefited from the forest changes, species closely associated with particular forest types are of special interest because they potentially represent irreplaceable biodiversity.

Our post-SOD estimates are further plausible given what is known about how the focal bird species depend on oaks for survival and reproduction. Consideration of these relationships reveals that the underlying oak-associations can be varied and complex. For example, reproductive success in the acorn woodpecker is determined primarily by acorn availability (Koenig and Mumme, 1987; Stacey and Ligon, 1987; Koenig et al., 1995), while in the oak titmouse by the distribution of natural cavities (Cicero, 2000). Hence, the two oak specialists predicted by our models to respond similarly to SOD will likely do so for very different reasons. The western scrub-jay, another acorn-dependent, may be less sensitive to SOD on account of its comparably varied diet and complex patterns of habitat use (Curry et al., 2002). Nuttall's woodpecker is mostly insectivorous and like the oak titmouse forages primarily in oaks (Lowther, 2000). Hutton's vireo often nests in coast live oaks and minimally requires breeding habitats with dense crown closure (Davis, 1995), which deteriorates following SOD (Swiecki and Bernhardt, 2003, 2004). Only in the case of Hutton's vireo and western scrub-jay did survey differences, specifically in CV of abundance, exceed overall average estimates (both BBS > CBC). Such results are not surprising given that these two species rely heavily on oak resources throughout breeding (Curry et al., 2002; Davis, 1995).

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
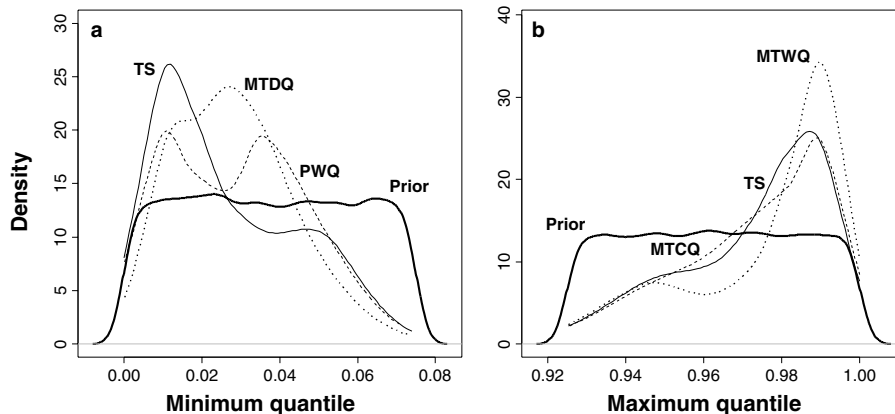
Fig. 6 – Prior and posterior density distributions for a subset of informative minimum (a) and maximum (b) climate model parameters obtained from approximate Bayesian analysis: TS = temperature seasonality; PWQ = precipitation of the warmest quarter; MTDQ = mean temperature of the driest quarter; MTCQ = mean temperature of the coldest quarter; MTWQ = mean temperature of the wettest quarter. The posterior distributions reveal that – for the selected variables – smaller minimum and larger maximum quantiles are associated with high model accuracy. Posteriors for most of the remaining variables (not shown) are similar to the priors, indicating that model performance as influenced by these variables will largely be unaffected by quantile choice within the prescribed minimum and maximum ranges.
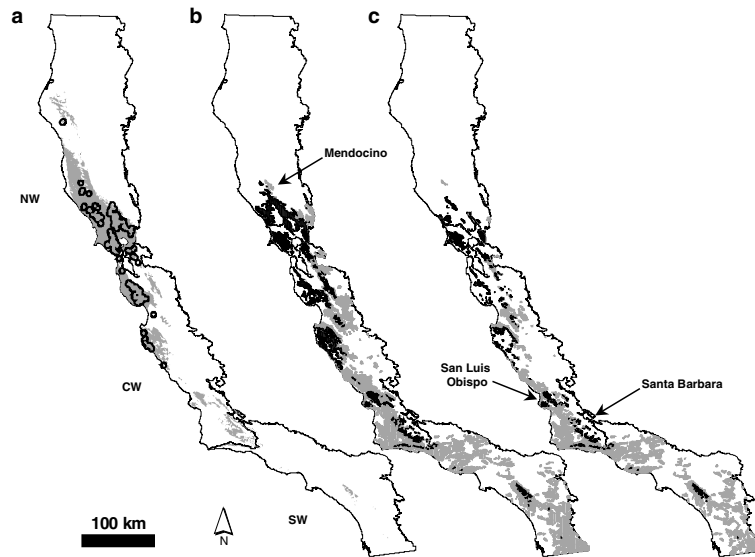
Fig. 7 – Current climatic SOD model (a, SOD model = gray areas, *P. ramorum* distribution = black buffer), intersected with the statewide *Q. agrifolia* range (b, *Q. agrifolia* = gray + black areas, SOD model ∩ *Q. agrifolia* = black areas), and intersected with habitats where oak species diversity is limited to *Q. agrifolia* (c, *Q. agrifolia* only = gray + black areas, SOD model ∩ *Q. agrifolia* only = black areas).
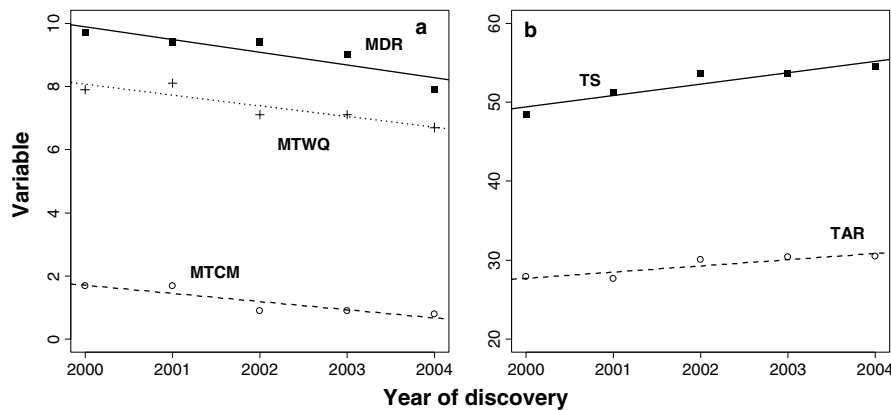

Fig. 8 – Regressions of minimum (a) and maximum (b) *P. ramorum* climate attributes on year of discovery: MDR = mean diurnal range, $y = -0.4x + 9.9$, $P < 0.05$; MTWQ = mean temperature of the wettest quarter, $y = -0.34x + 8.1$, $P < 0.05$; MTCM = minimum temperature of the coldest month, $y = -0.26x + 1.7$, $P < 0.05$; TS = temperature seasonality, $y = 1.4x + 49.4$, $P < 0.05$; TAR = temperature annual range, $y = 0.79x + 27.7$, $P < 0.05$.

allow certain insectivorous bird species such as chestnut-backed chickadee (*Poecile rufescens*) to switch foraging substrates (Apigian and Allen-Diaz, 2005). Even without this potential buffering capacity, stand-level tree mortality resulting from SOD has thus far never been complete (McPherson et al., 2002; Rizzo et al., 2002; Dodd et al., 2005), approaching only 50% for *Q. agrifolia* in areas of high *P. ramorum* infection (Brown and Allen-Diaz, 2005). Furthermore, if the disease locally eliminates the species, recolonization as in the case of *Eucalyptus* following *P. cinnamomi* infestation remains possible (Weste et al., 2002). Thus, the present post-SOD estimates likely represent extreme scenarios for oak woodland birds. In the absence of complete elimination of *Q. agrifolia*, understanding changes in stand structure may be key to accurately

estimating bird responses at smaller spatial scales (Winslow and Tietje, 2005), and a more detailed knowledge of ecosystem interdependencies may be required to estimate disturbance effects at larger scales (Plotnick and McKinney, 1993).

On the other hand, there are at least two potentially compensatory factors not explicitly considered by the models. Firstly, SOD represents only one of several common oak diseases (Swiecki et al., 2000), suggesting that the effects predicted from our models may be conservative for areas where disease dynamics are complex. Secondly, SOD is known to affect two additional tree species in California, *Q. kelloggii* and *L. densiflorus* (Garbelotto et al., 2001; Rizzo et al., 2002), whose statewide losses are expected to further negatively
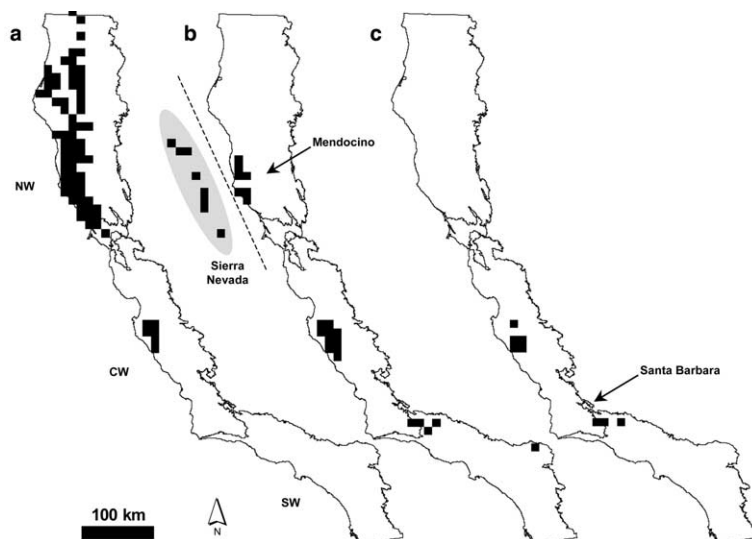
Fig. 9 – Future SOD models (black areas) given combined effects of *P. ramorum* range expansion and anthropogenic climate change: CCM3 (a), ECHAM4 (b), and CGCM1 (c).

impact populations of the focal bird species (Monahan and Koenig, 2002, 2005).

Despite uncertainty surrounding the spatiotemporal dynamics of SOD, most field and laboratory studies indicate that the ultimate influence of the disease will be to significantly reduce numbers of *Q. agrifolia* in California (Rizzo and Garbelotto, 2003). These findings are supported by our climatic SOD model, which conservatively predicts that *P. ramorum* could sweep through 24% of California's coast live oak woodlands, including 17% of habitats where oak diversity is limited to just *Q. agrifolia*. Coast live oak woodlands in San Luis Obispo and Santa Barbara counties are at high SOD-risk, and future projections suggest that long-term disease sweeps are possible for coastal counties south from Mendocino through Santa Barbara.

At a broader level, the methods presented here provide a framework for predicting how the rapid conversion of habitats over large geographic areas will adversely impact particular species in an ecosystem. For the conservation biologist, the real challenge is to accurately estimate both the magnitudes and locations of these negative effects in systems where experimental-based approaches are impractical. Prioritizing vulnerable habitats according to the projected losses of individuals, populations, or species will be key to allocating limited resources in ways that ensure the greatest possible conservation impact. Use of existing census data, such as the CBC and BBS used here and comparable schemes employed elsewhere, can clearly provide the kind of information necessary to guide such efforts.

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