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## Distributions and Habitat Models of Epiphytic *Physconia* in North-Central California

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*Abstract:*—I examined the distributions of eight *Physconia* species in northern and central California: *Physconia americana*, *P. californica*, *P. enteroxantha*, *P. fallax*, *P. isidiigera*, *P. isidiomuscigena*, *P. leucoleiptes*, and *P. perisidiosa*. Distributions are based upon lichen community data collected for the Forest Inventory and Analysis Program in over 200 permanent plots. *Physconia californica* was not found while *P. leucoleiptes* was infrequent across the landscape, occurring sporadically around the periphery of the Central Valley. *Physconia isidiomuscigena* occurred only once in the study plots, growing on *Quercus* sp. in Stanislaus county. This site is unusual in that this species is often saxicolous and known primarily from southern California. The remaining *Physconia* species were more frequent across the landscape with distributions centered in the Central Valley. I derived habitat models for these more common species using nonparametric multiplicative regression to help explain how distributions relate to environmental variables. Distributions of *P. enteroxantha*, *P. isidiigera*, and *P. perisidiosa* were well described by one or more environmental gradients while *P. fallax* and *P. americana* were only weakly associated with single predictors. Considering that many *Physconia* species are considered nitrophilous (nitrogen-loving), the habitat models would probably be better had an estimate of ammonia deposition been included. There are not, however, any comprehensive estimates of ammonia deposition for the study area.

### INTRODUCTION

Epiphytic *Physconia* species are common, conspicuous components of the lichen flora in northern and central California yet we know surprisingly little about their distributions and ecology. Several species, such as *P. americana*, *P. enteroxantha*, *P. isidiigera*, and *P. perisidiosa*, are characteristic of hardwood stands in the Central Valley and Sierra Nevada foothills, although distributions in surrounding regions like the Modoc Plateau, northwest coast, and central California coast are less clear. We know even less about the regional distribution of *P. leucoleiptes*, a species common in eastern North America, and the three most recently described species, *P. californica*, *P. fallax*, and *P. isidi-*

*omuscigena* (Esslinger 2000). Distribution maps for the latter three species were published for southern California (Esslinger 2001) although distributions for northern and central California, north of Ventura, remain largely unexplored. *Physconia fallax* is reported for northern California and Washington while most known *P. isidiomuscigena* and *P. californica* sites are reported from relatively dry Southern California counties (Los Angeles, Tulare, San Diego, and Riverside; Esslinger 2000).

Our first objective was to describe the distributions of eight epiphytic *Physconia* species in northern and central California using a large database of lichen community surveys. These species include *P. americana*, *P. californica*, *P. enteroxantha*, *P. fal-*

*fallax*, *P. isidiigera*, *P. isidiomuscigena*, *P. leucoleiptes*, and *P. perisidiosa*. Secondly, I used nonparametric multiplicative regression (NPMR) with a local mean estimator to build habitat models describing which climatic, topographic, and stand description variables best explain the distributions of the most common *Physconia* species. These models will provide a valuable first step towards understanding *Physconia* ecology in the region. As habitat modeling with NPMR methods is uncommon, the process will be briefly described in this paper although a more rigorous background can be found at <http://oregonstate.edu/~mccuneb/NPMR.pdf> and in the work of McCune et al. (2003), which describes a related form of NPMR.

#### METHODS

Distribution maps were derived from two databases of lichen community surveys conducted for the USDA Forest Inventory and Analysis program (FIA). Because of their usefulness as bioindicators, the FIA program collects extensive data on epiphytic lichens in forested areas throughout the United States. Field crews collected vouchers and estimated the abundance of each epiphytic macrolichen species occurring above 0.5 m on woody species or in the litter. Lichen community surveys lasted a minimum of 30 minutes and a maximum of two hours (methodology detailed in Jovan 2002 & McCune et al. 1997). To characterize forest stand structure, crews measured total basal area, basal area of hardwoods, basal area of softwoods, stand age, overstory species diversity, and dominant tree species at each plot. Climatic variables were extracted from the Precipitation-Elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994, 2001, 2002), which included mean annual dew temperature, maximum annual temperature, mean annual precipitation, mean number of wet days per year, mean annual relative humidity, and minimum annual temperature.

The larger of the two databases consists of 207 plots surveyed in 1994 and from 1998-2001. Sites covered all of northern and central California except the Great Basin region. Plots were located on a permanent sampling grid and were typically 27 km away from their nearest neighbor. Plots were not sampled in non-forested areas, causing lower plot densities in some parts of the study area such as the

southern San Joaquin Valley. The second database consists of 33 additional plots surveyed in 2002. Plots were located in urban parks throughout the greater Central Valley, which encompasses the Central Valley, greater Bay area, northern central coast, and Sierra Nevada foothills.

I re-examined all *Physconia* vouchers for *P. fallax*, *P. californica*, and *P. isidiomuscigena*, as most collections were identified before description of these species, and all three look similar to other species in the genus. I did not include data from other studies or herbaria, because environmental data needed for the models would not be available. However, plots in the two databases are well distributed over the study area and span a wide range of environmental conditions. Thus, the maps should approximate the larger distribution trends in northern and central California.

#### Habitat Modeling

I used NPMR with a local mean estimator to investigate how distributions of the most abundant *Physconia* species are associated with environmental gradients. Single-species habitat models were developed using the NPMR add-in module for the PCORD statistical software package (McCune & Mefford 1999). NPMR is a form of nonparametric regression. In essence, this method analyzes environmental data from sites where the target species occurs to build a habitat model. The models work by estimating species occurrence for new sites based upon the proportion of occurrences at known sites with similar environmental conditions.

Model building is an iterative process in which NPMR searches through all possible multiplicative combinations of environmental variables to determine which are the best predictors of a target species occurrence. I used a Gaussian kernel function in which weights between 0 and 1 were assigned to all data points (Bowman & Azzalini 1997). Thus, for a given point, not all known sites contributed equally to the estimate. The more similar the environmental conditions of the known sites are to the new site, the higher it is weighted in the model for that new site. The form of the Gaussian function used for weighting is based upon the standard deviation ("tolerance") of each environmental variable.

Model quality was appraised with leave-one-out cross validation: (1) one data point was removed from the dataset; (2) the dataset (minus the removed site) was used to estimate the response for that point, using various combinations of environmental variables and tolerances; (3) model accuracy was determined by comparing estimates of species occurrence for the removed site to actual species occurrence at that site; (4) this process was repeated for all plots in the dataset and; (5) a Bayesian statistic, the logB, was used to compare the accuracy (performance) of each model to the performance of a naïve model. In the naïve model I used, probability of occurrence at a given site equals the overall frequency in the study area. According to Kass and Raftery (1995), a model with a logB greater than 2 performs decisively better than a naïve model.

The *Physconia* habitat models were based upon all sites included in the distribution maps. The models were used to generate univariate species response curves that depict the probability of a species along an environmental gradient. These models may be used in the future to estimate species occurrence at other sites if the same environmental variables are provided.

RESULTS AND DISCUSSION

Species Distributions

*Physconia isidiomuscigena* and *P. leucoleiptes* were rare across the landscape while *P. californica* was absent. *Physconia isidiomuscigena* was found in only one site (specimen resides with author), growing epiphytically on *Quercus* sp. in Stanislaus county (Figure 1a). The collection was unusual in that

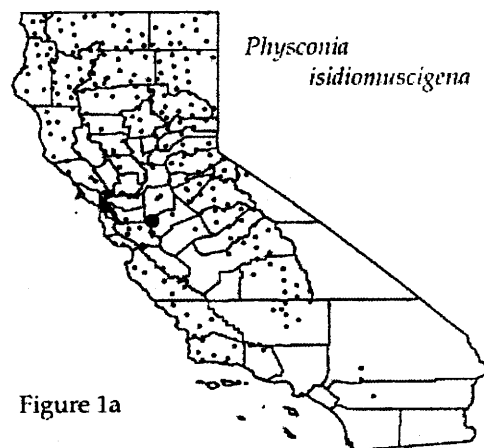


Figure 1a

this species is typically saxicolous and has been collected only a couple times in California from more southern locales near Los Angeles. *Physconia leucoleiptes* occurred in low abundance at 8 sites widely distributed around the periphery of the Central Valley, occurring in the Sierra Nevada foothills, as far south as Kern county, and as far north as Tehama county (Figure 1b). This species is known

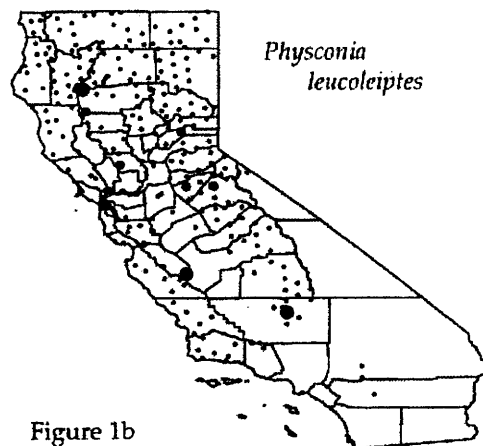


Figure 1b

to be much more common in the eastern United States so its low frequency is not surprising.

*Physconia fallax* was occasional within the study area but where it occurred it was typically abundant (Figure 1c). In 10 of the 15 sites I estimated there were over 10 thalli on the plot. The sites were widely spaced in the greater Central Valley, extending into the dry region of Lassen and Modoc counties. *Physconia fallax* was absent on the immediate coast but did occur within 15 miles of the ocean in a montane, *Quercus douglasii* stand in Los Padres National Forest.

Caption for distribution maps for *Physconia* species (Figures 1a through 1g). Abundance at each site is indicated by symbol size.

- None
- Rare (3 thalli or less)
- Uncommon (4-10)
- Common (>10 but not found on more than 50% of all boles and branches)
- ⊙ Abundant (found on more than 50% of all boles and branches)

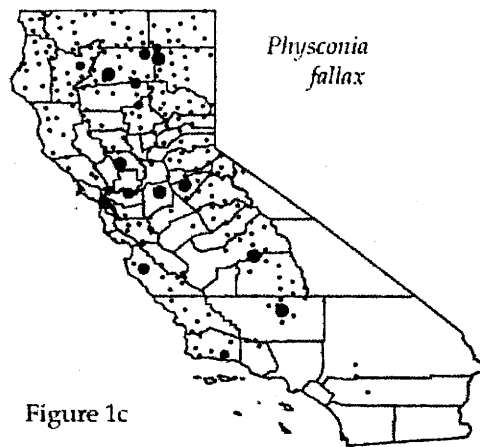


Figure 1c

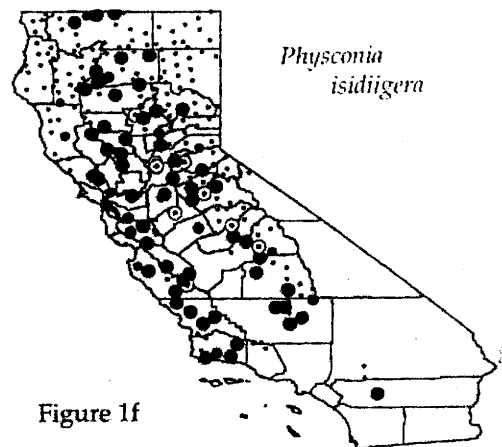


Figure 1f

*Physconia americana*, *P. enteroxantha*, *P. isidiigera* and *P. perisidiosa* were more common in the study area, having distributions centering in or near the Central Valley (Figure 1d, e, f & g). All species were sparse in high elevation plots and in the relatively

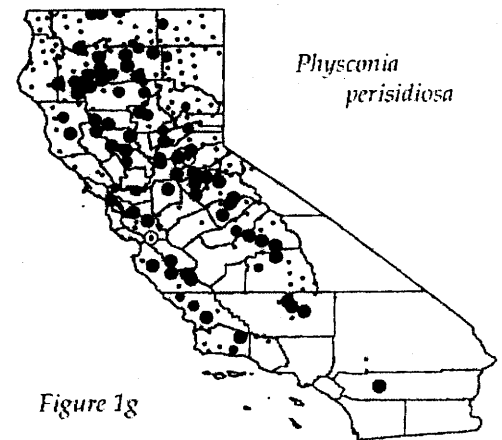


Figure 1g

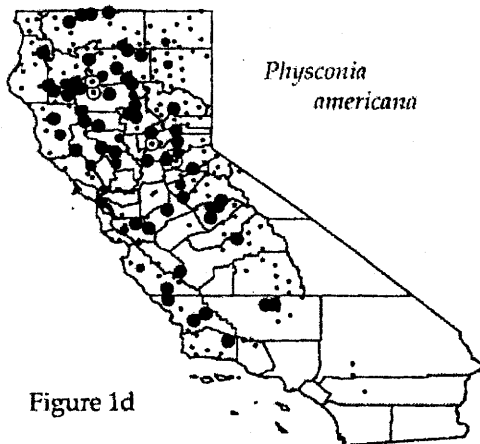


Figure 1d

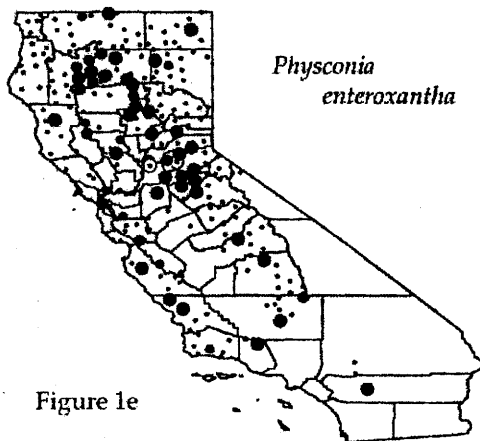


Figure 1e

cool Modoc Plateau and northwest coast. Distributions of these species were generally similar although modest variation is evident in figure 1. Most notably, *P. enteroxantha* and *P. americana* seem less common south of the Bay area than in the north. *Physconia americana* also appears to be more common in the northern California Coast Ranges than the other species I examined. *Physconia isidiigera* occurred in all urban plots, including parks in downtown Fresno, Merced, and San Jose where epiphytic lichen species richness was low, ranging from 3 to 7 species. Usually, however, multiple *Physconia* species were found on the same plot, often intermixed on the same tree. In the greater Central Valley urban plots where substrate data was collected, all four species occurred on a wide range of hardwood substrates but were consistently absent on coniferous trees.

*Species Response Curves*

Habitat models were constructed for the 5 most

Table 1: Summary of NPMR habitat models. Tolerances are reported for the multivariate models.

Response Variables	logB	Variable	Tolerance	Variable	Tolerance	Variable	Tolerance
<i>P. americana</i>	9.2	Elevation (m)	1137.36	Humidity (%)	2.16	*	*
<i>P. enteroxantha</i>	5.7	Elevation (m)	473.90	*	*	*	*
<i>P. fallax</i>	0.8	Max. Temperature (°C)	27.88	*	*	*	*
<i>P. isidiigera</i>	22.7	Dew Temperature (°C)	14.76	Max. Temperature (°C)	9.84	*	*
<i>P. perisidiosa</i>	19.6	Hardwood Richness	0.84	Humidity (%)	4.32	Mean Temperature (°C)	3.22

common species: *Physconia americana*, *P. enteroxantha*, *P. fallax*, *P. isidiigera*, and *P. perisidiosa* (Table 1). The distributions of most *Physconia* species were relatively well described by NPMR habitat models with high logB statistics (Table 1; Kass and Raftery 1995). Nonparametric multiplicative regression identified elevation as the best predictor of *P. enteroxantha* and maximum temperature as the best predictor for *P. fallax*. The remaining species were better described by more complex models: relative humidity and elevation were the best predictors of *P. americana* occurrence, dew temperature and

maximum temperature were the best for *P. isidiigera*, and mean temperature, relative humidity, and diversity of hardwood species were the best predictors of *P. perisidiosa*.

Species response curves for each predictor are shown in Figure 2. Any given response curve necessarily shows only the relationship between a species occurrence and a single environmental gradient. While the full multivariate NPMR models are useful for estimating occurrence across the landscape, the complex multiplicative relation-

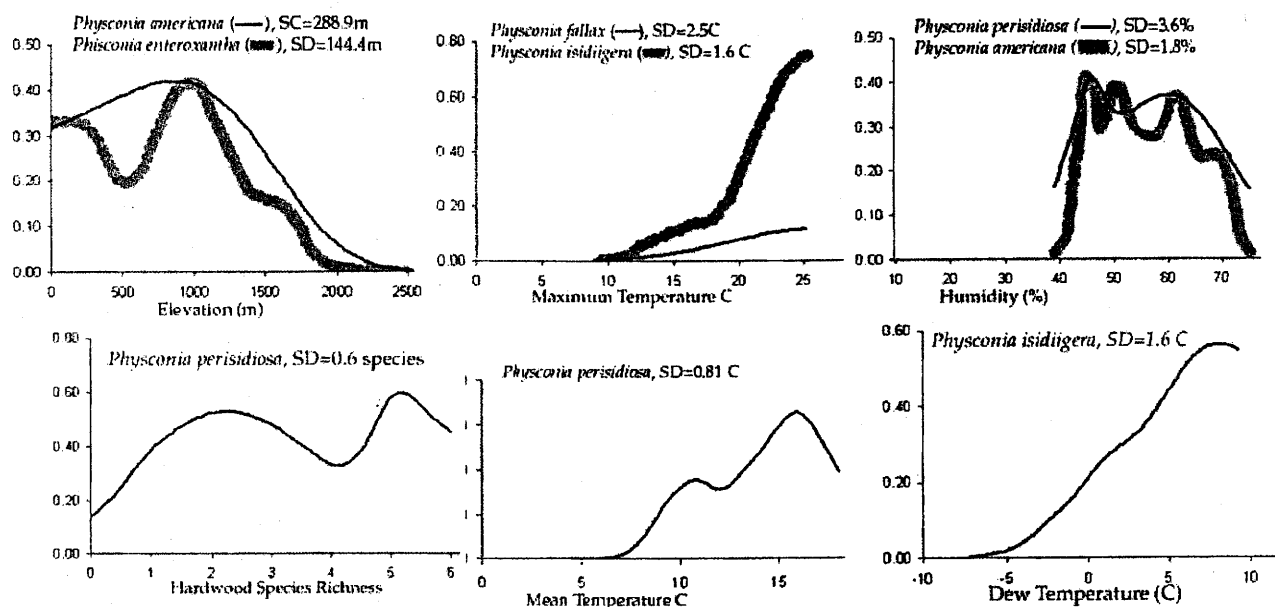


Figure 2: Species response curves from NPMR habitat models. Each species has 1-3 response curves. SD = standard deviations (tolerances) for univariate models.