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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. isid-*

iomuscigena (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-*

lax, *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

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)
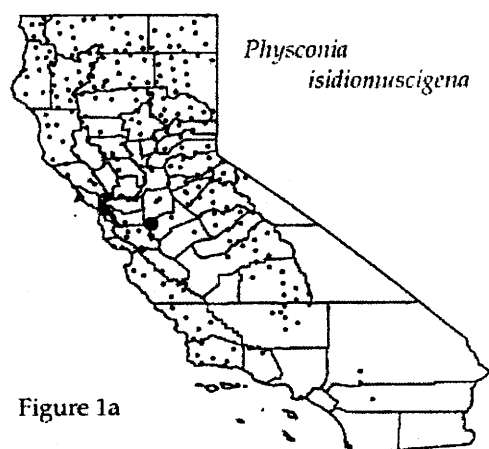

Figure 1a

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
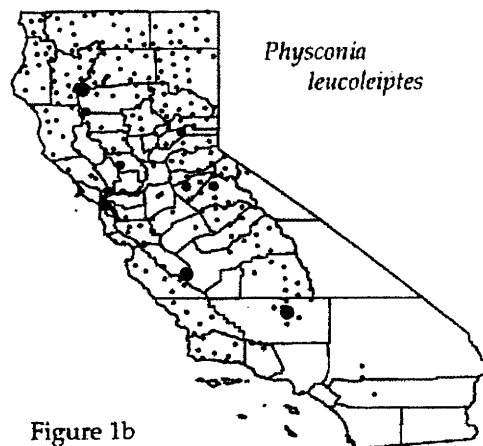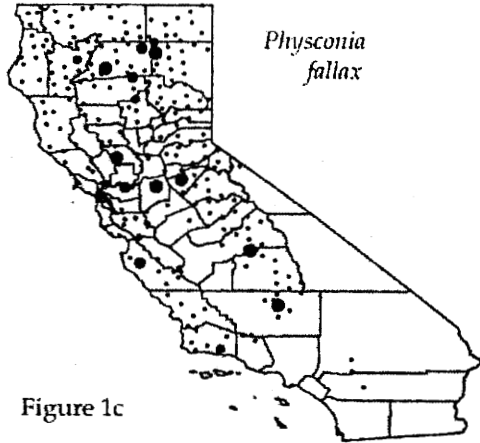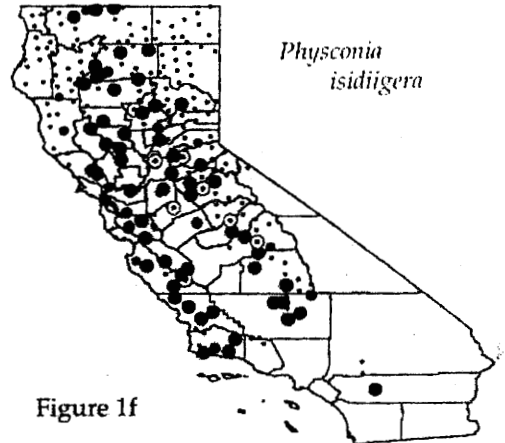

Figure 1b

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.

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Figure 1c

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
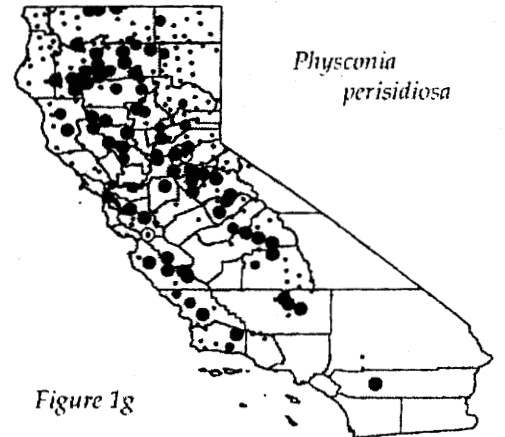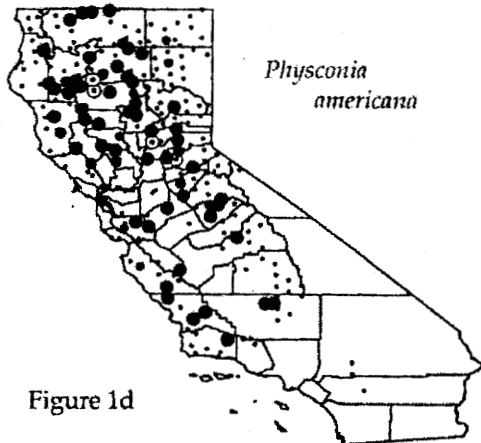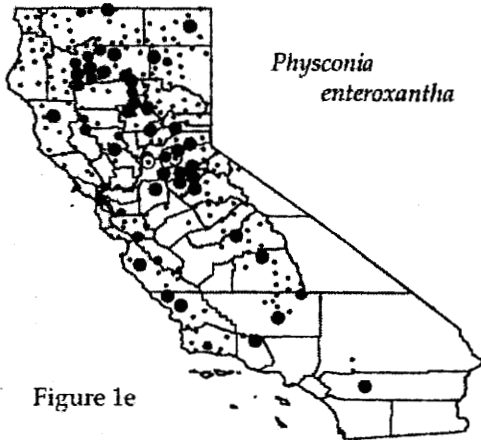

Figure 1d

Figure 1e

Figure 1f

Figure 1g

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	Toler-ance	Variable	Tolerance	Variable	Toler-ance
P. americana	9.2	Elevation (m)	1137.36	Humidity (%)	2.16	*	*
P. enteroxantha	5.7	Elevation (m)	473.90	*	*	*	*
P. fallax	0.8	Max. Temperature (°C)	27.88	*	*	*	*
P. isidiigera	22.7	Dew Temperature (°C)	14.76	Max. Temperature (°C)	9.84	*	*
P. perisidiosa	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-
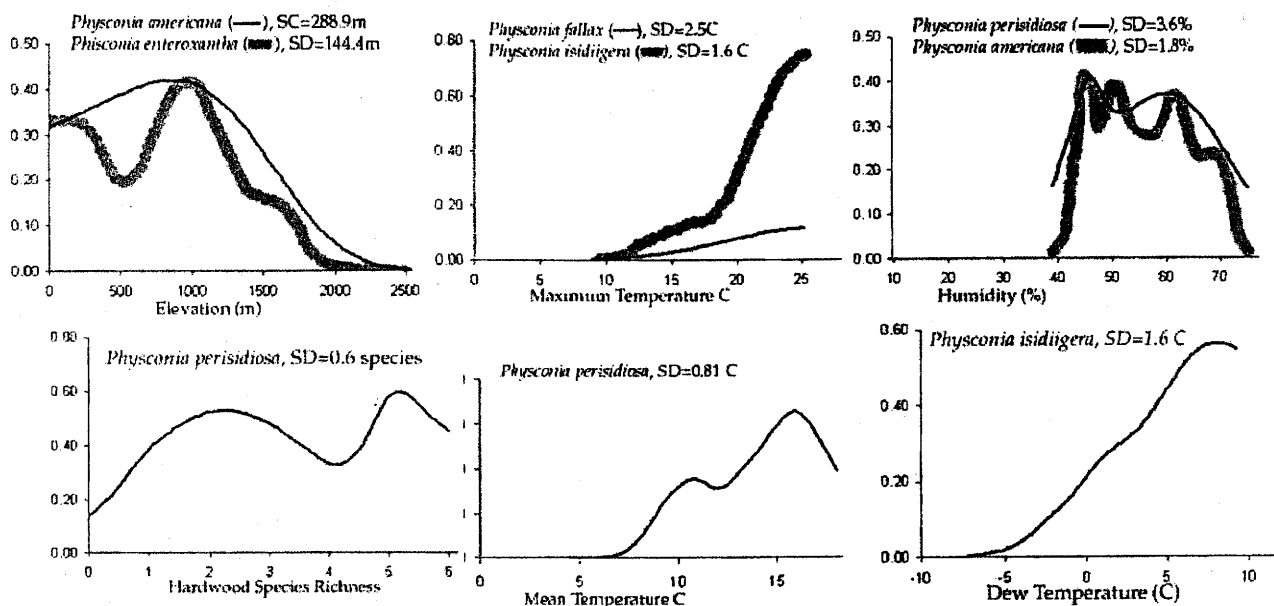

Figure 2: Species response curves from NPMR habitat models. Each species has 1-3 response curves. SD = standard deviations (tolerances) for univariate models.

ships between environmental predictors are difficult to visualize and interpret as graphics. Thus, for example, the response curve for *P. americana* and humidity does not account for the effects of elevation on occurrence. When the NPMR model is used to estimate *P. americana* occurrence at a particular site, however, both variables are considered simultaneously.

Interpretation of the single-gradient response curves is relatively straightforward. For example, the curves for *P. americana* would be interpreted as follows: relative humidity is a moderately strong predictor of *P. americana* occurrence and the probability of finding this species is relatively high (0.27-0.40) for humidity levels between 48-64%. The probability steeply declines at a relative humidity below 42% and above 69%. Elevation is also a moderately strong predictor of *P. americana* incidence. At elevations between 518-1097 m, incidence is expected to be high (0.40-0.41). Probability of *P. americana* is less than .05 at elevations over 2042 m. All response curves should be read in this fashion. Small fluctuations in the response curves (i.e. the response curves for *P. americana* and humidity) probably result from noise in the dataset or the action of other factors not accounted for in the analysis.

The *P. fallax* model was relatively weak as evidenced by the low logB and lack of strong environmental predictors (Table 1). There are two probable explanations: 1) the model was based upon relatively few sites and 2) I did not provide NPMR with the most relevant, defining habitat characteristics for this species. The number of *P. fallax* sites may be underestimated since most lichen community surveys were conducted before this species was described. Due to its yellow soralia, field workers could have easily overlooked this species as *P. enteroxantha*.

CONCLUSIONS

While climate and stand structure are typically important factors influencing lichen distributions, one can't conclude that the environmental predictors identified by NPMR are the cause of species presence or absence. A predictor may instead be a correlate of the actual causal factor that determines habitat suitability. However, the models inspire many questions about Physconia ecology. For instance, are *P. americana* distributions limited by atmospheric moisture as suggested by the habitat model? If that is the case, what morphological and physiological aspect of this species makes it so? Why do distributions of many of the other common species seem more related to temperature? These habitat models may also be used in practical applications like estimation of species occurrence across the landscape and identification of areas where each species is most likely to occur.

Understanding the distribution of Physconia species across the landscape is particularly important because of their potential utility as indicator species. Past research has shown it is possible to map NH_3 with the distributions of nitrophilous ("nitrogen-loving") species (van Herk 1999 & 2001). *Physconia enteroxantha* and *P. perisidiosa* are generally considered nitrophilous while *P. americana*, *P. fallax*, and *P. isidiigera* may also be nitrophilous or at least tolerant to high levels of NH_3 deposition. In this study, all five species seemed more abundant in areas where one would expect high NH_3 deposition, such as on wayside trees near livestock enclosures and near areas of high automobile traffic. A logical extension of this work would be to examine the relative influences of NH_3 deposition and climate on Physconia distributions, which would be an invaluable step towards realizing the full indicator potential of these species.

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