



Tracking lichen community composition changes due to declining air quality over the last century: the Nash legacy in Southern California

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Abstract: Southern California's South Coast Air Basin includes the heavily urbanized Los Angeles and Orange counties, the inland urban and suburban areas, and the surrounding mountain ranges. Historically high air pollution makes the region a natural laboratory for investigating human impacts on natural systems. Regional lichen distribution records from the early 1900s compared to more extensive montane data collected in the 1970s demonstrated declining species distribution ranges, attributed to increasingly heavy air pollution conditions. In 2008, we surveyed 21 sites in the mountains surrounding the basin for lichens, 18 of which were surveyed in 1976–77, and we quantitatively compared communities across the thirty-year span. The 1976–77 findings showed a marked decrease in species distribution in comparison to anecdotal evidence from early 1900s collections and a 1913 flora. Our findings show that additional community shifts occurred since the earlier surveys, suggesting a worsening of pollution impact. Of the species in the region, *Melanohalea subolivacea*, one of the most pollution-sensitive species remaining in the Basin's flora, decreased markedly in abundance between 1976–77 and 2008. Lichens in the more nitrophilous genera *Physcia*, *Physconia*, and *Xanthomendoza* increased in abundance. No sensitive species have re-appeared since the '76–77' inventories.

Keywords: air pollution, lichen community composition, nitrogen, ozone, Southern California

Introduction

Over the last three decades Dr. Tom Nash and his students have investigated lichen communities in Southern California, emphasizing their use as biomonitors of air pollution in the Los Angeles air basin. The accumulated body of work provides unique continuity for lichen research in North America, and a strong argument for the usefulness of lichens as bio-indicators in this heavily polluted region. The work we reference in this paper was conducted by a group that includes Dr. Nash's last graduate students before his retirement, and revisits work conducted by his first doctoral student.

Since the early 1900s, the L.A. Basin has changed from a large, sparsely populated agricultural basin to a highly urbanized region with a population of approximately 17 million people (SHEYA & HEIM 2008). The increased pollution load due to vehicle emissions combined with topographic and climatic conditions have interacted to create massive air quality problems. Pollutants moving downwind from urban sources into the mountain ranges surrounding the basin are trapped beneath the nearly constant summer inversion layers, creating a soup of toxic air (BYTNEROWICZ & FENN 1996, FENN et al. 1996). As a result, lichen communities in southern California have been exposed to some of the worst air pollution in the country for the last 70 years (FENN et al. 1996, LEE et al. 2003, COX 2009).

The first study of lichens in Southern California was conducted by Dr. Herman E. Hasse, an army surgeon stationed in Santa Monica in the early 1900s. He collected almost 500 species of lichens throughout the valleys and mountains of Southern California, including specimens from as far north as Yosemite Valley (TUCKER 2007). Hasse's *Lichen Flora of Southern California* (1913) was published at a time when there were few lichenologists working in the United States, thus it provides invaluable baseline information.

In the late 1970s, the first doctoral student of Dr. Tom Nash, Lorene Sigal, surveyed 55 lichen communities on oaks and conifers in five mountain ranges around the Los Angeles air basin (in the Los Padres, Angeles, San Bernardino, and Cleveland National Forests, and Cuyamaca State Park) (SIGAL 1979, SIGAL & NASH 1983, NASH & SIGAL 1998). Roughly 50% of the lichen species described and collected by Hasse in the montane regions of Southern California in the earlier part of the century were not present in her plots. Species were unevenly distributed between Sigal's sites. For example, *Hypogymnia imshaugii*, thought to be pollution tolerant, was present at polluted sites, but morphologically altered and bleached compared to specimens from clean sites. Sigal found that the regional ozone (O₃) gradient corresponded with patterns in species composition and thus concluded that O₃ was the primary driver of lichen decline in the montane regions surrounding the Los Angeles air basin. Preliminary results from peroxyacetyl nitrate (PAN) fumigations suggested that PAN might also negatively affect lichen physiology (SIGAL & TAYLOR 1979).

Several of Dr. Nash's subsequent students continued working in the Los Angeles air basin, and over time evolved a different explanation for the changing lichen communities. In the early 1980s, Lisa Ross surveyed lichen communities on coast live oaks (*Quercus agrifolia* Batt. & Trab.) in the Santa Monica Mts. north of Los Angeles (ROSS 1982). She found a significant reduction in the number of species present in the Santa Monica Mts. compared to the diversity of

species collected by HASSE (1913). Her work connected low species diversity and abundance with proximity to Los Angeles pollution and high O₃ concentrations. However, when Ross fumigated lichens with O₃, only one species showed deleterious responses, and only at unrealistically high concentrations (ROSS & NASH 1983).

Then, in the late 1980s Kansri Boonpragob began a transplant experiment with the pollution sensitive species *Ramalina menziesii* Taylor, a historically abundant species that had been locally extirpated. She transplanted thalli from clean sites north of the basin to the heavily polluted San Dimas Experimental Forest north of Los Angeles and monitored thallus response to ambient air quality (BOONPRAGOB 1987, BOONPRAGOB & NASH 1990, BOONPRAGOB & NASH 1991). Her transplanted lichens died within ten weeks in summer, the high pollution season, and leached considerable amounts of nitrate (NO₃-), fluoride, phosphate, chloride, and ammonium ions (NH₄+) when rinsed (BOONPRAGOB et al. 1989). Her results correlated the high NO₃- leaching with physiological decline.

A second transplant experiment in the Basin was initiated in 2004 by Ken Sweat and Dr. Nash who also began a preliminary resurvey of some conifers visited by Sigal in the 70s. Results strongly suggested that air pollution was quickly lethal to transplanted *Usnea* sp. and *Hypogymnia imshaugii* (SWEAT & NASH, unpublished) but results remain preliminary and do not identify a particular pollutant as the culprit.

In 2006–2009, a fumigation experiment conducted by Jennifer Riddell showed that gaseous nitric acid (HNO₃), an important pollutant in the mountains surrounding the basin, had a strong negative effect on lichen physiology while O₃ did not (RIDDELL et al. 2008, RIDDELL et al. 2010). This work clearly pointed to N pollutants as the probable driver of the lichen community changes observed by Sigal in the 1970s, a hypothesis supported by measurements of exceptionally high N loading to forests surrounding the Los Angeles air basin and surrounding mountains (BYTNEROWICZ & FENN 1996).

In a final study based out of the Nash lab, we revisited Lorene Sigal's sites in 2008 to quantitatively describe lichen community shifts. Here we report on observed changes in species' abundances since 1977 and discuss what air quality changes are indicated. We hope lichenologists will build upon the decades of research guided by Dr. Nash and continue revisiting these sites to chronicle the fates of these lichen communities.

Materials and methods

Site Data: We surveyed lichens at 21 sites in the Angeles National Forest, the San Bernardino National Forest, and the Mt. Palomar area of the Cleveland National Forest (Fig. 1, Tab. 1). Eighteen of these sites were visited by Lorene Sigal in 1976–77. We did not resurvey her sites in the Cuyamaca State Park due to a large wildfire that burned most of the park in 2004. Due to time constraints, we focused our efforts on the Forests within the air basin, and thus also excluded the Los Padres National Forest sites. Where possible, we located transects at the same locations surveyed by Sigal, although some sites had experienced recent forest fires, tree thinning, or urban development. When necessary, we located our new transects as close as possible to the old ones. We abandoned sites if we could not

sample close to the original location, and when original sites were too close to each other (in order to avoid pseudo-replication; HURLBERT 1984). In three cases we added sites close enough to Sigal's pseudoreplicated sites to capture the local community, but far enough away (at least one km) to avoid pseudoreplication. We used these new sites in overall analyses of forest species, but did not compare them directly to 1976–77 sites (Tab. 1). For each site, we recorded GPS coordinates, elevation, slope, aspect, azimuth, and tree density. Transects were more meandering than linear. We collected lichen data from 10 black oaks and 10 conifers, each at least 10 m from the last sampled conifer or oak. Transects ran north northeast, with the slope. Diameter at breast height (DBH, ~1.4 m above uphill ground level) was recorded for each sampled tree.

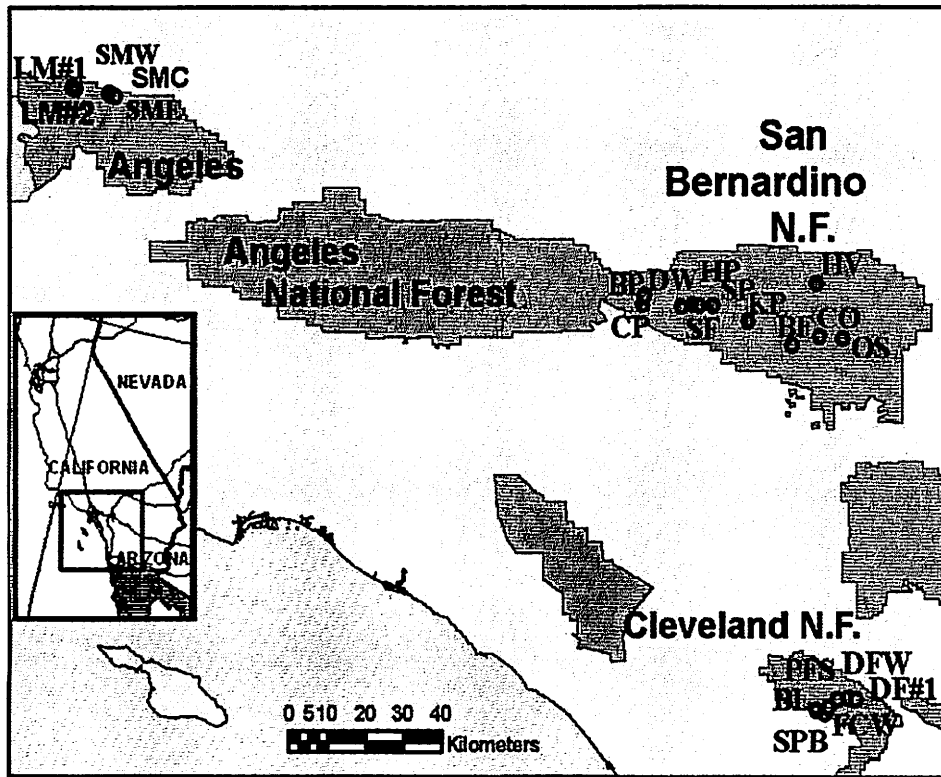


Fig.1. Map of study area with sites from 2008 surveys. Site codes are defined in Table 1.

Conifers: We surveyed 10 conifers per site; when possible, this included at least five *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., with the remainder made up of species present at the site, including *Pinus jeffreyi* Balf., *P. ponderosa* C. Lawson, and *Pseudotsuga macrocarpa* (Vasey) Mayr). Conifer species composition varied considerably between sites. We began with the first suitable tree >38 cm DBH bearing no obvious signs of recent burn damage, at least 20 meters in from stand edge in order to minimize edge effects. Subsequent trees had to be at least 10 m from the last surveyed tree, and we moved generally downhill with the slope to the next suitable tree. Following the method of SIGAL & NASH (1983), we used a measuring tape to demarcate a linear ‘transect’ around the tree

at breast height. We calculated the percent cover (the percent of the linear transect in contact with each lichen species) of *Letharia vulpina* (L.) Hue and *Hypogymnia imshaugii* Krog (the two species for which Sigal reported percent cover).

***Quercus kelloggii*:** We recorded lichen abundance on *Q. kelloggii* Newberry trees > 14 cm DBH that had no obvious signs of fire, damage or disease. Using a 5 × 16 cm wire mesh grid with 0.5 cm² squares (200 squares per grid), we estimated lichen cover by counting the number of squares filled by each lichen species (down to the half square) in each of the four cardinal directions of the bole at breast height (N, E, S, W). Percent cover was then calculated for each site as percent of the total grid area sampled across all oaks. Both macrolichen and crustose lichen cover were recorded, although due to uncertain field identifications, we do not use crustose lichens in comparisons of percent cover.

Lichen identification and statistical analysis of lichen communities shifts: Taxonomy was reconciled as much as possible to allow for comparisons between years (Tab. 2). Unknown lichen species were collected for further identification in the laboratory, and voucher specimens are housed at the Arizona State University Lichen Herbarium.

In the 1976–77 sampling period, percent cover was recorded for only four lichen taxa shared with the 2008 dataset on oaks, and two taxa on conifers. All other species found in Sigal's study were noted as present or were absent on trees within our plots. We separated the San Bernardino National Forest into eastern and western sections due to the large difference in air quality between these two regions (BYTNEROWICZ & FENN 1996). We compared percent cover values using two-way repeated measures ANOVA in SAS with Tukey-Kramer HSD multiple comparison tests, with forest and year as main factors. We log transformed percent cover data to meet the ANOVA assumptions of equal variance and normality. Because lichen percent cover on conifers was so sparse, we were unable to run quantitative analyses on conifer data.

Results and discussion

A total of 51 taxa were recorded in the 2008 survey and 56 in 1976–77. This discrepancy in number cannot be attributed to a loss of species, however, as the 1976–77 surveyors were more diligent in recording crustose species, and numerous taxonomic shifts occurred in the interval between studies (see Tab. 2). Many of the 1976–77 taxa were expanded into multiple species by 2008. Few of the species encountered are widely considered pollution-sensitive, exceptions being the *Alectoria* sp., *Cetraria canadensis*, and *Nodobryoria abbreviata* that Sigal found on conifers in 1976–77.

Table 1. 1976–77 and 2008 study sites. Some plots were not visited in both time periods, as indicated. See Methods for descriptions of site locations.

Site Name	Map Code	Location		1976-77	2008
<i>Palomar Mt. Area--Cleveland National forest</i>					
Boucher Lookout #1	BL	33.335	116.919		
<i>Boucher Lkt. #2</i>					*(SPB)
<i>Boucher Lkt. #3-4</i>					+
Deer Flat East	DF#1	33.36	116.826		
Deer Flat West	DFW	33.363	116.842	***	
<i>Deer Flat #3</i>					*(DFW)
Fry Creek West	FCW	33.344	116.889		
<i>Fry Creek West #2</i>					*(PFS)
<i>Observatory Camp.</i>					+
Palomar Fire Station	PFS	33.361	116.869	***	
Palomar State Park Boundary	SBP	33.329	116.898	***	
<i>San Bernardino National Forest</i>					
Barton Flat	BF	34.166	116.912		
Breezy Point	BP	34.257	117.32		
Camp Angelus	CA	34.147	116.976		
<i>Camp O'Ongo</i>					** (HP)
Camp Osceola	CO	34.163	116.857		
Camp Paivika	CP	34.238	117.324		
Dogwood	DW	34.237	117.206		
<i>Green Valley Creek</i>					<i>Burned</i>
Heap's Peak Arboretum	HP	34.235	117.161	***	
Holcomb Valley	HV	34.284	116.919		
Keller Peak/Deerlick	KP	34.201	117.08		
<i>NE Green Valley</i>					<i>Burned</i>
<i>Rock Camp</i>					<i>Logged</i>
Sky Forest	SF	34.236	117.191		
<i>Tunnel Two</i>					<i>Burned</i>
<i>U.C. Conf. Center</i>					<i>Developed</i>
<i>Sawmill Mtn. area--Angeles National Forest</i>					
Sawmill Mt. East	SME	34.697	118.567		
Liebre Mt #1	LM#1	34.716	118.659		
Liebre Mt #2	LM#2	34.718	118.668		
<i>Liebre Mt. #3</i>					+
Sawmill Mt Camp.	SMC	34.701	118.573		
Sawmill Mt. West	SMW	34.705	118.58		

* Site considered a pseudoreplicate. A substitute plot ≥ 1 km away was established; see code in parentheses, **Inaccessible private land, ***Site not sampled, + Site abandoned, considered a pseudoreplicate.

Tab. 2. Species list from surveys. Yearly columns indicate species found in surveys, and 1976–77 column lists older taxonomy.

Species List	2008	1976-77
<i>Alectoria</i> sp.		C
<i>Amandinea punctata</i> (Hoffm.) Coppins & Scheid., Mass.		<i>Buellia punctata</i> (Hoffm.) A. Massal O
<i>Aspicilia</i> sp.		O
<i>Buellia dakotensis</i> (H. Magn.) Bungartz	C, O	
<i>B. triphragmoides</i> Anzi		*
<i>Caloplaca</i> cf. <i>pinicola</i> Magn.		O
<i>C. californica</i> Zahlbr.		O
<i>Caloplaca</i> sp. (sorediate)		O
<i>Caloplaca</i> sp. (with apothecia)	O	
<i>Caloplaca</i> sp. (sorediate)	O	
<i>Candelaria concolor</i> (Dicks.) B. Stein	C, O	O
<i>Candelariella vitellina</i> (Hoffm.) Müll. Arg.	C, O	O
<i>Cetraria canadensis</i> (Räs.) Räs.		C
<i>C. merrillii</i> Du Rietz	*	C
<i>Collema furfuraceum</i> (Arnold) Du Rietz	O, *	
<i>C. nigricans</i> (Huds.) DC.	*	O
<i>Evernia prunastri</i> (L.) Ach.		*
<i>Hypocenomyce scalaris</i> (Ach. ex Lilj.) M. Choisy		<i>Lecidea scalaris</i> (Ach.) Ach.; O
<i>Hypogymnia imshaugii</i> Krog	C, O	<i>Hypogymnia enteromorpha</i> (Ach.) Nyl.; C
<i>Lecanora hagenii</i> group		O
<i>Lecanora mutabilis</i> Somm.		O
<i>Lecanora</i> sp. (w/ brown apothecia)		O
<i>L. subfusca</i> group	O	O
<i>Lecidella glomerulosa</i> (DC.) Steud.		O
<i>Lecidea scalaris</i> (Ach.) Ach.		O
<i>Lecidea</i> sp.	O	
<i>Lecidea</i> sp. (brown thallus)		*
<i>Lecidea</i> sp. (white thallus)		O
<i>Leptogium californicum</i> Tuck.		*
<i>Letharia columbiana</i> (Nutt.) J.W. Thomson	C	
<i>Letharia vulpina</i> (complex)		<i>L. vulpina</i> and <i>L. columbiana</i> grouped; C
<i>Letharia vulpina</i> (L.) Hue	C, O	
<i>Megaspora verrucosa</i> var. <i>mutabilis</i> (Ach.) Nimis & Cl. Roux	O	
<i>Melanelixia fuliginosa</i> (Schaer.) O. Blanco et al.	*	

O= found on oaks; C = found on conifer; * = found on soil, or rocks, or off plot

Tab. 2. Species list from surveys (continued)....

Species List	2008	1976-77
<i>Melanelixia glabra</i> (Schaer.) O. Blanco et al.	C, O	<i>Parmelia glabra</i> (Schaer.) Nyl.; C, O
<i>Melanohalea elegantula</i> (Zahlbr.) O. Blanco et al.	C, O	<i>Parmelia elegantula</i> (Sahlbr.) Szat; C, O
<i>Melanohalea subolivacea</i> (Nyl.) O. Blanco et al.	C, O	<i>Parmelia subolivacea</i> group; C, O
<i>Trapeliopsis viridescens</i> (Schr.) Coppins & P. James		<i>Micarea viridescens</i> (Schr.) Brodo*
<i>Nodobryoria abbreviata</i> (Müll. Arg.) Common & Brodo	*	<i>Bryoria abbreviata</i> (Müll. Arg.) Brodo & D. Hawksw.; C
<i>Ochrolechia</i> sp.		O
<i>Ochrolechia</i> sp. A. Massal.	C, O	
<i>Parmelia saxatilis</i> (L.) Ach.	*	
<i>Parmelia</i> sp.	*	
<i>P. sulcata</i> Tayl.	*	C, O
<i>Parmelina quercina</i> (Willd.) Hale	O, *	C, O
<i>Peltigera collina</i> (Ach.) Ach.		*
<i>P. rufescens</i> (Weiss) Humb.		*
<i>Pertusaria</i> sp.		O
<i>Phaeophyscia ciliata</i> (Hoffm.) Moberg	*	<i>Physcia ciliata</i> (Hoffm.) Du Rietz; O
<i>Phaeophyscia orbicularis</i> (Necker) Moberg	C, O	<i>Physcia orbicularis</i> (Neck.) Poetsch;
<i>Phaeophyscia sciastra</i>		<i>Physcia sciastra</i> (Ach.) Du Rietz; O
<i>Phaeophyscia</i> sp. Moberg	C, O	
<i>Physcia aipolia</i> (Humb.) Fürnrohr	C, O	O
<i>P. biziana</i> (A. Massal.) Zahlbr.	C, O	O
<i>P. callosa</i> Nyl.		O
<i>P. dimidiata</i> (Arnold) Nyl.	*	
<i>P. leptalea</i> (Ach.) DC.		O
<i>Physcia</i> sp.	C, O	
<i>Physcia</i> complex: <i>P. adscendens</i> (Fr.) H. Olivier and <i>P. tenella</i> (Scop.) DC.	C, O	C, O
<i>P. stellaris</i> (L.) Nyl.	*	O
<i>Physcia tribacia</i> (Ach.) Nyl.	C, O	
<i>Physconia americana</i> Essl.	O, *	
<i>P. californica</i> Essl.	*	
<i>Physconia</i> complex: <i>P. americana</i> , <i>P. enteroxantha</i> , <i>P. fallax</i> , <i>P. isidiigera</i> , <i>P. perisidiosa</i>		<i>Physconia grisea</i> (Lam.) Poelt; C, O
<i>P. musigena</i> , <i>P. americana</i> , and <i>P. distorta</i>		<i>Physconia pulverulenta</i> (Schreb.) Poelt; O

O= found on oaks; C = found on conifer; * = found on soil, or rocks, or off plot

Tab. 2. Species list from surveys (continued)....

Species List	2008	1976-77
<i>P. enteroxantha</i> (Nyl.) Poelt	C, O	
<i>P. fallax</i> (Zahlbr.) Essl.	*	
<i>P. isidiigera</i> (Zahlbr.) Essl.	C, O	
<i>P. perisidiosa</i> (Erichsen) Moberg	O, *	
<i>Platismatia glauca</i> (L.) W. Culb and C. Culb.	O, *	C
<i>Polychidium albociliatum</i> (Desm.) Sahlbr.	*	
<i>Ramalina farinacea</i> (L.) Ach.		*
<i>Ramalina</i> sp.	*	
<i>Rinodina</i> cf. <i>laevigata</i> (Ach.) Malme		O
<i>R. cf. pyrina</i> (Ach.) Arn.		O
<i>Rinodina</i> sp. (gray thallus)	O	
<i>Strangospora ochrophora</i> (Nyl.) R. Anderson		O
<i>Usnea</i> sp.		C
<i>Xanthomendoza</i> complex: <i>X. fallax</i> , <i>X. fulva</i> , <i>X. oregana</i>		<i>Xanthoria fallax</i> (Hepp.) Arn.; C, O
<i>X. fallax</i> (Hepp ex Arnold) Søchting, Kärnefelt & S. Kondratyuk	C, O	
<i>X. fulva</i> (Hoffm.) Søchting, Kärnefelt & S. Kondratyuk	C, O	
<i>X. galericulata</i> L. Lindblom	O, *	
<i>X. hasseana</i> (Räsänen) Søchting	O, *	
<i>X. oregana</i> (Gyeln.) Søchting, Kärnefelt & S. Kondratyuk	O, *	
<i>Xanthoria candelaria</i> (L.) Th. Fr.	O	O
<i>X. polycarpa</i> (Hoffm.) Th. Fr. ex Rieber	O, *	O

O= found on oaks; C = found on conifer; * = found on soil, or rocks, or off plot

Conifers: Macrolichen communities on conifers were consistently very species-poor in 2008, ranging from one to seven species found per site, using Sigal's methods. None of these conifer-dwelling species were abundant. Total lichen cover per site was less than 5% at 10 sites, and 10% or less at 16 of 19 sites. Among the 22 species recorded on conifers in 2008, the most abundant was by far the highly N-tolerant *Candelaria concolor*, which had a mean percent cover of 1.1%; most *C. concolor* abundance comes from conifers at two of the most N-impacted sites in our dataset, Breezy Point and Camp Paivika (Fig. 1; FENN et al. 2008, RIDDELL et al. 2010).

Letharia vulpina and *Hypogymnia imshaugii* are the only two conifer dwellers that Sigal characterized in terms of percent cover. If N impacts were increasing, we'd expect to witness a decline at least in *H. imshaugii*. Both species have

apparently decreased in cover since 1976–77 (Fig. 2) although results are not significant ($p > 0.05$). More convincing, but anecdotal, evidence of increasing N comes from the apparent colonization of conifers by nitrophytic (i.e. highly N-tolerant) species such as *Phaeophyscia orbicularis*, *Physcia* spp. complex, *Physconia* spp. complex, and *Xanthoria polycarpa*. These species are typically hardwood dwellers and Sigal did not detect them on conifer substrates (Tab. 2). Moreover, as mentioned previously, conifers in 2008 lacked the sensitive species detected by Sigal (*Alectoria* sp., *Cetraria canadensis*, *Nodobryoria abbreviata*), except at one site in the Sawmill Mt. area.

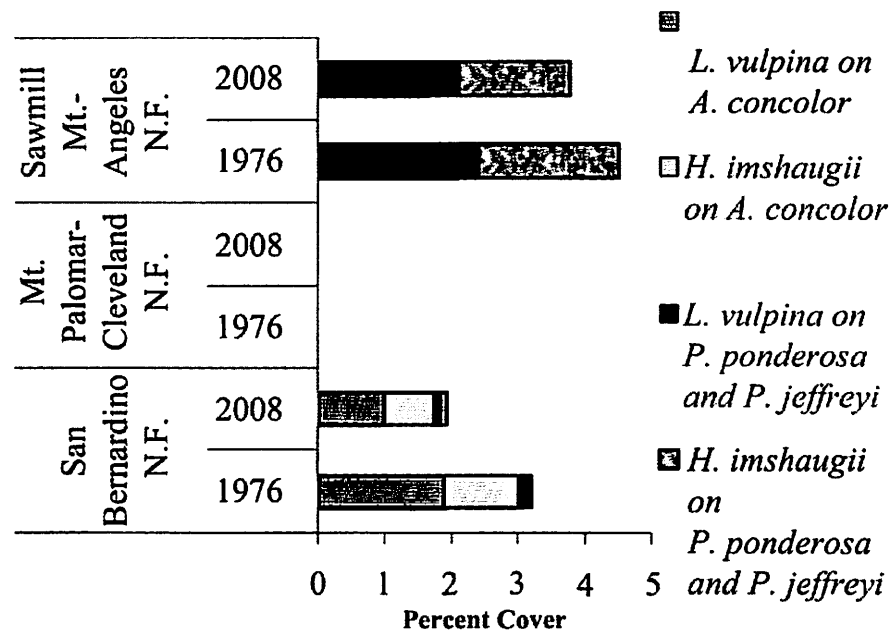


Fig. 2. Mean percent cover of *Letharia vulpina* and *Hypogymnia imshaugii* on *Abies concolor*, and *Pinus ponderosa* and *P. jeffreyi* in each forest in 1977 and 2008 surveys.

***Quercus kelloggii*:** In 2008, lichen cover on California black oaks varied between sites and between forests. The five taxa with the highest mean percent cover (averaged across all sites) were: *Xanthomendoza* spp. complex, 3.8%; *Physcia* spp. complex, 4.0%; *Physconia isidiigera* and *P. enteroxantha*, 5.2% (treated as one taxon, since they were difficult to differentiate in the field); *Candelaria concolor* and *Candelariella vitellina*, 2.0% (also treated as one taxon, since they were difficult to differentiate in the field), and *Melanohalea subolivacea*, 4.0%. Species complexes are defined in Table 2. These taxa made up a large portion of the percent cover overall, sometimes blanketing the oak boles.

Shifts in *Quercus kelloggii* lichen communities: We compared lichen communities between 1976–77 and 2008 using the four taxonomic groups SIGAL (1979) characterized in terms of percent cover (Fig. 3, Tab. 2): *Physcia* spp. complex, *Physconia* spp. complex, *Xanthomendoza* spp. complex, and *Melanohalea subolivacea*. The first three complexes describe nitrophilous groups

of species while *M. subolivacea* is generally considered more moderately N-tolerant (JOVAN 2008); SIGAL (1979) identified this latter species as the primary indicator of “clean air” in the 1976 *Q. kelloggii* surveys.

Overall the ANOVA models indicate that total abundance of nitrophilic species increased, while Sigal’s clean air indicator, *M. subolivacea*, decreased in forests of the L.A. Basin between 1976–77 and 2008. Percent cover of *Xanthomendoza* spp. differed significantly by year ($F = 4.24$, $p = 0.05$), while cover differed between both years and forests for *M. subolivacea* ($F = 10.33$, $p = 0.03$; $F = 7.12$, $p = 0.001$) and the *Physconia* complex ($F = 9.9$, $p = 0.004$; $F = 29.2$, $p < 0.001$). The interaction between forest and year was significant for *Physcia* spp. ($F = 5.8$, $p = 0.022$). Ten of 12 Tukey contrasts detected an increase in percent cover of

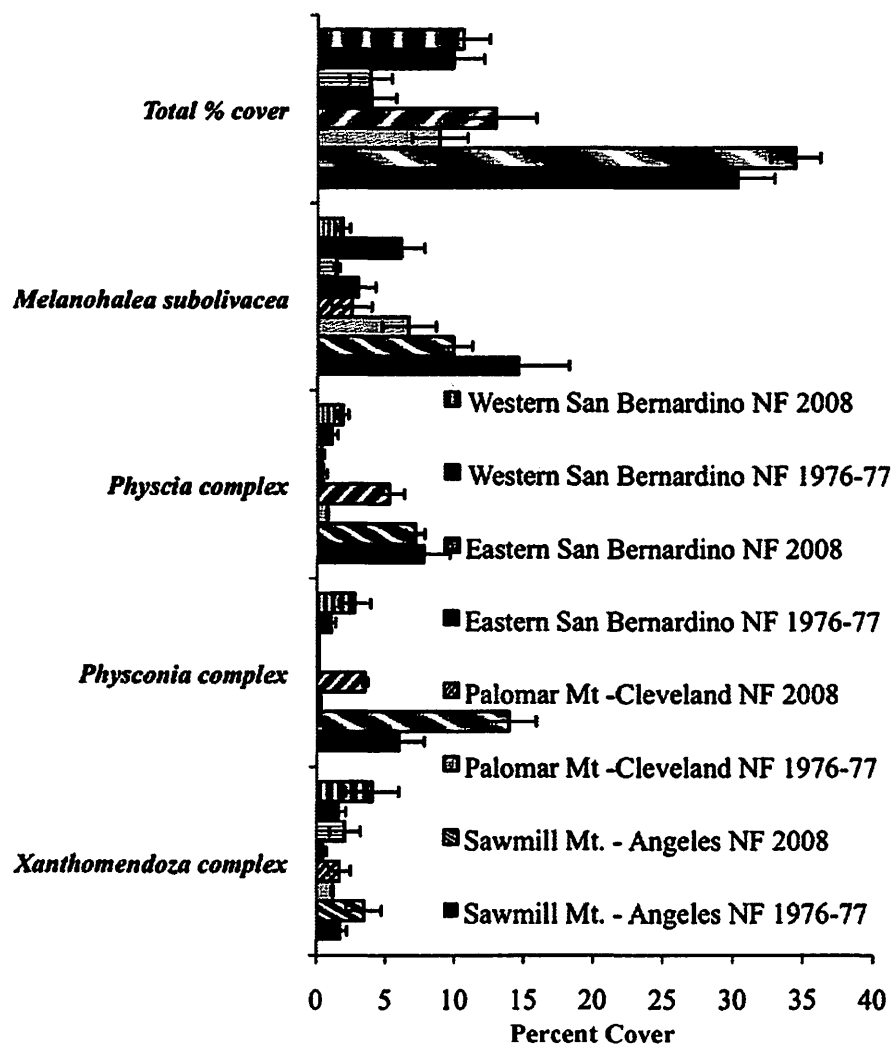


Fig. 3. Comparison of percent cover of four taxa from Sigal (1979) with percent cover from 2008 surveys on *Quercus kelloggii* bark. Error bars represent one standard error from the mean. See Table 2 for definitions of the species complexes.

nitrophilic species while all 4 contrasts concerning *M. subolivacea* detected a percent cover decrease over time (Tab. 3). Several of the contrasts lack statistical significance although they do consistently estimate a positive trend in nitrophilic cover and negative trend in *M. subolivacea* cover, which altogether suggests that the flora has become increasingly N-compromised.

Sites within the Palomar region, which Sigal considered relatively “clean” in her 1976–77 study, and the western San Bernardino Mts., which Sigal considered the most impacted, appear to have endured the most dramatic shift towards an N-tolerant community between 1976–77 and 2008 (Table 3). In the Palomar region, median percent cover of *M. subolivacea* significantly decreased by a factor of 4.31 (95% confidence interval: 1.24, 14.99; $p = 0.03$), meaning that we estimate median percent cover was more than 4 times greater in 1976–77. Conversely, *Physconia* spp. and *Physcia* complex cover increased significantly by factors of 11.1 (95% C.I. 1.8, 62.5; $p = 0.014$) and 7.3 (95% C.I. 2.4, 20; $p = 0.001$), respectively. Similarly, in the western San Bernardino Mts., *Physcia* complex spp. and *Xanthomendoza* complex spp. significantly increased in abundance by factors of 3.0 (0.76, 12.5; $p = 0.02$) and 4.3 (1.27, 7.14; $p = 0.04$), respectively.

It is clear that the lichen communities have not recovered from their depauperate condition of the late 1970s. If anything, the data suggest a worsening situation for lichens, as evidenced by the continued lack of sensitive lichen species and decreased abundance of *M. subolivacea*, one of the more sensitive remaining species in the southern California flora. Communities of *Quercus kelloggii* and conifers tell the same story; significantly increasing species on oaks are traditionally regarded as nitrophilic (i.e. *Physcia* spp., *Physconia* spp., and *Xanthomendoza* spp.) and since the late 70s these species have increasingly colonized Southern California montane conifers, as well.

Even though data were sparse and non-significant, the observed downward trend in percent cover for *Letharia vulpina* and *Hypogymnia imshaugii* on conifers indicates that these moderately pollution tolerant species could be continuing to lose ground. Lorene Sigal’s survey suggested these two species were already impacted by pollution patterns of the late 1970’s. For future studies evaluating lichen communities on conifers, a broader survey method that covers more tree surface area within a plot would be more appropriate.

Table 3. Mean percent cover of lichen species on oak trees for each forest, and results from a Tukey-Kramer HSD multiple comparisons between 1976-77 and 2008 in each forest. The data were log transformed to meet ANOVA assumptions, and ANOVA estimates were back-transformed. The estimate represents the median ratio of % cover 1976-77:2008. Upper and lower 95 % critical intervals are in parentheses.

		Total % cover	<i>Melanohalea subolivacea</i>	<i>Phycia</i> complex	<i>Physconia</i> complex	<i>Xanthomendoza</i> complex
Sawmill Mtn. Angeles National Forest	1976-77 mean	30.4	14.7	7.8	6.1	1.8
	2008 mean	34.4	9.9	7.1	13.9	3.5
	Estimate ($\pm$ CI)	0.87 (0.44, 1.74)	1.38 (0.45, 4.21)	.099 (0.37, 2.64)	0.38 (0.08, 1.86)	0.61 (0.14, 2.71)
	P	0.7049	0.5758	0.989	0.2402	0.5171
Palomar Mt. Cleveland National Forest	1976-77 mean	8.9	6.7	0.8	0.3	1.2
	2008 mean	12.9	2.5	5.2	3.5	1.7
	Estimate ($\pm$ CI)	1.77 (0.77, 4.07)	4.31 (1.24, 14.99)	0.14 (0.05, 0.41)	0.09 (0.02, 0.55)	0.75 (0.14, 4.03)
	P	0.1901	0.0284	0.0012	0.0136	0.7439
Eastern San Bernardino National Forest	1976-77 mean	3.9	2.9	0.4	0.04	0.5
	2008 mean	3.9	1.4	0.3	0.1	2.1
	Estimate ($\pm$ CI)	1.25 (0.58, 2.71)	2.89 (0.83, 10.07)	1.85 (0.62, 5.52)	0.45 (0.08, 2.65)	0.36 (0.07, 1.92)
	P	0.5718	0.1048	0.2809	0.3815	0.2401
Western San Bernardino National Forest	1976-77 mean	9.9	6.1	1.1	1.1	1.6
	2008 mean	10.6	1.9	1.9	2.8	4.0
	Estimate ($\pm$ CI)	0.66 (0.36, 1.21)	2.55 (0.96, 6.81)	0.33 (0.14, 0.79)	0.33 (0.08, 1.32)	0.23 (0.06, 0.88)
	P	0.1865	0.0703	0.0181	0.1265	0.0388

During the last 30 years, very high N deposition levels have been documented for sites at the western end of the San Bernardino Mt. range, which lies downwind of the urban Los Angeles air basin and the agricultural areas of San Bernardino County (BREINER et al. 2007). Little air quality data exist for either the Sawmill Mt. area or Mt. Palomar region although the observed lichen community shifts toward increased abundance of nitrophytic lichen species and decreased *M. subolivacea* indicate potentially worsening N inputs to these regions as well. We recommend air quality monitoring be initiated or increased in these regions, most especially in the Palomar area, where air quality is generally considered relatively “clean” despite minimal substantiating pollution measurements.

This study provides a rare insight into temporal changes in lichen communities in Southern California. Its data are especially useful because we chose to copy, as closely as possible, the methods of the previous survey, which allowed us to compare surveyed taxa with relative confidence. The findings we discuss in this paper are proving to be valuable in assessing air quality across the basin (paper forthcoming).

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