



ELSEVIER

Contents lists available at ScienceDirect

## Urban Forestry &amp; Urban Greening

journal homepage: [www.elsevier.com/locate/ufug](http://www.elsevier.com/locate/ufug)

# Urban forested parks and tall tree canopies contribute to macrolichen epiphyte biodiversity in urban landscapes

Hannah M. Prather\*, Sarah M. Eppley, Todd N. Rosenstiel

Portland State University, Center for Life in Extreme Environments and Department of Biology, 1719 SW 10<sup>th</sup> Avenue, SRTC rm 246, Portland, OR, 97201, USA



## ARTICLE INFO

## Keywords:

Air quality  
Biodiversity  
Bioindicators  
Forest canopies  
*Pseudotsuga menziesii*  
Urban forests  
Urban parks

## ABSTRACT

Land use changes through urbanization can dramatically impact floral and faunal species-specific survival and alter patterns of regional biodiversity. These changes can lead to complex, ecosystem scale interactions that yield both positive and negative impacts on urban and ex-urban biota. The Pacific Northwest region is one of the most rapidly urbanizing areas of the United States, with the human population estimated to increase more than fifty percent by 2050. Despite rapid population growth in the Pacific Northwest and a forest system known to provide extraordinary ecosystem services, relatively little is known about how human activities affect urban tree biology and the services these trees provide. Specifically, little is known about how urbanization impacts tall tree canopy epiphyte communities, a unique and sensitive component of Pacific Northwest trees which are known to contribute essential ecosystem functions. Here, we revisit a historic study of urban epiphytic lichen communities, initially conducted 18 years ago in Portland, Oregon, USA. Additionally, to compare ground and canopy-based survey methods and to gain a broader understanding of urban epiphytic communities, we comprehensively investigated the biodiversity of stratified urban canopy epiphyte lichen communities, for the first time. Our results show that tall, urban conifer trees and urban parks and forested areas can provide both heterogeneous and stratified habitats for urban-tolerant epiphytic lichens. We found significant and highly eutrophied lichen communities in all epiphytic surveys, suggesting that continued urbanization in the Portland metro region may further impact these communities despite overall gains in regional air quality during the 18 year study period. Our results support the distinct homogenization of urban epiphytic lichen communities, suggesting that it may be necessary to expand beyond measures of biodiversity to consider community composition and functional biodiversity in assessments of the ecology and potential ecosystem services of epiphyte communities within urbanizing landscapes.

## 1. Introduction

The process of urbanization—transitioning landscapes from predominately rural to predominately urban—is a major threat to global biodiversity (Vitousek et al., 1997; Chapin et al., 2000; Foley et al., 2005; Hillebrand and Matthiessen, 2009; Pereira et al., 2010), altering ecosystem processes and the resiliency of ecosystems to environmental change (Naeem et al., 1999; Chapin et al., 2000). The expansion of urban areas is on average twice as fast as urban population growth; the unprecedented speed and scale of change in the 21st century will result in significantly greater urbanization than the cumulative urban expansion in all of human history to date (IPCC 5th Assessment Report, 2014). The effects of urbanization on biodiversity have generated mixed results, indicating both positive and negative impacts for biota. Traditionally, urban environments have been thought to negatively impact biotic communities (McKinney, 2002; Seto et al., 2012;

Newbold et al., 2015), as urbanization can result in reduced biodiversity from habitat loss, physiological stress (*i.e.* air pollution, urban heat island effect), fragmentation, and disturbance. In contrast, more recent work has shown the potential of urban environments to contribute to biodiversity. Specifically, habitat heterogeneity and green infrastructure in the urban environment has been shown to foster plant biodiversity and harbor sensitive/rare plant species (Kowarik, 2011; Nielsen et al., 2014; Guénard et al., 2015; Pinho et al., 2016). Parks and urban forested areas, in particular, have been shown to significantly increase the biodiversity of multiple groups of species in urban landscapes (*i.e.* birds, *etc.*) (Nielsen et al., 2014; Pinho et al., 2016).

Urban forests have been well recognized as important ecological infrastructure of urban cities, and the benefits of urban trees have been well established in urban areas (Nowak et al., 2010; Elmqvist et al., 2015; Livesley et al., 2016). Urban trees, and the larger urban forest they comprise, contribute similar ecological services as that of natural

\* Corresponding author.

E-mail address: [pratherh@pdx.edu](mailto:pratherh@pdx.edu) (H.M. Prather).

<https://doi.org/10.1016/j.ufug.2018.04.012>

Received 6 December 2017; Received in revised form 18 April 2018; Accepted 18 April 2018

Available online 22 April 2018

1618-8667/ © 2018 Elsevier GmbH. All rights reserved.

forest ecosystems. Urban trees influence microclimate, improve air quality, regulate hydrologic cycles and provide habitat for wildlife (Ordóñez and Duinker, 2012; Rao et al., 2014).

The Pacific Northwest (PNW) region of the United States is known for its temperate rain forests dominated by large coniferous species, including Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco. The ecosystem services of PNW forest trees, including *P. menziesii*, are well-described (e.g. Kline et al., 2016; Clark et al., 2017). Similarly, the benefits of urban trees in the PNW are well-documented (Donovan and Prestemon, 2012; Sun et al., 2015; Chen et al., 2016; Mills et al., 2016), and include benefits directly to humans, including crime reductions (Chen et al., 2016), pollution mitigation (Rao et al., 2014), as well significant effects on hydrology (Wissmar et al., 2004) and wildlife populations (Donnley and Marzluff, 2004).

Within natural forest systems, PNW trees have a rich epiphytic flora with high biodiversity and biomass of canopy dwelling macrolichens (McCune, 1993; Jovan, 2008), and these epiphytes have been shown to be fundamental in ecological processes, including nutrient cycling, regulation of canopy microclimate, wildlife habitat, nesting material, etc. (Coxson and Nadkarni, 1995; Pettersson et al., 1995; McCune, 2000; Antoine, 2004; Wolf, 2009). However, few studies have examined how urbanization may affect biodiversity and the functional role of sensitive tree canopy dwelling epiphytes, despite their fundamental importance in many ecological processes across many ecosystems worldwide (Elbert et al., 2012; Porada et al., 2013, 2014). Unlike our understanding of the role of epiphytes contributing to ecosystem services in native forest landscapes, the role of epiphytes in urban landscapes remains mostly unknown.

It is well known that lichen epiphytes are particularly sensitive and responsive to changes in air quality and climatic variables (Geiser and Neitlich, 2007; Jovan, 2008; Geiser et al., 2010; Root et al., 2015) and dramatic shifts in lichen community structure can occur with urbanization, thus making community-level response a useful, early indicator of ecosystem degradation (Geiser and Neitlich, 2007; Davies et al., 2007). Lichen community shifts often result in replacement of sensitive species by nitrogen-tolerant, weedy eutrophic species (Jovan and McCune, 2005; Jovan et al., 2012). The dramatic shift in lichen communities near urban environments can also shift the functional biodiversity and ecological contributions of canopy dwelling lichen epiphytes, yet few studies exist on the scope of these functional and ecological shifts.

Here, we aim to understand how urbanization in the PNW impacts canopy macrolichen communities and how macrolichen community composition has changed over time. To address this aim, we conducted two complimentary surveys of epiphytic lichens in urban parks in Portland, Oregon. First, we conducted a ground-based surveys of epiphytic lichens in eight urban parks in the rapidly urbanizing Portland, Oregon, USA, which was paired with an existing, 18 year-old historical survey of lichen and air quality plots by the United States Forest Service (USFS) Air Resource Management Program (ARM) from the same sites. This survey allowed us to assess past and present day air quality, as derived from lichen community analyses and lichen community generated air-scores (Geiser and Neitlich, 2007) for the Portland Metro area. Second, we used stratified vertical canopy surveys of lichen biodiversity (species presence and abundance) in a native conifer tree species, *Pseudotsuga menziesii* (Mirb.) Franco, resulting in the first ever evaluation of the biodiversity and functional role of macrolichens within canopies of urban environments. Vertical canopy surveys were paired with ground-level surveys in three of Portland's large, urban forested parks to validate ground-based measures of urban canopy lichen biodiversity. Ground-based surveys of epiphytic lichens are commonly used, particularly by the USFS (McCune, 2000; Geiser and Neitlich, 2007; Jovan, 2008; Root et al., 2015), and have been shown to be good estimators of epiphytic biomass (McCune, 1994; Berryman and McCune, 2006) and of epiphytic species richness (McCune et al., 1997b); however, their reliability for evaluating epiphytic biodiversity,

**Table 1**

Eight Portland, Oregon parks used in the study, summarized by land classification and the number of survey plots installed by the USDA Forest Service Air Resources and Management regional air quality and lichen study.

Year of Historic Survey	Land Classification	Number of Survey Plots
1995, 1996	<b>Urban Parks:</b> Delta Park (DP), Riverfront Park (RP), Oregon Zoo (OZ)	4
1995, 2007	<b>Urban Forested Parks:</b> Forest Park (FP), Mt. Tabor Park (MTTP), Tryon Creek State Natural Area (TCSNA)	7
1996	<b>Suburban Parks:</b> Oxbow Regional Park (ORP), Sandy River Delta (SRD)	2

particularly in changing urban canopies is unknown. We predicted that distinct changes in macrolichen biodiversity would occur with increasing urbanization and that shifts in macrolichen community composition, as a result of urban air exposure, would be more evident in tall tree canopies when compared to ground-based studies, with implications for forest canopy function in rapidly urbanizing landscapes.

## 2. Materials and methods

### 2.1. Study area

The study was carried out in metropolitan Portland, Oregon, USA, across eight urban and ex-urban parks (Table 1). The Portland Metro area covers 33,000 ha, with parklands comprising just over 17% (5748 ha) of the metro city area (ParkScore, 2016). Portland park landscapes are variable and range from fully developed inner city park areas to undisturbed, natural urban forest parks. The diversity of park landscapes creates a tree canopy matrix of non-native tree cultivars as well as native tree species, a distinctive feature of the Portland Metro area. Most notably in the study is Forest Park, the largest urban forest park in the United States, encompassing 2064 ha along the northwest section of downtown Portland. The overstory canopy of Forest Park is comprised of native conifer species such as Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western reedcedar (*Thuja plicata* Donn.) and native hardwoods: bigleaf maple (*Acer macrophyllum* Pursh) and red alder (*Alnus rubra* Bong.). Five of the eight parks selected in this study (Forest Park, Mt. Tabor, Oxbow Regional Park, Tryon Creek State Natural Area and Washington Park Zoo) have *Pseudotsuga menziesii*, a native conifer species, as the primary overstory tree species.

### 2.2. Historic ground-based lichen community data

During 1995-96 & 2007 the United States Department of Agriculture (USDA) Forest Service Air Resources Management (ARM) Program surveyed ground-based epiphytic macrolichen biodiversity at thirteen urban plots, located in the eight Portland, Oregon area parks (Table 1). The historic study was part of a larger regional sampling effort to understand gradients in epiphytic macrolichen community in response to regional air pollution and climatic gradients, with particular interest on regional gradients of N deposition away from the large, urban metropolitan areas of Seattle, Washington and Portland, Oregon extending east towards the Cascade Mountain Range (Geiser and Neitlich, 2007; Geiser et al., 2010). Trained field technicians collected voucher specimens and estimated the visual abundance of each epiphytic macrolichen detected in 0.38 ha circular plots, following the USFS Forestry Inventory and Analysis (FIA) lichen community protocol (USDA-Forest Service, 2011). The ground-based sampling method designates the collection of macrolichen epiphytes that occur on woody substrates between 0.5 m to approximately 1.8 m in height, excluding ground-dwelling epiphytes below 0.5 m. The method also includes sampling

**Table 2**

Lichen species list from historic (1995–96, 2007) and current year (2012–13) ground-based community surveys of eight Portland, Oregon, USA parks ( $n = 13$ ). Detections are the number of times a species was found in the 13 unique study plots. The N functional group (E = eutroph, M = mesotroph, O = oligotroph) for each lichen species is shown in the leftmost column.

N-Rating	Scientific Name	Historic Number of Detections	Current Number of Detections
M	<i>Bryoria capillaris</i> (Ach.) Brodo & D. Hawksw.	1	
O	<i>Bryoria fuscescens</i> (Gyelnik) Brodo & D. Hawksw.		1
E	<i>Candelaria concolor</i> (Dickson) Stein	9	10
E	<i>Cetrelia cetrarioides</i> (Duby) Culb. & C. Culb.	4	
O	<i>Cladonia carneola</i> (Fr.) Fr.		1
E	<i>Cladonia fimbriata</i> (L.) Fr.		1
E	<i>Cladonia macilenta</i> (Hoffm.)	4	
M	<i>C. ochrochlora</i> , <i>C. coniocraea</i> (Florke) Sprengel	1	2
E	<i>Cladonia squamosa</i> (Hoffm.)	2	3
O	<i>Cladonia transcendens</i> (Vainio) Vainio		7
M	<i>Cladonia umbricola</i> (Tonsberg & Ahti) <i>Cladonia</i> spp.	1	1
E	<i>Collema nigrescens</i> (Hudson) DC.	1	
E	<i>Evernia prunastri</i> (L.) Ach.	13	13
E	<i>Flavopunctelia soledica</i> (Nyl.) Hale		2
O	<i>Hypogymnia apinnata</i> (Goward & McCune)	1	3
O	<i>Hypogymnia enteromorpha</i> (Ach.) Nyl.	3	4
O	<i>Hypogymnia imshaugii</i> (Krog)		1
M	<i>Hypogymnia inactiva</i> (Krog) Ohlsson	4	8
E	<i>Hypogymnia physodes</i> (L.) Nyl.	10	12
M	<i>Hypogymnia tubulosa</i> (Schaerer) Hav.	9	13
O	<i>Hypotrachyna revoluta</i> (Florke) Hale		1
O	<i>Hypotrachyna sinuosa</i> (Sm.) Hale	1	2
M	<i>Leptogium polycarpum</i> (P.M. Jorg. & Goward)	2	
O	<i>Lobaria oregana</i> (Tuck.) Mull. Arg.	1	
O	<i>Lobaria pulmonaria</i> (L.) Hoffm.	1	
M	<i>Melanelia exasperatula</i> (De Not.) Essl.	5	4
E	<i>Melanelixia fuliginosa</i> (Fr. Ex Duby) O. Blanco et al.	5	7
E	<i>Melanelixia subargentifera</i> (Nyl.) O. Blanco et al.		1
E	<i>Melanelixia subaurifera</i> (Nyl.) O. Blanco et al.	8	9
E	<i>Melanohalea subelegatula</i> (Essl.) O. Blanco et al.	3	8
	<i>Melanohalea</i> spp.		1
O	<i>Menegazzia terebrata</i> (Hoffm.) A. Massal.	2	
M	<i>Parmelia hygrophila</i> (Goward & Ahti)	10	10
O	<i>Parmelia pseudosulcata</i> (Gyelnik)	1	
E	<i>Parmelia saxatilis</i> (L.) Ach.	1	2
E	<i>Parmelia sulcata</i> (Taylor)	13	13
O	<i>Parmotrema arnoldii</i> (Du Rietz) Hale	3	7
O	<i>Parmotrema chinense</i> (Osbeck) Hale & Ahti		1
M	<i>Peltigera collina</i> (Ach.) Schrader	3	1
O	<i>Peltigera membranacea</i> (Ach.) Nyl.	1	
E	<i>Phaeophyscia nigricans</i> (Florke) Moberg		1
E	<i>Phaeophyscia orbicularis</i> (Necker) Moberg	1	3
E	<i>Phaeophyscia sciastra</i> (Ach.) Moberg		1
E	<i>Physcia adscendens</i> (Fr.) H. Olivier	9	11
E	<i>Physcia aipolia</i> (Ehrh. Ex Humb.) Furnr.	3	4
E	<i>Physcia tenella</i> (Scop.) DC.	4	12
E	<i>Physcia</i> spp.		1
E	<i>Physconia enteroxantha</i> (Nyl.) Poelt	1	
M	<i>Physconia isidiigera</i> (Zahlbr.) Essl.	1	
E	<i>Physconia perisidiosa</i> (Erichsen) Moberg	2	2
M	<i>Platismatia glauca</i> (L.) Culb. & C. Culb.	9	9
M	<i>Platismatia herrei</i> (Imshaug) Culb. & C. Culb.	5	3
E	<i>Punctelia perreticulata</i> (Rasanen) G. Wilh. & Ladd		2
E	<i>Ramalina dilacerata</i> (Hoffm.) Hoffm.	2	2
E	<i>Ramalina farinacea</i> (L.) Ach.	11	12
E	<i>Ramalina subleptocarpa</i> (Rundel & Bowler)	3	9
O	<i>Sphaerophorus globosus</i> (Hudson) Vainio	1	1
O	<i>Sticta fuliginosa</i> (Hoffm.) Ach.	2	

**Table 2 (continued)**

N-Rating	Scientific Name	Historic Number of Detections	Current Number of Detections
M	<i>Tuckermannopsis chlorophylla</i> (Willd.) Hale	5	3
O	<i>Tuckermannopsis orbata</i> (Nyl.) M.J. Lai	1	3
O	<i>Usnea cornuta</i> (Korber)	6	
O	<i>Usnea filipendula</i> (Stirton)	3	2
M	<i>Usnea fulvovireagens</i> (Rasanen) Rasanen	1	1
O	<i>Usnea glabrata</i> (Ach.) Vainio	2	5
O	<i>Usnea longissima</i> (Ach.)		1
O	<i>Usnea scabrata</i> (Nyl.)	1	2
E	<i>Usnea subfloridana</i> (Stirton)	4	6
O	<i>Usnea wirthii</i> (P. Clerc)	5	12
	<i>Usnea</i> spp.	3	6
E	<i>Xanthomendoza fallax</i> (Hepp ex. Arn.) Soechting, KSnfelt & S. Kondratyuk	2	4
E	<i>Xanthoria candelaria</i> (L.) Th. Fr.	1	
E	<i>Xanthoria parietina</i> (L.) Th. Fr.	2	10
E	<i>Xanthoria polycarpa</i> (Hoffm.) Rieber	7	10
E	<i>Xanthoria</i> spp.		1

from recently fallen branches and canopy throughfall within the plot area, thus the sampling method is intended to provide a ‘capture’ of the canopy dwelling lichen community. However, due to difficulties and limitations of climbing trees, only a few paired canopy to ground validation surveys exist, and have focused on non-urban areas (McCune, 1994; Berryman and McCune, 2006). These historic lichen community data are housed on the USFS Lichen and Air Database (<http://gis.nacse.org/lichenair/index.php>), and the expansive network of regional sampling, which encompasses gradients of both air quality and environmental variables across 1416 forested plots, has resulted in a robust model where macrolichen community assemblages can be used to predict N deposition and climate environments across the PNW region (Geiser and Neitlich, 2007; Geiser et al., 2010; Root et al., 2015). Additionally, lichen community derived air scores can be generated for plots and ran amongst the larger 1416 plot network (Geiser and Neitlich, 2007).

We used matched urban site locations as the historically established USFS plot survey array to examine urbanized lichen communities in the Portland, Oregon Metropolitan area. The historical lichen data are indicated in Table 2, further plot specific data can be accessed from the USFS Lichen and Air Database (<http://gis.nacse.org/lichenair/index.php>). We conducted repeat, ground-based macrolichen community surveys at all of the thirteen historic plots in 2012–13 to capture current and historic air quality as indicated by epiphytic lichen communities. We replicated the survey methods of the historical surveys; original plot locations were relocated with precise GPS coordinates. Lichens were identified using McCune and Geiser (2009) from morphology, spot tests, and thin layer chromatography.

### 2.3. Canopy-based lichen community data

We selected a subset of three urban parks from the existing urban USFS plot array for vertical tree canopy surveys. One tall *P. menziesii* tree (55–60 m) at each park was chosen for vertical survey and comparison to a paired ground-based plot. The small sample size reflects both the difficulty of finding tall and mature conifer trees with structurally intact crowns (*i.e.* not mechanically or naturally topped) near the urban center as well as the challenges of rigging and climbing tall conifer trees. The parks were searched for mature trees that had topographic exposure (not located in creek beds or steep drainages) to the surrounding urban air plumes. Tree selection criteria were based on trees that were over 100 cm DBH (diameter at breast height), tree heights between 55 and 60 m, full and structurally intact canopies that were safe for climbing access.

Trees were rigged for climbing by propelling a weighted throwbag attached to high-tensile strength throwline over suitable climbing limbs

in the uppermost canopy. Climbing ropes were then pulled through to allow vertical ascent into the crown. Single rope climbing techniques (SRT) were used to access the crown and were used for in-canopy movements. Tree height was measured to the top of the most apical portion of the crown; depth of crown was measured from the lowest live branch whorl to the most apical portion of the crown. The crown was divided vertically into three canopy stratification layers: top, mid, and lower crown. We used a modification of the FIA lichen community protocol survey (USDA-Forest Service, 2011) to describe canopy macrolichen communities at each of the canopy survey layers. Each canopy layer was surveyed for a maximum of 1 h, or until no new species had been recorded in a ten minute period. Epiphytic macrolichens were collected from all substrates (branches and bole) within the canopy survey layers, an approximately 9 m vertical section. Each unique macrolichen species was vouchered and an ocular abundance value was recorded (Geiser, 2004; USDA-Forest Service, 2011).

#### 2.4. Lichen elemental data

At each of the three canopy stratification sections (top, mid and lower crown), 5–10 g of two epiphytic macrolichen species were collected, where possible, for total nitrogen and sulfur tissue analysis following methods of Geiser (2004). A matched ground level collection of the two species, where possible, was made following standard USFS methods (Geiser, 2004). The target species was *Platismatia glauca* (L.) Culb. & C. Culb., but since the frequency and overall health of this species decreases in highly urbanized areas (USDA-Forest Service, 2016), we also collected *Parmelia sulcata* (Taylor), a frequent and abundant species detected in the study area. Both species varied in presence, abundance and health in the study trees and became uncommon in the very top layer of the subject tree canopies. Sterile gloves were used to sample lichens from the bole and branches of the study trees at each canopy stratification sections. Because *P. sulcata* has not yet been widely used as a target species for tissue accumulation in the PNW, we further collected paired collections of *P. sulcata* and *P. glauca* across a larger regional deposition gradient, as identified in Geiser and Neitlich 2007. We linearly regressed combustion analyzed N and S content (%) of *P. sulcata* and *P. glauca* using JMP Version 9.0 (JMP Version 9.0., 2009) and the correlation indicated ( $r^2 = 0.91$ ) a strong relationship. We further tested binned values of N and S content (%) for *P. glauca* and *P. sulcata* for all urban collections and found values did not differ significantly (ANOVA,  $n = 17$ ,  $F = 3.82$ ,  $p = .06$ , &  $n = 18$ ,  $F = 0.02$ ,  $p = .88$ , respectively), which allowed us to pool all N and S (%) values for both species.

Lichen samples were cleaned of non-lichen debris and necrotic tissue and sent to the USFS Northern Research Station, Forest Science Analytic Laboratory in Grand Rapids Minnesota. Samples were dried and homogenized to a constant weight and total C, N, and S was determined by combustion analysis as percent (%) dry weight using a LECO FP-528. Measured mean  $\pm$  std err total C, N, and S concentrations in a certified barley check standard (Leco 502-277) were  $44.91 \pm 0.03$ ,  $1.734 \pm 0.004$ , and  $0.149 \pm 0.001$ , respectively. These are all within the Leco-certified ranges of these elements (C: 44.58–45.63, N: 1.66–1.81, S: 0.137–0.159), indicating the combustion analysis data for these elements were highly accurate.

#### 2.5. Statistical analyses

To reveal changes in lichen community assemblages between the historical and current ground-based surveys, a species by site abundance matrix was ordinated using non-metric multidimensional scaling (NMDS) in R studio (RStudio Team Version 0.99.473, 2015) using package “Vegan” (Oksanen et al., 2016). Using Bray-Curtis distance measures, and square root data transformation, we chose a two-dimensional solution with the best stress (0.17) based on 20 runs of 1000 permutations. An analysis of similarity (ANOSIM) was used to

statistically test for differences between past and present site species assemblages.

We further used the Geiser and Neitlich (2007) regional lichen, air quality and climate model to ordinate a lichen species by site abundance matrix from both historic and current park surveys and canopy-base surveys within the larger archive of regional sites (1416, 0.4 ha regional forested plots) and generated ‘air scores’ within the parameters described in Geiser and Neitlich (2007), using non-metric multidimensional scaling (NMS) in PC-ORD (McCune and Mefford, 2011). Positive air score values indicate polluted sites, while negative air score values indicate clean sites.

Two-way ANOVA were used to determine the effect of year of survey (historic or current), altitude of survey (ground or canopy), and the interaction of these factors on species number, N functional groups (eutroph, mesotroph, oligotroph) and ecological classified groups (eutroph, green algal, alectoroid, cyanolichen). Two-way ANOVA were also used to determine the effect of year of survey (historic or current), park location (8 Portland parks), and the interaction of these factors on lichen derived air scores. Unpaired *t*-test was used to determine the effect of binned survey year (historic or current) on mean lichen derived air scores. Tukey’s tests were used to determine significance among factors. Analyses were conducted using JMP Version 9.0 (JMP Version 9.0 2009). Discrimination between N functional groups (eutroph or nitrophilous ( $> 4.6 \text{ kg N/ha}^{-1}\text{yr}^{-1}$ ), mesotroph ( $2.5\text{--}4.5 \text{ kg N/ha}^{-1}\text{yr}^{-1}$ ), or oligotroph ( $< 2.4 \text{ kg N/ha}^{-1}\text{yr}^{-1}$ ) followed McCune and Geiser (2003). Lichen ecological groups were modeled after classifications by McCune et al. (1997a) and Sillett and Rambo (2000); eutroph (*Candelaria* sp., *Physcia* sp., *Xanthoria* sp.), green algal (*Hypogymnia* sp., *Platismatia* sp.), alectoroid (*Alectoria* sp., *Bryoria* sp., *Usnea* sp.), and cyanolichens (*Lobaria* sp.).

### 3. Results

#### 3.1. Historic versus current ground-based lichen community data

NMDS ordination was used to visualize changes in lichen community assemblages (lichen species presence and abundance) between the historical and current ground-based surveys (Fig. 1). A species by site abundance matrix was ordinated using non-metric multidimensional scaling, using Bray-Curtis distance measures and square root data transformation, we chose a two-dimensional solution with the best stress (0.17) based on 20 runs of 1000 permutations. An analysis of similarity (ANOSIM) was used to statistically test for differences between past and present site species assemblages. The distances between points are proportional to the dissimilarities between entities, circles represent 95% CI (Fig. 1). A significant change in urban macrolichen community assemblages (lichen species presence and abundance) occurred between historic (1995–96, 2007) and current (2012–13) ground based FIA surveys (NMDS, Stress = 0.17; ANOSIM test statistic,  $n = 13$ ,  $p = .005$ ; Fig. 1). These differences indicate that over time, both the presence and abundance of lichen species has significantly changed.

We found 60 unique epiphytic macrolichen species in the 8 urban parks surveyed (Table 2), compared to 61 total species found in the historic surveys. Macrolichen species richness varied by park location; the highest species richness was found in Oxbow Regional Park [30] and the lowest was in Riverfront Park [11]. These findings are fairly consistent with historic surveys; highest species richness recorded at Oxbow Regional Park [30], the lowest species richness at both Riverfront Park and the Oregon Zoo [8]. Species richness was lowest in parks that were nearer the downtown center [Riverfront Park] or abutted a major freeway corridor [Delta Park and Oregon Zoo] and had epiphytic communities comprised of primarily all eutrophic species. Species richness was highest in parks that were further from the downtown center and contained a unique assemblage of both eutrophic and oligotrophic species, which resulted in high measures of species richness [Oxbow Regional Park]. Species diversity, calculated using the

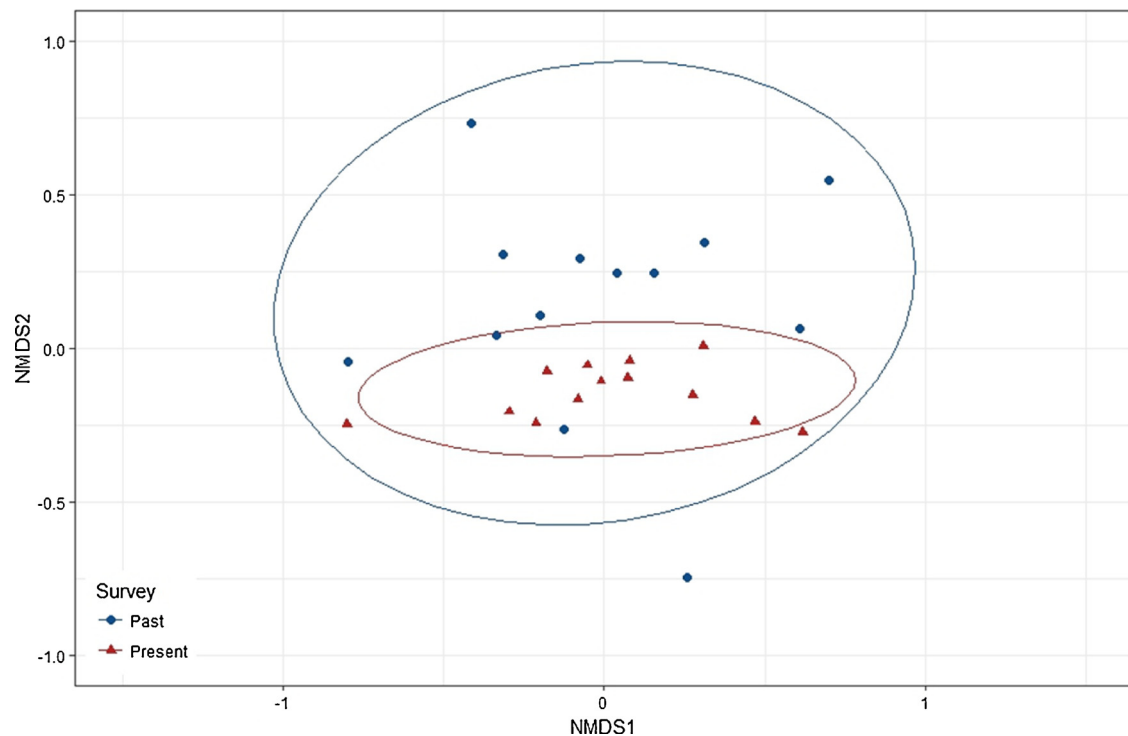


Fig. 1. NMDS ordination was used to explore lichen community structure in historic and current surveys. Historic (1995–96, 2007) and current (2012–13) lichen biodiversity in 8 urban parks located in Portland, Oregon, USA showed a significant change in lichen community assemblages (species presence and abundance); stress = 0.17; ANOSIM test statistic  $p = .005$ ,  $n = 13$ . Bray-Curtis distance measure was for analysis; distances between points are proportional to the dissimilarities between entities. Circles represent 95% CI.

Shannon-Wiener diversity index, increased from historical survey levels at all but one park. Overall, parks with historically high diversity remained the highest in current year surveys and parks with historically low diversity also remained lowest.

We found both historic and current park surveys revealed highly eutrophied macrolichen communities. A significant increase in total number of eutrophic species occurred between historic and current ground based surveys (two-way ANOVA,  $n = 13$ ,  $F = 5.95$ ,  $p = .02$ ; Fig. 2a). A high frequency of eutrophic, nitrophilous species, (greater than 35% eutrophic species) within the total proportion of macrolichen community indicates ecosystem N inputs are high, ranging upwards of  $3 \text{ kg N/ha yr}^{-1}$ , in all urban parks surveyed (USDA-Forest Service, 2016) (Fig. 2b). The total proportion of eutrophic species in the ground based surveys ranged from 26%–91% of total community composition; no significant changes were seen between historic and current surveys (two-way ANOVA,  $n = 13$ ,  $F = 0.00$ ,  $p = .98$ ; Fig. 2b) therefore, both the historic and current urban macrolichen communities remain dominated by eutrophic, nitrophilous species. When categorized by functional groupings, we found a significant increase in mean number of eutrophic lichen species (two-way ANOVA,  $n = 13$ ,  $F = 110.66$ ,  $p = .0001$ ; Fig. 3a) and mean number of green algal species (two-way ANOVA,  $n = 13$ ,  $F = 110.66$ ,  $p = .0001$ ; Fig. 3a) between historic and current surveys.

### 3.2. Ground-based versus canopy-based lichen community data

We found a total of 29 macrolichen species across the three urban canopy sampling locations (Table 3). On average, 7 species were found only in canopy surveys and 8 species were found only in ground surveys and not in canopy surveys. Overall, the vertical canopy species surveys did accurately reflect paired ground level surveys in all three urban parks; mean ground level species capture was 81% of canopy and comparably, mean canopy species capture was 68% of ground-based species records. No macrolichen species were found unique to only the

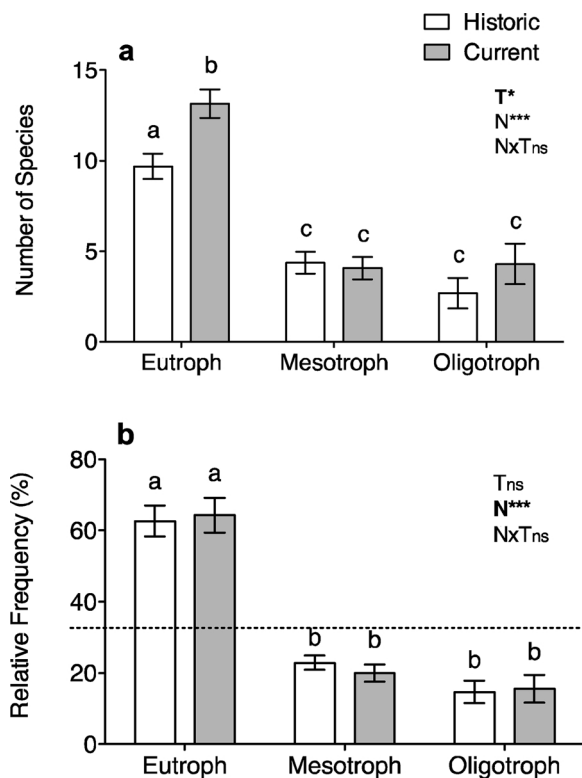
canopy surveys, however each urban survey type (ground vs. canopy) had a limitation of  $\pm 7$ –8 species, with ground level surveys often overestimating diversity of large overstory conifer tree canopies, likely due to the larger sampling area (0.4 ha) and greater availability of microsites.

Canopy surveys revealed a high frequency of eutrophic species; the proportion of eutrophic species ranged from 42%–67% of total community composition, which was also reflected in the paired ground level plots; no significant differences occurred between ground and canopy level surveys (two-way ANOVA,  $n = 9$ ,  $F = 0.00$ ,  $p = .99$ ). When lichens were grouped by their ecological classification, we further showed low occurrences of alectoroid species and a total absence of cyanolichen species in the paired urban conifer canopies and ground-based plots (two-way ANOVA,  $n = 13$ ,  $F = 1.33$ ,  $p = .27$ ; Fig. 3b). Cyanolichens *Lobaria pulmonaria* and *Lobaria oregana* were absent and not detected in any of the canopy- or ground-based surveys.

The canopy surveys revealed an unexpected amount of visual macrolichen tissue damage, bleached and necrotic tissues were visible in both *Platismatia glauca* and *Parmelia sulcata*, *in situ*, otherwise not detectable in ground-based surveys. Many canopy lichen species (*Hypogymnia* sp., *Platismatia* sp., *Usnea* sp.) showed visual signs of air pollution injury, as evidenced by extremely stunted and compact thalli.

### 3.3. Lichen elemental data

We found that lichen tissue N and S concentrations in *Platismatia glauca* and *Parmelia sulcata* exceeded regional values of critical load thresholds in both ground- and canopy-based collections (Table 4). Ground-level collected lichen tissues in the urban sites exceeded N and S (%) threshold values for elemental concentrations of *P. glauca*, 0.6% and 0.07% respectively, as determined from lichen tissues collected across regional background sites in PNW forests (USDA-Forest Service, 2016) (mean N% = 0.98 & mean S% = 0.08; Table 4). Mean tissue concentrations of N and S (%) were highest in the topmost canopy

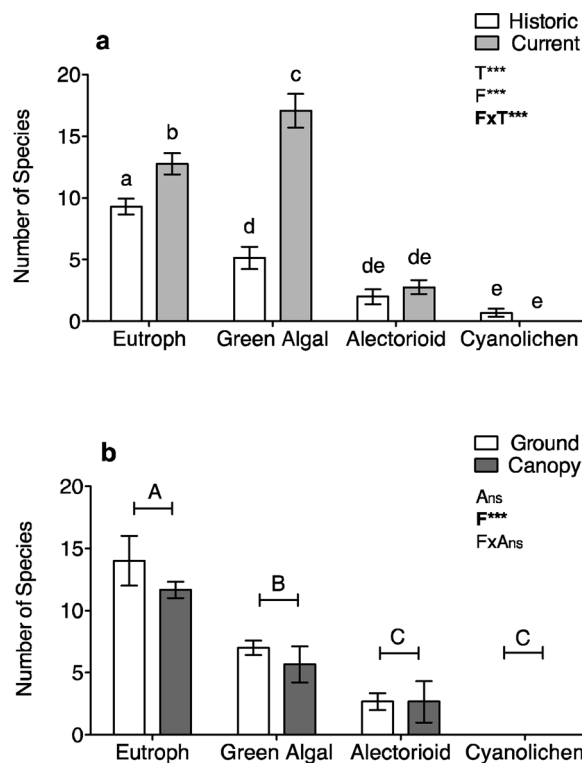


**Fig. 2.** a) Mean ( $\pm$  SE) number of lichen species in historic and current ground-level lichen community surveys in eight urban parks located in Portland, Oregon, USA. A significant increase in number of eutrophic species was found between current and historic surveys ( $p = .02$ ,  $n = 13$ ); b) Mean ( $\pm$  SE) relative frequency (%) of lichen species in historic and current ground-level lichen community surveys; lichen species are categorized by functional N rating; eutroph or nitrophilous ( $> 4.6 \text{ kg N/ha}^{-1}/\text{yr}^{-1}$ ), mesotroph ( $2.5\text{--}4.5 \text{ kg N/ha}^{-1}/\text{yr}^{-1}$ ), or oligotroph ( $< 2.4 \text{ kg N/ha}^{-1}/\text{yr}^{-1}$ ). Hashed line indicates  $> 35\%$  proportion of eutrophic species, signifying elevated ecosystem N inputs. Two-way ANOVA results are shown on graph: T indicates effect of survey time (historic or current), N indicates effect of functional N rating (eutroph, mesotroph, oligotroph), and NxT indicates the interaction of survey time on functional N rating of lichen species. Asterisks indicate level of significance: ns  $p > 0.05$ , \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ . Lowercase letters indicate significant differences for the interaction shown in bold.

samples, with values nearly two-fold greater than regional threshold values ( $N\% = 2.05$  and  $S\% = 0.14$ ).

### 3.4. Lichen community derived air scores

Air scores are derived from macrolichen community gradients in the larger, regional NMS ordination model (Geiser and Neitlich, 2007). High air score values indicate polluted sites; all air scores in this urban study indicate polluted sites (clean air sites return a negative air score value). The highest air scores (indicating polluted sites) occurred in parks with low species richness, a high proportion of eutrophic species, and were closest to the downtown urban center or a main freeway corridor. The lowest air scores (indicating cleanest sites) were found at parks with high species richness, a wide range of lichen N functional groups and furthest from the downtown center. No significant difference occurred between mean historic and current park air scores ( $t$ -test,  $n = 13$ ,  $F = 0.00$ ,  $p = .91$ ; Fig. 4b), however park location had a significant effect on air score (two-way ANOVA,  $n = 13$ ,  $F = 18.58$ ,  $p = .0001$ ; Fig. 4a).



**Fig. 3.** a) Mean ( $\pm$  SE) number of lichen species categorized by ecological classification group in matched historic and current ground-based lichen community surveys in eight urban parks located in Portland, Oregon, USA; a significant increase in number of eutrophic lichen species ( $p = .0001$ ,  $n = 13$ ) and number of green algal species ( $p = .0001$ ,  $n = 13$ ) occurred between historic and current surveys. Two-way ANOVA results are shown on graph: T indicates time of survey (historic or current), F indicates # of species in ecological grouping and Tx F indicates the interaction of survey time and ecological groupings of lichen species; b) Mean ( $\pm$  SE) number of lichen species categorized by ecological group in paired ground and canopy surveys; no significant differences between ground to canopy based surveys were revealed ( $p = .27$ ,  $n = 13$ ); canopy surveys are a mean of three vertical sampling layers (top, mid, low canopy); lichen species are categorized by ecological group; eutroph (*Candelaria* sp., *Physcia* sp., *Xanthorhiopsis* sp.), green algal (*Hypogymnia* sp., *Platismatia* sp.), alectorioid (*Alectoria* sp., *Bryoria* sp., *Usnea* sp.), and cyanolichens (*Lobaria* sp.). Two-way ANOVA results are shown on graph: A indicates survey altitude (canopy or ground), F indicates # of species in ecological grouping and Ax F indicates the interaction of survey altitude and ecological groupings of lichen species. Asterisks indicate level of significance: ns  $p > 0.05$ , \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ . Lowercase and uppercase letters indicate significant differences for the interaction shown in bold.

### 4. Discussion

In this study, we investigated tree canopy macrolichen communities in a native urban-dwelling coniferous tree species, nested in a larger historic urban park lichen plot network in Portland, Oregon, USA. We are interested in the effects of rapid urbanization of the Portland region on canopy macrolichen communities, which provide vital ecosystem functions to the dominant Pacific Northwest conifer forests (Coxson and Nadkarni, 1995; Pettersson et al., 1995; McCune, 2000; Antoine, 2004; Wolf, 2009). Our results suggest that urban forest areas and tall coniferous trees can function as heterogeneous habitats, containing a surprising biodiversity of urban-tolerant epiphytic lichens. However, while these urban canopy macrolichen communities demonstrate the capacity to maintain substantial biodiversity, we found evidence for biotic homogenization of canopy macrolichen communities, where ecologically important, functional groups are replaced by functionally redundant, urban-tolerant species (McKinney and Lockwood, 1999;

**Table 3**

Lichen species list from paired ground- and canopy-based surveys of three Portland, Oregon, USA urban forested parks; the number indicates which species was detected during a specific survey type. Species code is the abbreviated genus and species name (see also Table 2). The N functional group (E = eutroph, M = mesotroph, O = oligotroph) for each lichen species is shown in the leftmost column.

N-Rating	Species Code	Mt. Tabor Park		Forest Park		Tryon Creek	
		Ground	Canopy	Ground	Canopy	Ground	Canopy
E	<i>Cancon</i>	1	1	1	1	1	1
E	<i>Clafim</i>				1		
E	<i>Clasqu</i>			1			
O	<i>Clatra</i>			1	1	1	
E	<i>Evepru</i>	1	1	1	1	1	1
M	<i>Hypapi</i>	1					
O	<i>Hypent</i>					1	
M	<i>Hypina</i>	1		1	1	1	1
E	<i>Hypphy</i>	1	1	1	1	1	1
M	<i>Hyptub</i>	1	1	1	1	1	1
M	<i>Melexau</i>	1	1	1	1		1
E	<i>Melful</i>	1	1	1	1		1
E	<i>Melsubau</i>	1				1	
E	<i>Melsube</i>					1	1
O	<i>Pararn</i>	1					1
M	<i>Parhyg</i>	1	1	1	1	1	1
E	<i>Parsax</i>			1			
E	<i>Parsul</i>	1	1	1	1	1	1
E	<i>Phaorb</i>	1					
E	<i>Phyads</i>	1			1	1	
E	<i>Phyaip</i>					1	
E	<i>Phyper</i>	1					
E	<i>Phyten</i>	1	1	1	1	1	1
M	<i>Plagla</i>	1	1	1	1	1	1
M	<i>Plaher</i>			1			
E	<i>Punper</i>	1	1				1
E	<i>Ramdil</i>					1	
E	<i>Ramfar</i>	1	1	1	1	1	1
E	<i>Ramsub</i>	1			1	1	
M	<i>Tucchl</i>	1	1		1		1
O	<i>Tucorb</i>						1
E	<i>Unssubl</i>			1			1
	<i>Usnea sp.</i>	1	1			1	1
O	<i>Usnfil</i>					1	1
O	<i>Usnglaa</i>					1	1
O	<i>Usnhir</i>						1
O	<i>Usnwir</i>	1		1	1	1	1
E	<i>Xanfal</i>	1			1	1	1
E	<i>Xanpar</i>	1				1	
E	<i>Xanpol</i>	1	1	1	1	1	1

McKinney, 2006).

#### 4.1. Effects of urbanization on lichen biodiversity

Despite the high air scores associated with the urban ecosystem, we found that urban parks and forested areas provide a heterogeneous environment, leading to species rich community of macrolichen epiphytes. Using the historic FIA lichen survey plot array, we found a significant shift in macrolichen community assemblages (presence/absence and abundance) occurred between historic and current ground-based surveys (Fig. 1). Unexpectedly, we further found that urban parks gained new species and biodiversity of species (presence and abundance) also increased over time. The frequency of pollution tolerant, N-loving species showed little change over the 18-year period, suggesting a saturation of eutrophic lichen species in this system (Fig. 2b), which resulted in no significant change in macrolichen community gradient derived air scores between historic and current surveys (Fig. 4b). Further, the recruitment of new species was primarily N loving, eutrophic species (Figs. 3a and 3a). The increase of eutrophic species over time and a eutroph dominated macrolichen community may suggest that despite distinct improvements in regional air quality across the same time period, as implemented by the 1990 Clean Air Act Amendments, these air quality regulations may not be significant enough to show

detectable improvements in sensitive macrolichen epiphyte communities. The continued presence of a highly eutrophic macrolichen community suggests that urban ecosystem N inputs likely prohibit N sensitive oligotrophic species from establishing, however it is also possible that a dominance of eutrophic species themselves may competitively limit the establishment of sensitive oligotrophic species. Either mechanism may contribute in an absence of sensitive, and functionally important, epiphytes from establishing in this urban park and tree canopy environment.

#### 4.2. Effects of urbanization on canopy function and ecology

Though our results suggest urbanization can foster macrolichen biodiversity, we also found evidence of dramatic homogenization of epiphyte functional diversity in urban forest canopies. Using both ground-based and canopy-based surveys, we found that urban canopies were highly eutrophied. While urban tree canopies still contained a moderate number of species, we found that primarily all species detected were indicating a highly nitrogenous environment with a low frequency of N sensitive species occurring. Urban canopies also lacked ecologically important groups of alectorioid lichens and a complete absence of canopy-dwelling cyanolichens (Fig. 4b). Our research suggests that generally in this rapidly urbanizing environment, ground-

**Table 4**

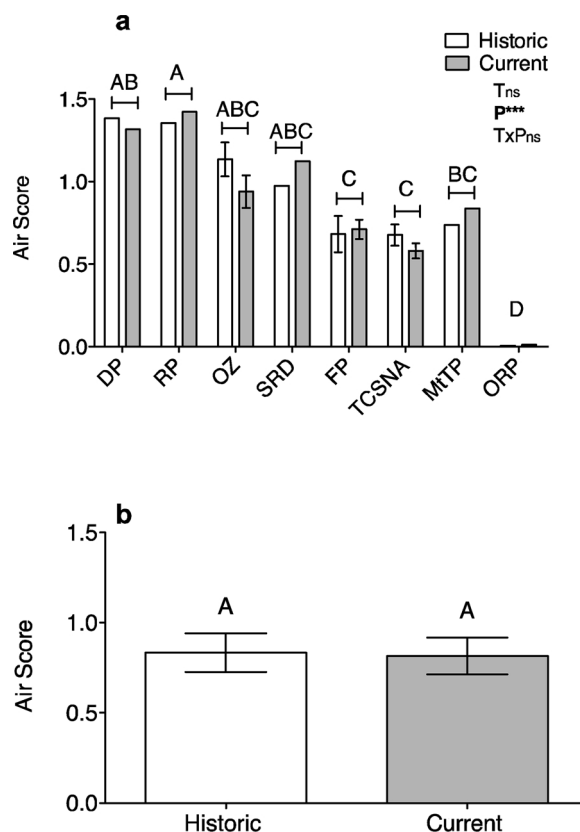
Summary statistics of lichen tissue accumulated nitrogen and sulfur in ground- and canopy-based collections of *Platismatia glauca* & *Parmelia sulcata*, expressed as parts per million per dry weight. Values that exceed the *P. glauca* threshold value (ppm) indicate deposition levels that exceed the established regional PNW threshold value for clean air sites. Bolded values indicated sites where mean values exceed regional threshold values.

<i>P. glauca</i> Regional Threshold Value		%N	%S
		0.59	0.07
Ground-based <i>n</i> = 4	mean	<b>0.98</b>	<b>0.08</b>
	std dev	0.06	0.02
	std err	0.03	0.01
	max	1.07	0.10
	min	0.93	0.06
Low-canopy <i>n</i> = 4	mean	<b>1.92</b>	<b>0.13</b>
	std dev	0.90	0.04
	std err	0.37	0.02
	max	3.72	0.21
	min	1.32	0.11
Middle-canopy <i>n</i> = 3	mean	<b>1.49</b>	<b>0.11</b>
	std dev	0.27	0.01
	std err	0.16	0.01
	max	1.72	0.12
	min	1.19	0.10
Top-canopy <i>n</i> = 3	mean	<b>2.05</b>	<b>0.14</b>
	std dev	0.90	0.06
	std err	0.52	0.03
	max	3.08	0.21
	min		

based surveys do provide a good estimate of epiphyte lichen biodiversity and functional type. We found that our exhaustive canopy surveys were not significantly different than the ground based surveys in number of species, function type and air score. This supports previous work in natural systems, suggesting that ground-based sampling is a sufficient estimate of epiphytic lichen biomass, species richness and function (McCune, 1994; McCune et al., 1997b; Berryman and McCune, 2006). Interestingly, many of the eutrophic species found in the arboreal study are those that would typically be preferentially to hardwood tree substrates and not occur on acidic substrate of conifer bark. This may suggest that N inputs, or other pollutants, are so high that eutrophic species are less specific to substrate pH, or that substrate pH may be altered (buffered) by urban deposition.

The urban canopy surveys also revealed a surprising amount of bleached and necrotic macrolichen damage *in situ*, not otherwise observable in ground-based surveys. *Platismatia glauca*, *Parmelia sulcata*, and *Usnea* spp. were visibly stunted in the arboreal surveys, suggesting that presence or absence of species cannot determine ecological contribution as many macrolichen epiphytes also become physically altered in urban areas. Stunted thalli size of otherwise larger biomass species, as well as the overall compact thalli sizes of many eutrophic species (*Candelaria* sp. *Physcia* sp., *Xanthoria* sp.), may affect tree canopy microclimate, as reduced biomass of epiphytes may lower canopy water retention. Additionally, tissue damage and stunted thalli may affect habitat quality of epiphytes for invertebrates within tree canopies.

We found that lichens affixed in urban tall tree canopies intercept atmospheric N and S and show two-fold higher concentrations (%) than lichen tissues collected in matched ground-based collections. This study is the first that we know of documenting elemental concentrations of lichens collected *in situ*, across the vertical gradient of large conifer tree canopies. We suspected that ground-based collections made from litterfall and branch fall may have lower macronutrient concentrations than those affixed in the canopy because these nutrients are fairly mobile and can leach or mobilize from thalli quickly when in contact with other substrates, which may underestimate lichen tissues concentrations (%) from sites which occur along distinct urbanization



**Fig. 4.** Urban Park historic and current survey air scores derived from plot scores on lichen community gradients using non-metric multidimensional scaling ordination. a) Park location (see Table 1) had a significant effect on air score ( $p = .0001$ ,  $n = 13$ ) and mean values ( $\pm$  SE) are shown for parks with replicate plots. Two-way ANOVA results are shown on graph: T indicates effect of survey time (historic or current), P indicates effect of park location, and **NxP** indicates the interaction of survey time on mean air score by park location. Asterisks indicate level of significance: ns  $p > 0.05$ , \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ . Uppercase letters indicate significant differences for the interaction shown in bold; b) No significant difference occurred between binned mean historic and current park air scores ( $p = .91$ ,  $n = 13$ ) in an 18-year re-assessment of matched historic and current urban park lichen community surveys. Highest air score values indicate the most polluted sites.

gradients. These results highlight the important role of tall urban trees and canopy depth in contributing to nutrient retention and pollutants uptake in urban environments

Collectively, these results suggest that urbanization can foster macrolichen biodiversity, yet results in homogenization of the functional role of canopy epiphyte communities, as observed in other regional, ground-based studies (Geiser and Neitlich, 2007; Root et al., 2015). This is in contrast to some studies, where low species richness equated to biotic homogenization (Buczowski and Richmond, 2012; Deguines et al., 2016). The combined sensitivity of many functionally and ecologically important macrolichen species and the rapid spread of urbanization in the PNW region will have a significant result on Pacific Northwest forest ecosystem processes such as canopy N fixation, canopy microclimate regulation, and habitat and forage sources. The resulting impacts of a homogenized, urban-tolerant macrolichen community on tree canopy communities and ecosystem functioning have not been well examined in either urban cities or in rapidly urbanizing areas along the rural-urban fringe, yet is a pressing issue in regards to increasing urbanization and the growing interest in the role of peri-urban forests and transitional areas in mitigating air pollution from adjacent urban areas (Godefroid and Koedam, 2003; Baumgardner et al., 2012).



## 5. Conclusions

This study is the first to our knowledge to examine urbanization impacts on tree canopy macrolichen biodiversity and the resulting impacts of epiphyte community shifts on functional biodiversity within urban tree canopies. Our results suggest that tall urban conifer trees, such as *P. menziesii*, can serve as important, stratified habitats for macrolichen epiphytes. Additionally, we found that urban parks and forested areas can harbor a species rich community of macrolichens epiphytes and that such biodiversity has been sustained over an 18 year time period in the urban area of Portland, OR. Measures of biodiversity are important indicators for environmental assessment; however, a critical limitation of many biodiversity indices is that community composition and functional biodiversity are not always interpretable (Di Battista et al., 2016). Therefore, despite the maintained biodiversity, the pattern of biotic homogenization in urban forest epiphytes observed here, resulting in the replacement of sensitive, endemic canopy species with functionally redundant generalists (McKinney and Lockwood, 1999; McKinney, 2006; Concepción et al., 2015), may have profound implications on the function of both urban and natural forest canopies as well as larger forest ecosystem processes. If we wish to conserve biodiversity and the ecological processes of forests in urban areas, tall, stratified tree canopies should be considered a vital component of urban forests and parks, and the functional role of epiphytes in urban and peri-urban forests more thoroughly investigated.

## Acknowledgements

We would like to thank USFS Region 6 Air Program, Linda Geiser, Amanda Hardman and Doug Glavich for access to the historic survey database. Portland Parks and Recreation, Kendra Petersen-Morgan and Oregon State Parks for permitting the tree canopy surveys. Special thanks to Tyler Zuniga for climbing expertise and volunteer of time on this project. Doug Glavich for help with lichen identification. Orion Coleman, Isaac Brocker, Seth Bailey and John Brown for additional climbing support and to Laura Holloway, Scott Kiel and April Fong for lab and field assistance. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## References

- Antoine, M.E., 2004. An ecophysiological approach to quantifying nitrogen fixation by *Lobaria oregana*. *Bryologist* 107, 82–87.
- Baumgardner, D., Varela, S., Escobedo, F.J., Chacalo, A., Ochoa, C., 2012. The role of a peri-urban forest on air quality improvement in the Mexico City megalopolis. *Environ. Pollut.* 163, 174–183.
- Berryman, S., McCune, B., 2006. Estimating epiphytic macrolichen biomass from topography, stand structure and lichen community data. *J. Veg. Sci.* 17, 157–170.
- Buczowski, G., Richmond, D.S., 2012. The effect of urbanization on ant abundance and diversity: a temporal examination of factors affecting biodiversity. *PLoS One* 7, 1–9.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Chen, Y., Li, Y., Li, J., 2016. Investigating the influence of tree coverage on property crime: a case study in the city of Vancouver, British Columbia, Canada. *Int. Arch. Photogramm. Remote Sens. Spatial Inf. Sci.* 695–702 XLI-B2.
- Clark, C.M., Bell, M.D., Boyd, J.W., Compton, J.E., Davidson, E.A., Davis, C., Fenn, M.E., Geiser, L., Jones, L., Blett, T.F., 2017. Nitrogen-induced terrestrial eutrophication: cascading effects and impacts on ecosystem services. *Ecosphere* 8, 1–28.
- Concepción, E.D., Moretti, M., Altermatt, F., Nobis, M.P., Obrist, M.K., 2015. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. *Oikos* 124, 1571–1582.
- Coxson, D.S., Nadkarni, N.M., 1995. In: Lowman, M.D., Nadkarni, N.M. (Eds.), *Ecological Roles of Epiphytes in Nutrient Cycles of Forest Ecosystems*. Forest Canopies. Academic Press Incorporated, pp. 495–543.
- Davies, L., Bates, J.W., Bell, J.N.B., James, P.W., Purvis, O.W., 2007. Diversity and sensitivity of epiphytes to oxides of nitrogen in London. *Environ. Pollut.* 146, 299–310.
- Deguine, N., Julliard, R., de Flores, M., Fontaine, C., 2016. Functional homogenization of flower visitor communities with urbanization. *Ecol. Evol.* 6, 1967–1976.
- Di Battista, T., Fortuna, F., Maturro, F., 2016. Environmental monitoring through functional biodiversity tools. *Ecol. Indic.* 60, 237–247.
- Donnley, R., Marzluff, M., 2004. The importance of reserve size and landscape context to urban bird conservation. *Conserv. Biol.* 18, 733–745.
- Donovan, G.H., Prestemon, J.P., 2012. The effect of trees on crime in Portland, Oregon. *Environ. Behav.* 44, 3–30.
- Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M.O., Pöschl, U., 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nat. Geosci.* 5, 459–462.
- Elmqvist, T., Setälä, H., Handel, S.N., van der Ploeg, S., Aronson, J., Blignaut, J.N., Gomez-Baggethun, E., Nowak, D.J., Kronenberg, J., de Groot, R., 2015. Benefits of restoring ecosystem services in urban areas. *Curr. Opin. Environ. Sustain.* 14, 101–108.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309, 570–574.
- Geiser, L.H., Neitlich, P.N., 2007. Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens. *Environ. Pollut.* 145, 203–218.
- Geiser, L.H., Jovan, S.E., Glavich, D.A., Porter, M.K., 2010. Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA. *Environ. Pollut.* 158, 2412–2421.
- Geiser, L.H., 2004. Monitoring Air Quality Using Lichens on National Forests of the Pacific Northwest: Methods and Strategy. Page USDA- Forest Service Pacific Northwest Regional Technical Paper.
- Godefroid, S., Koedam, N., 2003. Distribution pattern of the flora in a peri-urban forest: an effect of the city-forest ecotone. *Landscape Urban Plann.* 65, 169–185.
- Guénard, B., Cardinal-De Casas, A., Dunn, R.R., 2015. High diversity in an urban habitat: are some animal assemblages resilient to long-term anthropogenic change? *Urban Ecosyst.* 18, 449–463.
- Hillebrand, H., Matthiessen, B., 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecol. Lett.* 12, 1405–1419.
- IPCC 5th Assessment Report, 2014. Climate Change 2014: Mitigation of Climate Change. Chapter 12.1, 12.2 Human Settlements, Infrastructure and Spatial Planning.
- JMP Version 9.0. 2009. SAS Institute Inc., Cary, NC.
- Jovan, S., McCune, B., 2005. Air-quality bioindication in the greater central valley of California, with epiphytic macrolichen communities. *Ecol. Appl.* 15, 1712–1726.
- Jovan, S., Riddell, J., Padgett, P., Nash III, T.H., 2012. Eutrophic lichens respond to multiple forms of N: implications for critical levels and critical loads research. *Ecol. Appl.* 22, 1910–1922.
- Jovan, S., 2008. Lichen Bioindication of Biodiversity, Air Quality, and Climate: Baseline Results from Monitoring in Washington, Oregon, and California. USDA Forest Service General Technical Report PNW-GTR-737.
- Kline, J.D., Harmon, M.E., Spies, T.A., Morzillo, A.T., Pabst, R.J., McComb, B.C., Schneckeburger, F., Olsen, K.A., Csuti, B., Vogeler, J.C., 2016. Evaluating carbon storage, timber harvest, and potential habitat possibilities for a Western Cascades (USA) forest landscape. *Ecol. Appl.* 26, 2044–2059.
- Kowarik, I., 2011. Novel urban ecosystems, biodiversity, and conservation. *Environ. Pollut.* 159, 1974–1983.
- Livesley, S.J., McPherson, G.M., Calfapietra, C., 2016. The urban forest and ecosystem services: impacts on urban water, heat, and pollution cycles at the tree, street, and city scale. *J. Environ. Qual.* 45, 119–124.
- McCune, B., Geiser, L.H., 2009. *Macrolichens of the Pacific Northwest*, 2nd edition. Oregon State University Press.
- McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, Oregon, USA.
- McCune, B., Amsberry, K.A., Camacho, F.J., Emerson, C., Felder, G., French, P., Greene, D., Peterson, E.B., Pendergrass, K., Parker, G.G., Hutten, M., Larson, B., Lesko, M., Maiors, S., Peterson, T., Platt, J., Proctor, J., Rambo, T., Rosso, A., Turner, R., Widmer, M., 1997a. Vertical profile of epiphytes in a Pacific Northwest old-growth forest. *Northwest Sci.* 71, 145–152.
- McCune, B., Dey, J.P., Peck, J.E., Cassell, D., Heiman, K., Will-wolf, S., Neitlich, P.N., 1997b. Repeatability of community data: species richness versus gradient scores in large-scale lichen studies. *Bryologist* 100, 40–46.
- McCune, B., 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington. *Bryologist* 96, 405–411.
- McCune, B., 1994. Using epiphyte litter to estimate epiphyte biomass. *Bryologist* 97, 396–401.
- McCune, B., 2000. Lichen communities as indicators of forest health. *Bryologist* 103, 353–356.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. *Bioscience* 52, 883–890.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127, 247–260.
- Mills, J.R., Cunningham, P., Donovan, G.H., 2016. Urban forests and social inequality in the Pacific Northwest. *Urban For. Urban Green.* 16, 188–196.
- Naem, S., Chapin III, F.S., Costanza, R., Ehrlich, P.R., Golley, F.B., Hooper, D.U., Lawton, J.H., O'Neil, R.V., Mooney, H.A., Sala, O.E., Symstad, A.J., Tilman, D., 1999. Biodiversity and ecosystem functioning: maintaining natural life support processes. *Issues Ecol.* 4, 2–11.
- Newbold, T., Hudson, L.N.L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverri-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhuseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.J.P.W., Purvis, A., Börger, L., Bennett, D.J., Choimes, A.,

- Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhousseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha Pinto Correia, D., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50.
- Nielsen, A.B., van den Bosch, M., Maruthaveeran, S., Konijnendijk van den Bosch, C., 2014. Species richness in urban parks and its drivers: a review of empirical evidence. *Urban Ecosyst.* 17, 305–327.
- Nowak, D.J., Stein, S.M., Randler, P.B., Greenfield, E.J., Comas, S.J., Carr, M.A., Alig, R.J., 2010. Sustaining America's Urban Trees and Forests. USDA Technical Report, Northern Research Station NRS-62:27.
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2016. *Vegan: Community Ecology Package*. R Package Version 2.4-0. <https://cran.r-project.org/package=vegan>.
- Ordóñez, C., Duinker, P.N., 2012. Ecological integrity in urban forests. *Urban Ecosyst.* 15, 863–877.
- ParkScore. 2016. <http://parkscore.tpl.org/city.php?city=Portland>.
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. *Science* 330, 1496–1501.
- Pettersson, R.B., Ball, J.P., Renhorn, K.-E., Esseen, P.-A., Sjöberg, K., 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biol. Conserv.* 74, 57–63.
- Pinho, P., Correia, O., Lecoq, M., Munzi, S., Vasconcelos, S., Gonçalves, P., Rebelo, R., Antunes, C., Silva, P., Freitas, C., Lopes, N., Santos-reis, M., Branquinho, C., 2016. Evaluating green infrastructure in urban environments using a multi-taxa and functional diversity approach. *Environ. Res.* 147, 601–610.
- Porada, P., Weber, B., Elbert, W., Pöschl, U., Kleidon, A., 2013. Estimating global carbon uptake by lichens and bryophytes with a process-based model. *Biogeosci. Dis.* 10, 3735–3846.
- Porada, P., Weber, B., Elbert, W., Pöschl, U., Kleidon, A., 2014. Estimating impacts of lichens and bryophytes on global biogeochemical cycles. *Global Biogeochem. Cycles* 28, 71–85.
- RStudio Team Version 0.99.473, 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA.
- Rao, M., George, L.A., Rosenstiel, T.N., Shandas, V., Dinno, A., 2014. Assessing the relationship among urban trees, nitrogen dioxide, and respiratory health. *Environ. Pollut.* 194, 96–104.
- Root, H.T., Geiser, L.H., Jovan, S., Neitlich, P., 2015. Epiphytic macrolichen indication of air quality and climate in interior forested mountains of the Pacific Northwest, USA. *Ecol. Indic.* 53, 95–105.
- Seto, K.C., Guneralp, B., Hutyrá, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci.* 109, 16083–16088.
- Sillett, S.C., Rambo, T.R., 2000. Vertical distribution of dominant epiphytes in Douglas-fir forests of the Central Oregon Cascades. *Northwest Sci.* 74, 44–49.
- Sun, N., Yearsley, J., Voisin, N., Lettenmaier, D.P., 2015. A spatially distributed model for the assessment of land use impacts on stream temperature in small urban watersheds. *Hydrol. Processes* 29, 2331–2345.
- USDA-Forest Service, 2011. *FIA Field Methods for Forest Health Guide (phase 3) Measurements Version 5.1. Section 21: Lichen Communities*.
- USDA-Forest Service, 2016. *National Forest Air Quality and Lichen Database and Clearinghouse*. <http://gis.nacse.org/lichenair/index.php>.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of earth's ecosystems. *Science* 277, 494–499.
- Wissmar, R.C., Timm, R.K., Logsdon, M.G., 2004. Effects of changing forest and impervious land covers on discharge characteristics of watersheds. *Environ. Manage.* 34, 91–98.
- Wolf, A.L., 2009. Bird Use of Epiphyte Resources in an Old-growth Coniferous Forest of the Pacific Northwest.