

# Relative effects of vehicle pollution, moisture and colonization sources on urban lichens

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## Summary

1. Lichens are sensitive to pollution and have therefore been used as air quality indicators. While the distribution of lichens within cities may reflect the distribution of traffic pollution, other factors affecting urban lichens are correlated with this pollution – particularly moisture and the presence of lichen colonization sources.

2. Our objective was to determine the relative importance of these three factors – vehicle pollution, moisture and colonization sources – in determining lichen distribution within a city. We surveyed macrolichen richness and cover on 420 trees within 84 sites across urban Ottawa, Canada. The sites were selected to minimize correlations among vehicle pollution, moisture and colonization sources. Model-averaged standardized regression coefficients were used to compare the relative effects of these three variables on macrolichen richness and cover.

3. We found that macrolichen cover was most strongly related to vehicle pollution and that this effect occurred within 300 m of a site.

4. However, macrolichen species richness responded more strongly to both moisture (at the site centre) and colonization sources (within 1000 m of the site) than to vehicle pollution.

5. *Synthesis and applications.* Our results suggest that macrolichen cover, but not macrolichen species richness, can be used as an indicator of urban traffic pollution. Our results also suggest that, to promote urban macrolichen diversity, it would be more effective to increase the availability of lichen colonization sources (nearby trees) than to control traffic pollution.

**Key-words:** bioindicators, conservation, greenspace, habitat restoration, impervious surfaces, landscape ecology, multi-scale analysis, road ecology, soil sealing, urban design

## Introduction

Lichens absorb nutrients from the air and water. Harmful molecules are absorbed with these nutrients, and lichens are often unable to metabolically process or isolate these harmful molecules quickly enough to avoid damage. This makes lichens very sensitive to air pollution (Brodo, Sharnoff & Sharnoff 2001). There is a large body of literature showing the impacts of various forms of air pollution on lichens, reviewed by Conti & Cecchetti (2001), Asta *et al.* (2002) and Nash (2008). In fact, urban lichen distributions are often attributed to the pattern of urban air pollution, leading some to map urban air pollution using lichens. For example, two classic studies published in 1970 presented detailed pollution mapping techniques using lichens: the Index of Atmospheric Purity was developed in

Montreal, Canada (LeBlanc & De Sloover 1970), and a lichen scale calibrated with sulphur dioxide pollution levels was developed in England and Wales (Hawksworth & Rose 1970). More recent examples include Käffer *et al.* (2011) who mapped air quality in urban areas of southern Brazil using lichen distributions, and Estrabou *et al.* (2011) who mapped air quality in the city of Córdoba, Argentina, using lichen distributions. Pollution mapping using lichens was originally designed in the context of industrial pollution emissions, and lichens are still used to document effects of industrial pollution, including industrial agriculture, on natural and semi-natural areas (e.g. Pinho *et al.* 2011; Wannaz *et al.* 2012). However, in today's cities, automobiles and other vehicles typically emit the bulk of air pollution in the province of Ontario, Canada (Ontario Ministry of the Environment 2011). If vehicle pollution affects lichens, then the distribution of lichens in cities should reflect patterns of vehicle pollution. Support for this idea comes from experiments showing

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that vehicle pollution hinders lichen growth. Fumigation experiments show that nitric acid pollution from vehicle exhaust is damaging to both algal and fungal cells in lichens (Riddell, Nash & Padgett 2008). By deploying 'bags' of healthy lichens for short time periods in polluted areas, it has been shown that lichens bio-accumulate heavy metals from vehicles (Garty, Kauppi & Kauppi 1996), and heavy metals are known to compromise the absorption of light by chlorophyll, hindering lichen metabolism (Puckett 1976).

However, the fact that vehicle pollution affects lichen growth does not necessarily mean that lichen distributions in cities are determined primarily by vehicle pollution. Many variables other than pollution have been observed to affect lichens in their natural habitats (Smith 1921; Barkman 1958; De Wit 1976). Within a city, lichen cover and richness at a site should also depend on the local site microclimate (primarily moisture level: Brodo 1966; Tretiach *et al.* 2012) and on the rate of influx of lichen dispersal units (both vegetative and sexual) from nearby colonization sources (Öckinger, Niklasson & Nilsson 2005; Werth *et al.* 2006a,b; Johansson, Ranius & Snäll 2012). Gombert, Asta & Seaward (2004) found that patterns of the Index of Atmospheric Purity corresponded with general 'human impact' rather than major pollution sources, supporting the idea that urban lichen distributions may respond to factors other than, or in addition to, major pollution sources.

It is important to test the hypothesis that lichen distributions in cities are primarily related to air pollution (rather than moisture or colonization sources) for two reasons. First, as macrolichen cover is easy to measure, it could be used as an indirect way of detecting and mapping local pollution levels if the relationship with air pollution is strong. Second, if local urban lichen richness is controlled by air pollution then management actions for conservation of lichens in cities should focus on controlling air pollution.

However, untangling the effects of pollution, moisture and colonization on lichen distributions is difficult because patterns of both local moisture and lichen colonization sources are likely to covary with patterns of vehicle pollution across cities. Vehicle traffic levels are positively correlated with impervious surface area because vehicles travel on roads, which are typically paved. Pavement cover renders the road surface impervious to water, reducing local moisture by increasing runoff of precipitation and thereby reducing evaporation. Vehicle traffic levels are negatively correlated with treed area as trees cannot grow in the roadway; by reducing the treed area, the lichen habitat (trees) from which colonists disperse is reduced.

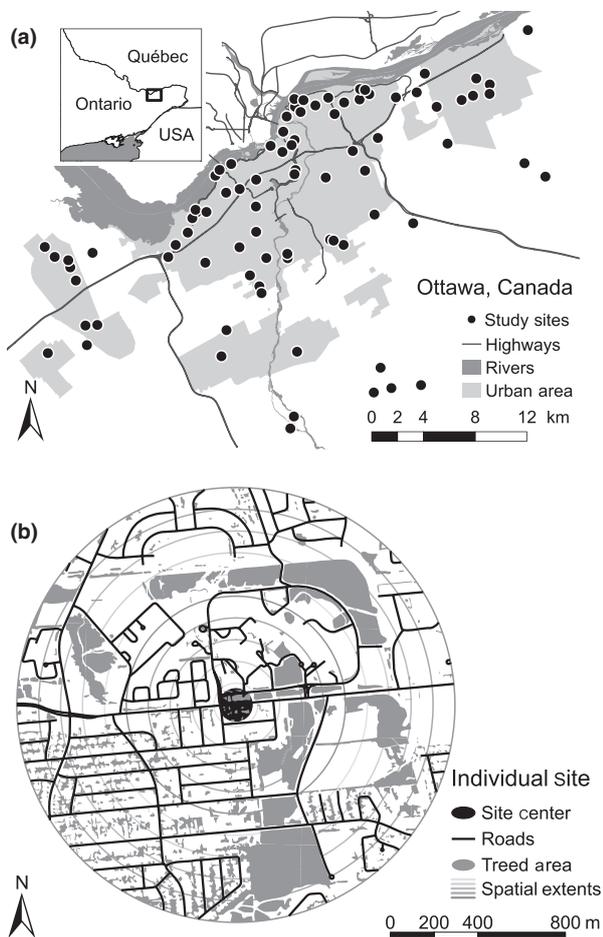
The purpose of this study was to test predictions (below) of the relative effects of vehicle pollution, moisture and colonization sources on lichen distributions within a city, with the aim of developing recommendations for lichen conservation and monitoring of urban air pollution. To do this we designed a 'mensurative experi-

ment' (*sensu* Hurlbert 1984; e.g. Ethier & Fahrig 2011; Munro, Bowman & Fahrig 2012) in which we selected lichen survey sites in a design aimed at reducing the correlations among the three predictor variables. In a mensurative experiment, site selection is used to mimic a real experiment, in which each potential predictor would be varied while controlling for the other potential predictors. Landscape variables are often highly correlated across randomly selected landscapes, which means that the inferential strength of such studies is low, and teasing apart the separate effects of the landscape variables with confidence is difficult (Eigenbrod, Hecnar & Fahrig 2011). Estimating independent effects of predictors is particularly important in an applied context, as it allows for higher confidence in management recommendations based on the study results. A disadvantage of the mensurative experimental approach is that the data collected cannot be used to estimate the distributions of the variables across the study area, because the study sites are specifically selected from within the portions of the predictor distributions that reduce correlations among the predictors. However, we note that this is not a concern in the present study where our objective was not to describe the distributions of the variables but rather to test specific *a priori* predictions about the relative importance of the predictors on lichen richness and abundance, from which we could produce guidelines for lichen conservation and air quality monitoring. The mensurative experimental approach allows higher confidence in such guidelines.

We conducted the study in Ottawa, Canada (pop. 812 129, Statistics Canada 2007), a city in which the only major air pollution source is vehicle traffic (City of Ottawa 2011). Our focus was on urban streets rather than expressways: the highest average annual daily traffic along a road at a study site was 28 120 vehicles (City of Ottawa 2010). Two prior studies have shown that lichen richness is lower in the Ottawa urban area than in surrounding areas (Bégin-Robitaille 1978; Manga 1989–1990). We predicted that sites within the city with higher vehicle pollution, lower moisture and fewer trees (colonization sources) in the surrounding area would have lower lichen cover and lichen species richness. However, we also predicted that vehicle pollution effects on lichen cover and species richness would be stronger than the effects of moisture and treed area, based on the emphasis on pollution effects in prior literature.

## Materials and methods

In 2009 and 2010, we sampled lichen cover and lichen species richness on 420 trees along city streets at 84 sites in Ottawa, Canada (Fig. 1). First, over 800 possible roadside sites were identified, one in each grid cell of a 1 × 1 km grid placed over the city. From among these, we selected a subset 84 sample sites that minimized the correlations among vehicle pollution, impervious surface area (a correlate of local moisture), and colonization sources at the site centres (75 m radius).



**Fig. 1.** Map of 84 study sites across urban Ottawa, Canada (a), and an example site (b) showing the lichen sample site at the centre, and the surrounding multi-scale landscape. Lichen cover and species richness (response variables) were sampled on five trees at the centre of each site; moisture (a predictor variable) was measured on one of these trees at each site; and vehicle pollution and lichen colonization sources (predictor variables) were measured at multiple spatial extents, from 100 m to 1 km, around each sample site.

We measured three predictor variables, representing the three hypothesized effects: vehicle pollution, moisture and colonization sources around each site. We estimated vehicle pollution by adding together ranged values (Legendre & Legendre 1998) of road density and bus traffic at each site, for a unit-less index of pollution between zero and two. Road density and bus traffic were measured at multiple spatial extents (landscapes) around each lichen sampling site (Fig. 1). Road density was the length of all roads within the landscape and was ranged between zero and one. Bus traffic was the average annual daily bus traffic (OC Transpo 2009) multiplied by the length of the corresponding bus route in each landscape, and also ranged between zero and one. Moisture in the boundary layer of tree trunks (in units of MPa) was measured using a shaded iButton (DS1923 Hygrochron, Maxim; Dallas, USA) mounted one meter above the ground on the north side of one tree at each site. Water potential was calculated from temperature and humidity (equation 2.24 in Nobel 2009) every half an hour of daylight over 5 days. Sites were randomly assigned to 5-day periods between July and

November 2010. The average water potential for each site was subtracted from the average of all sites monitored within the same 5-day period, to correct for climatic variation between monitoring periods.

We assumed that lichens would colonize trees at the site centres from nearby trees, or more precisely the lichens established on the tree branches, in the surrounding area. We estimated the influence of colonization sources around a site by using the area in  $\text{m}^2$  of all tree crowns in the landscape surrounding each lichen sample site (see also Shei *et al.* 2012). We made these estimates using data available from the City of Ottawa (2009). Colonization sources were then the standardized natural logarithm of treed area, calculated at multiple spatial extents around each site (Fig. 1).

Vehicle pollution and colonization sources were calculated within landscapes at multiple spatial extents (radius in meters) around each site (Fig. 1). Lichens can be affected by mechanisms operating at different spatial scales. *A priori*, the spatial extent over which vehicle pollution and colonization sources might influence lichen cover and lichen species richness in urban areas was unknown. Therefore, we estimated these variables at ten spatial extents, ranging from 100 m to 1 km. The lower limit of 100 m was chosen to capture the influence of vegetative dispersal at small scales; 1 km was considered sufficient to capture variations in air pollution. The scale of effect for each predictor variable was estimated as the spatial extent with the highest Pearson correlation coefficient with the response variable. In further statistical modelling, we used the predictor variable measured at its scale of effect. Note that we did not use the results from the multi-scale analyses to estimate the effects of the predictors or to test our predictions, as the only predictor included in each multi-scale analysis was the variable of interest for that analysis. To estimate the effect of a predictor relative to other variables and while controlling for their effects, we included all the variables in mixed effects multiple regression models in which we also controlled for the effects of tree species and diameter.

For the lichen surveys, we selected five trees at the centre of each site. Tree selection criteria followed Asta *et al.* (2002). *Acer* (Maple) and *Fraxinus* (Ash) were preferred due to local availability and similar lichen flora (based on preliminary fieldwork). We chose straight trees at the site centre (within a 75 m radius). Trees were only used if they had no branches or knots below 1.5 m from the ground and were easily accessible to light and air pollution from all sides. Tree species and diameter at breast height (measured 1.3 m above the ground) were recorded.

We sampled macrolichen cover and species richness on each tree. We limited our surveys to macrolichens, the species that grow in leafy or bushy forms and are only loosely attached to the tree bark, as opposed to those growing within the bark. Macrolichens are suitable indicators of the diversity of all lichens growing on trees (Bergamini *et al.* 2005, 2007). They can be definitively identified in the field and are those most commonly used in public monitoring protocols (e.g. OPAL, [www.OPAL.explorenature.org](http://www.OPAL.explorenature.org)). Identification of lichens growing within the tree bark is much more time-consuming and can require laboratory identification, so is not feasible for extensive surveys such as ours or those of most monitoring programs. Throughout this study, we use the word 'lichens' to refer to macrolichens unless otherwise specified. A lichen ladder (vertical set of five 10 by 10 cm microquadrats) was placed on four sides of each tree, 90° apart (Asta *et al.* 2002), with the first side parallel to and facing

the road. Lichens were identified in twenty regularly spaced, one centimetre diameter circles in each microquadrat (Fig. S1, Supporting Information). The species of lichen (or bare bark) with the highest cover in each circle was recorded. Reference specimens were collected for the Canadian Museum of Nature's herbarium (CANL). Lichen species richness was the number of lichen species recorded on each tree; lichen cover was the number of circles (of 400 per tree) with lichens present.

We used linear mixed effects modelling to estimate the relative effects of vehicle pollution, moisture and colonization sources on lichen cover and lichen species richness. We analysed the data at the tree level so that we could account for tree diameter and for tree species as random effects in the models. Tree species is highly correlated with a number of 'micro' scale variables such as pH and bark texture (Giordani 2006), so we have used tree species as a microcontrol variable. All seven possible models of the three standardized predictor variables – vehicle pollution, moisture and colonization sources – were fit for each of the two response variables (lichen cover and richness). All models also included tree diameter and tree species. We compared the support for the models using the Akaike Information Criterion (AIC, Burnham & Anderson 2002). Inclusion of tree diameter was supported by a decrease of at least eight points in AIC values when tree diameter was included in any of our models as a fixed effect. Inclusion of tree species was supported by an AIC decrease of 12 points. We compared the relative effects of the predictor variables using weighted model-averaged standardized parameter estimates (Burnham & Anderson 2002; Smith *et al.* 2009). Residual plots supported model assumptions of linear responses. Statistical modelling was conducted using the *nlme* package for R (Zuur *et al.* 2009; Pinheiro *et al.* 2010).

## Results

We found eighteen macrolichen species, covering 27% of the total sampled trunk surface area (occupied/total circles). *Candelaria concolor*, *Xanthomendoza fallax* and *Physciella chloantha* were most commonly found across sites (see Esslinger 2011 for authorities). The percentage of sites where each species was found and the cover of each species across all sites are reported in Table 1. Moisture varied considerably among 5-day periods, supporting our use of the residual values from each week's mean. The two *Fraxinus* (Ash) tree species had the highest macrolichen cover and species richness, while different *Acer* (Maple) tree species varied considerably in their macrolichen cover and species richness (Fig. S2, Supporting Information).

The scales of effect for the two landscape predictors (vehicle pollution and colonization sources) are the spatial extents with the largest absolute correlation coefficient with each of the lichen responses (cover and species richness); hence, there is one scale of effect identified for each of the four predictor–response pairs (Fig. S3, Supporting Information). The scales of effect for vehicle pollution were 300 m and 1000 m for lichen cover and richness, respectively. At 300 m, the length of roads in the landscape was between zero and 0.0200 m of road per m<sup>2</sup> of landscape. The average annual daily bus traffic per kilometre of road varied between zero and 45.7 vehicles per

**Table 1.** Summary of macrolichens found at 84 lichen survey sites in Ottawa, Canada. Cover is the percentage of all 168 000 of the 1-cm diameter sample circles surveyed (i.e. 400 circles on each of five trees at each of 84 sites), in which the species was most abundant. The sites column reports the percentage of the 84 sites at which the species was found

Lichen species	Cover (%)	Sites (%)
<i>Candelaria concolor</i>	7.18	100
<i>Evernia mesomorpha</i>	0.00	1
<i>Flavoparmelia caperata</i>	0.04	12
<i>Hyperphyscia adglutinata</i>	0.93	73
<i>Parmelia sulcata</i>	0.35	32
<i>Phaeophyscia adiantola</i>	2.36	100
<i>Phaeophyscia ciliata</i>	0.04	15
<i>Phaeophyscia orbicularis</i>	0.00	1
<i>Phaeophyscia pussiloides</i>	0.22	44
<i>Phaeophyscia rubripulchra</i>	0.47	44
<i>Physcia adscendens</i>	2.62	74
<i>Physcia aipolia</i>	1.10	73
<i>Physcia millegrana</i>	2.29	67
<i>Physcia stellaris</i>	1.29	63
<i>Physciella chloantha</i>	3.34	93
<i>Physciella melanchnra</i>	0.02	6
<i>Physconia detersa</i>	0.54	42
<i>Xanthomendoza fallax</i>	5.54	96

km. At 1000 m, these were 0.000637–0.0192 m of road per m<sup>2</sup> of landscape and zero to 300 vehicles per km, respectively. The scale of effect for colonization sources (treed area) was at 1000 m for both lichen cover and species richness. At this scale, treed area varied from  $6.82 \times 10^4$  to  $2.24 \times 10^6$  m<sup>2</sup>. The correlation coefficients between predictor variables (with the landscape variables measured at their scales of effect) were low, as expected by design: –0.37 between vehicle pollution and moisture, 0.34 between moisture and colonization sources, and –0.19 between vehicle pollution and colonization sources.

Mixed model results are presented in Table 2. The signs of the coefficients across all models were consistent with expectations: the influence of vehicle pollution was negative and the influences of moisture and colonization sources were positive. The best models for lichen cover ( $\Delta\text{AIC}_i$  within two points of best model) all included vehicle pollution as a predictor variable. In contrast, all models for lichen species richness had similar support (small  $\Delta\text{AIC}_i$  values). Comparisons of model-averaged standardized parameter estimates for each response variable suggest that vehicle pollution is the strongest predictor of lichen cover, while moisture and colonization sources predict lichen species richness better than vehicle pollution.

## Discussion

Our results have important implications for the use of macrolichens as traffic pollution indicators and for conservation of macrolichen diversity. We found that while

**Table 2.** Comparison of all seven possible models of lichen cover (a) and species richness (b) predicted by standardized vehicle pollution, moisture and treed area. All models included tree diameter (fixed effect) and tree species nested within site (random effect). Direction of effect, difference between 'best' model Akaike Information Criterion (AIC) and AIC of model  $i$  ( $\Delta\text{AIC}_i$ ), and Akaike weight of the model ( $w_i$ ) are shown. Model-averaged standardized parameter estimates ( $\hat{\beta}$ ) summarize the predictor strength and direction across models

(a) Models of lichen cover				
Vehicle pollution (300 m)	Moisture (Local)	Colonization sources (1000 m)	$\Delta\text{AIC}_i$	$w_i$
–	+		0	0.379
–			0.679	0.270
–	+	+	1.87	0.149
–		+	2.04	0.136
	+		4.29	0.0443
	+	+	5.99	0.0189
		+	9.42	0.00340
$\hat{\beta} = -19.7$	$\hat{\beta} = 7.53$	$\hat{\beta} = 1.29$		
(b) Models of lichen species richness				
Vehicle pollution (1000 m)	Moisture (Local)	Colonization sources (1000 m)	$\Delta\text{AIC}_i$	$w_i$
	+		0	0.238
		+	0.064	0.230
–			0.704	0.167
	+	+	1.24	0.128
–	+		1.80	0.0965
–		+	1.89	0.0925
–	+	+	3.22	0.0475
$\hat{\beta} = -0.0514$	$\hat{\beta} = 0.113$	$\hat{\beta} = 0.109$		

macrolichen cover on Ottawa's urban trees is an indicator of vehicle pollution within 300 m, macrolichen species richness does not respond strongly to vehicle pollution at scales from 100 to 1000 m. This suggests that macrolichen cover (but not macrolichen species richness) could be used to estimate the spatial distribution of vehicle pollution in the city. From the perspective of the conservation or enhancement of macrolichen richness, our results suggest that efforts should focus on increasing treed area (to provide dispersal sources) throughout the city, rather than on trying to control traffic pollution because urban macrolichen species richness responds more strongly to treed area than to vehicle pollution in Ottawa. Note that our results apply specifically to macrolichens. Other components of the lichen community may be more or less sensitive to different environmental conditions in urban areas (Llop *et al.* 2012). We focussed on macrolichens here because these are most readily surveyed in the field and therefore most amenable for use as bioindicators.

These results support the use of 'Lichen Diversity Values' (LDV, Asta *et al.* 2002) as an indicator of urban vehicle pollution patterns because, despite its name, LDV

is actually more closely related to total lichen cover than to lichen richness. Across the 84 sample sites, the Pearson correlation coefficient between lichen cover (number of occupied circles) and LDV was 0.885, whereas lichen species richness and LDV had a 0.643 correlation. This is because LDV is calculated as the sum of presences of each species in each of 20 quadrats per tree, divided by the number of trees sampled (Asta *et al.* 2002). Therefore, the contribution of each species to the LDV ranges from 0 to 20, depending on its cover (as there were 20 quadrats per tree), resulting in an increase in the index with total lichen cover. The usefulness of the LDV as an indicator of urban vehicle pollution may be further enhanced by limiting the species included in the index to a subset of species that are known to be particularly sensitive to traffic pollution (Llop *et al.* 2012).

While we were able to estimate the separate effects of vehicle pollution, moisture and colonization sources reasonably well, we were not able to select sites such that the correlations were zero. To estimate relative effects of the predictors, we used standardized coefficients, as they are generally robust to correlations among predictor variables (Smith *et al.* 2009). In fact, completely eliminating correlations between vehicle pollution, moisture and colonization sources is not possible because, as outlined in the introduction, all three variables are related to roads. In addition, there are likely to be some interactions among the predictors. For example, experiments have shown that effects of vehicle pollution on lichen respiration and photosynthesis are lower in more moist conditions; this seems to be because the higher humidity levels increase the metabolic activity of the lichens, allowing them to repair damage from pollution (Riddell, Nash & Padgett 2008). Also, as vegetation can remove pollutants from the air (Forsyth & Musacchio 2005), the effect of a given level of vehicle pollution on lichens should be reduced in landscapes containing more trees (more colonization sources).

Lichen cover responded most strongly to vehicle pollution within 300 m of the lichen sampling sites. This scale of vehicle pollution effect is smaller than the scale of effect of industrial air pollution: the classic lichen air quality study in Montreal (LeBlanc & De Sloover 1970) extrapolated the 'index of atmospheric purity' between sites 1600 m apart. We note, however, that Perlmutter (2010) did not find a significant correlation between lichen cover or species richness and traffic levels, when traffic was measured in 1600 m radius landscapes. It is possible that a relationship (at least with lichen cover) might have been found in that study if traffic had been measured at a smaller spatial scale. We hypothesize that the scale of response in our study (300 m) results from the scale at which urban traffic varies. Ottawa's city blocks are about 100 m wide and 200–500 m long. The 300 m scale response suggests lichens are responding to vehicles travelling along the adjacent street, not along other neighbouring streets.

In contrast to lichen cover, urban lichen species richness was more sensitive to moisture and colonization sources than to vehicle pollution. This result is supported by a recent study suggesting that urban lichens may be less sensitive to pollution than to drought stress (Tretiach *et al.* 2012). However, the relatively weak effect of vehicle pollution on species richness was unexpected given that lichen species have been classified based on their tolerances to sulphur dioxide pollution (Hawksworth & Rose 1970) and to nitrogen enrichment (Gadsdon *et al.* 2010) associated with vehicle exhaust. The implication is that certain species should be absent in areas with higher traffic pollution, which should result in an effect of traffic pollution on species richness. In apparent support of this, Llop *et al.* (2012) showed an effect of urban pollution on the lichen diversity values (LDV) of pollution-sensitive species. However, as the LDV is a combined index of species richness and species cover (as discussed earlier), their results may indicate an effect on lichen cover rather than on lichen richness. We did observe an effect of vehicle pollution on lichen cover, so traffic levels were high enough to affect lichens. The two results together – an effect of vehicle pollution on lichen cover but little effect on species richness – suggest that vehicle pollution may have its strongest effect on common (high cover) species, thus having a relatively small effect on overall species richness. We conducted a *post hoc* test of this hypothesis in which we divided the lichen data into two sets, one containing the three most common species and the other containing the remaining species. In support of our *post hoc* hypothesis, we found that pollution had four times the effect of colonization sources on the common species, but only 1.3 times the effect of colonization sources on the rare species (Table S1, Supporting Information).

We interpret the positive effect of treed area on lichen species richness as predominantly an effect of increased lichen colonization sources. While, as mentioned earlier, treed area is expected to be negatively correlated with vehicle pollution as vegetation can remove pollutants from the air (Forsyth & Musacchio 2005), we selected our sample sites to minimize this correlation. If treed area were simply an index of vehicle pollution, we would have expected vehicle pollution itself to be more strongly related to lichen richness than treed area. The reverse was true, with treed area having four times the effect of vehicle pollution on lichen richness (the model-averaged standardized parameter estimate for treed area is four times the parameter estimate for vehicle pollution).

The spatial scale of effect of colonization sources on urban lichens occurred within a 1000 m radius from lichen sample sites. As the correlation coefficients increased up to one kilometre, colonization sources may have their strongest effect at scales beyond 1000 m (Fig. S3, Supporting Information). This is larger than hypothesized based on vegetative dispersal distances (Öckinger, Niklasson & Nilsson 2005; Werth *et al.* 2006a), and also larger than

empirically estimated short-range lichen dispersal distances (e.g. Buckley 2011; Johansson, Ranius & Snäll 2012). However, the assumption that short-range dispersal is the dominant component of lichen colonization may be faulty. Johansson, Ranius & Snäll (2012) estimated that longer-range 'background' dispersal accounted for up to 50% of colonists, depending on the species, and Buckley (2011) found that the distance of isolated trees from a forest remnant several hundred meters away significantly negatively affected the probability of occurrence of many lichen species. In combination with our results, these studies suggest that an important component of lichen colonization of trees occurs over much larger distances than previously thought.

In conclusion, this study explicitly distinguished the effects of vehicle pollution, moisture and colonization sources on urban macrolichen cover and species richness. We found that macrolichen cover responded to vehicle pollution within 300 m of the lichen sample site, indicating that lichen cover is suitable for monitoring traffic pollution. This is a particularly useful result because lichen cover can be estimated quickly without any knowledge of lichen species identification. Our results also suggest that urban air quality monitoring, where vehicle pollution is at comparable levels to those in Ottawa, can be based on macrolichen cover, but should not be based on macrolichen species richness. Species richness was more strongly related to moisture and colonization sources than to vehicle pollution. For the conservation and enhancement of lichen diversity in cities, our results suggest that measures aimed at conserving and increasing treed area should be a primary objective. On a general level, we have shown that variables other than vehicle pollution, namely moisture and colonization sources, are important for understanding urban lichen ecology.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Measuring lichen cover and species richness using circles.

**Fig. S2.** Boxplots of lichen species richness and percentage cover on the most commonly surveyed tree species.

**Fig. S3.** Correlations between predictor variables at multiple spatial extents and response variables, used to determine the scale of effect for each predictor–response pair.

**Table S1.** Comparison of all seven possible models of lichen cover predicted by standardized vehicle pollution, moisture and treed area analysed separately for common and rare species.

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