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# An epiphyte desert no more: considerable epiphytic lichen diversity on common lane tree species in Amsterdam under contemporary urban environmental conditions

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## Abstract

Recording the epiphytic lichen flora in Amsterdam on 576 trees distributed over eight common lane tree species shows that the urban epiphytic diversity alone is considerable, representing 15.2%, or 100 species, of the total lichen diversity in the Netherlands. The species recorded include many rarities and some that can be viewed as urban opportunists. Trees bear 15 lichen species on average but are greatly influenced by local factors. Species-specific bark qualities such as water-holding capacity, texture and bark-shedding, influence species richness greatly but are often overshadowed by dominant environmental factors. Tree species with a higher water-holding capacity and texture generally bear the highest species richness. Bark qualities are more indicative of species richness than tree species, showing few significant differences between species richness linked to tree species. *Platanus* × *hispanica* is the only observed species whose frequent bark shedding causes it to consistently have the lowest lichen species richness, regardless of environmental factors. In general, bark desiccation and eutrophication are the most dominant factors in influencing urban epiphytic lichen diversity, resulting in xerophytic and nitrophytic lichen species being the most common. Pollution is no longer observed to be the main limiting factor for urban lichen diversity as it was in the past. Instead, bark desiccation associated with the Urban Heat Island (UHI) and low air humidity (drought) is the most damaging factor in contemporary urban conditions in Amsterdam, but it rarely reduces species richness to zero or near zero levels. Areas in which eutrophication and desiccation are much less dominant were repeatedly observed. Such areas sometimes showed local dominance of acidophytes or other distinctive communities. In line with long-term improvements to Dutch air quality, the city now offers a niche to a wider range of species. Three ecological groups (acidophytic, lithophytic-minerotrophic, xerophytic-nitrophytic) are described in this context to characterize reoccurring lichen communities in the city that are indicative of contemporary urban conditions. The term 'lithification' is proposed in an ecological context to describe the frequently observed urban phenomenon of tree bark taking on the properties of rock and consequently bearing lithophytic communities. Additionally, we show the potential use of lichen species and ecological groups to monitor urban climate factors such as the UHI on a very local and accurate scale.

**Keywords:** air pollution; ecological groups; eutrophication; lithification; species richness; urban ecology

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## Introduction

Lichens are a major component of urban biodiversity and provide many important ecosystem services, such as nitrogen and carbon fixation as well as provision of food, microhabitats and nesting material for other organisms (Prather 2017; Llewellyn *et al.* 2020 and references therein). Furthermore, epiphytic lichens especially are widely known for their value as indicators of environmental conditions, in particular air pollution (encompassing acidic, nitrogen-based and other kinds of pollution; e.g. Conti & Cecchetti 2001; Seaward 2008; Prather 2017; Allen & Lendemer 2021). In urban areas with reduced pollution levels, lichens could also be useful as indicators of local differences in humidity and temperature. The latter utility could be especially indicative of the urban heat island effect (UHI) (Munzi *et al.* 2014). Lichen biodiversity (species richness, community composition and functional diversity) is therefore an important factor not only for studying urban ecology, but also for determining the quality of the urban environment for city dwellers, including humans (Munzi *et al.* 2014; Prather 2017; Llewellyn *et al.* 2020).

Although lichens have gained more attention within the field of urban ecology (Munzi *et al.* 2014; Sujetovienė & Galinytė 2016; Koch *et al.* 2019; Mikhaylov 2020; Allen & Lendemer 2021), knowledge is still limited on how lichen biodiversity is distributed within cities, and which species characterize urban lichen communities. In the Netherlands, the only comprehensive study of urban lichen diversity was produced by Barkman (1958), who focused on the

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phytosociology and ecology of epiphytic communities across the country. Among other inferences, Barkman concluded that the diversity, abundance and coverage of epiphytic lichens was lower in urban than in natural areas, that nitrophytes and xerophytes were most common in urban areas, and that areas with the poorest diversity ('epiphyte deserts') were rather large and included industrial areas, cities like Amsterdam, but also parts of the rural areas. The latter was considered to be caused by high $SO_2$ concentrations coupled with generally low humidity in the Netherlands (Barkman 1958; Nash 2008).

The environment in the Netherlands has undergone significant changes since Barkman's era. Notably, sulphur dioxide emissions have shown a sharp decline since the 1980s, while nitrogen emissions, which only began to decrease in the 1990s (Compendium voor de Leefomgeving 2022), remain elevated. Additionally, global warming has impacted the country's lichen flora (Aptroot & van Herk 2007). Urban areas have expanded from 8% to 16% of the total surface area of the Netherlands in the period 1970–2008 (Compendium voor de Leefomgeving 2008, 2013), but on the other hand, awareness of the necessity to make cities greener and more climate adaptive is rising (Carter *et al.* 2015).

Although a small number of studies have considered the effects of changing environmental conditions in the Netherlands, mainly with respect to pollution (e.g. van Dobben & ter Braak 1998; van Herk 2001, 2009), patterns of species diversity and community composition of lichens in Dutch cities under contemporary environmental conditions remain unexplored. Munzi *et al.* (2014) recently showed for Almada (Portugal) that pollution might no longer be the dominant driver of lichen diversity in cities. Instead, locally differing climatic factors influencing lichen microclimates, such as the UHI, were found to be more significant drivers of diversity.

To investigate these patterns in the Netherlands, we studied lichen species diversity and community composition on the most common lane phorophyte species in Amsterdam. Amsterdam is situated in Western Europe close to the coast of the North Sea, and experiences a temperate oceanic climate. This study aimed to identify how lichen biodiversity is distributed across the most common urban lane tree species in Amsterdam and to use this information to infer characteristics of contemporary urban environments.

We hypothesize that there is a low overall lichen diversity, characterized mainly by nitrophytic and xerophytic species. This is expected due to the stressful urban environmental factors driving diversity, such as eutrophication from traffic emissions as well as drought and heat-stress caused by low air humidity and the UHI (Barkman 1958; Munzi *et al.* 2014; Prather 2017). The resulting urban environment is therefore expected to be limited in its available niches. However, although being significantly influenced by these environmental factors, we also hypothesize that lichen species diversity differs for each tree species, due to tree-specific bark qualities (pH, water capacity, nutrient availability, as taken from Barkman (1958) and other literature) and the locally observed urban microclimate effect (e.g. shaded to exposed localities, humid to dry habitats). For example, tree species with bark qualities that are most effective at buffering against prominent stressful urban environmental factors such as drought, heat and pollutants are expected to show the highest lichen diversity overall. These would include common urban phorophytes such as *Fraxinus excelsior* L., *Populus* × *canadensis* Moench and *Ulmus* × *hollandica* Mill., as their bark is characterized by either a medium to high water capacity, and rough or deep texture, or both (Barkman 1958).

Additionally, we analyze which species and communities are most characteristic of the urban environment and how such ecological groups could serve as indicators of specific urban conditions and phenomena such as the UHI.

## Material and Methods

### Study area

Amsterdam is the largest city in the Netherlands, with a population of close to 932 000 inhabitants in 2024 (Smits & de Jonge 2024). Between 1901 and 2010, annual precipitation in Amsterdam increased by 25%, from 768 to 933 mm $y^{-1}$. Since 1950, the average annual temperature rose by 1.6 °C to 10.9 °C in 2015 (KNMI 2018). According to van Moorselaar & van der Zee (2024), $NO_2$ emissions come primarily from traffic and have been decreasing on a national scale since the 1990s, with a 2.3 $\mu g\ m^{-3}$ annual decrease in the last decade. From 2022 to 2023, emissions decreased from 25.2 $\mu g\ m^{-3}$ to 21.8 $\mu g\ m^{-3}$ near roads with much traffic, and from 19.3 $\mu g\ m^{-3}$ to 16.5 $\mu g\ m^{-3}$ near roads with little traffic. No recorded $NO_2$ emissions have ever gone below the WHO standard of 10 $\mu g\ m^{-3}$. $SO_2$ emissions have been stable around 0.50 $\mu g\ m^{-3}$ a year. Particulate matter (PM) density was 17.3 $\mu g\ m^{-3}$ (much traffic) and 14.8 $\mu g\ m^{-3}$ (little traffic) for PM10 (< 10 μm) in 2023, and 8.9 $\mu g\ m^{-3}$ (much traffic) and 7.3 $\mu g\ m^{-3}$ (little traffic) for PM2.5 (< 2.5 μm), respectively. Both PM10 and PM2.5 levels are primarily caused by traffic and have never, or only marginally, gone below the WHO standards (15 $\mu g\ m^{-3}$ and 5 $\mu g\ m^{-3}$, respectively) as of 2023.

### Sampling design

Phorophyte species were selected based on their abundance in the Amsterdam urban environment and to represent different tree genera and corresponding bark characteristics, using the public online tree map of the Municipality of Amsterdam (GISIB 2023). The eight phorophyte species investigated were: *Acer campestre* L., *Alnus glutinosa* (L.) Gaertn., *Fraxinus excelsior*, *Platanus* × *hispanica* Münchh. (*P. orientalis* L. × *P. occidentalis* L.), *Populus* × *canadensis* (*P. nigra* L. × *P. deltoides* Marsh.), *Quercus robur* L., *Tilia* × *europaea* L. (*T. cordata* Mill. × *T. platyphyllos* Scop.) and *Ulmus* × *hollandica* (*U. glabra* Huds. × *U. minor* Mill.). Each phorophyte species was studied at two sites as replicates in different parts of Amsterdam (Fig. 1), so that local environmental factors at a single site did not mask the influence of tree-species specific bark qualities on lichen species richness. The only requirement for site selection was the presence of 36 street trees of the same species positioned in two rows along a straight or sometimes curved street. Apart from avoiding localities clearly deviating from typical urbanized environments (e.g. streets along large parks), topological differences between sites were not considered as a factor in the selection. For example, selected sites could have buildings, canals or small greenspaces on one or both sides of the street.

Trees whose bark was atypical of the mature stage, or trees that were obviously slanted, impaired by disease or otherwise damaged were excluded. Local conditions such as shade and exposure were observed in the field and used for interpretation of the results, but not sampled quantitatively. Within the context of this paper, the following terms are used: exposed (permanently sun-exposed); shaded (never sun-exposed, permanently shaded by buildings or foliage); half-shaded (periodically sun-exposed or shaded during the day, or permanently partially lit and shaded during the day).

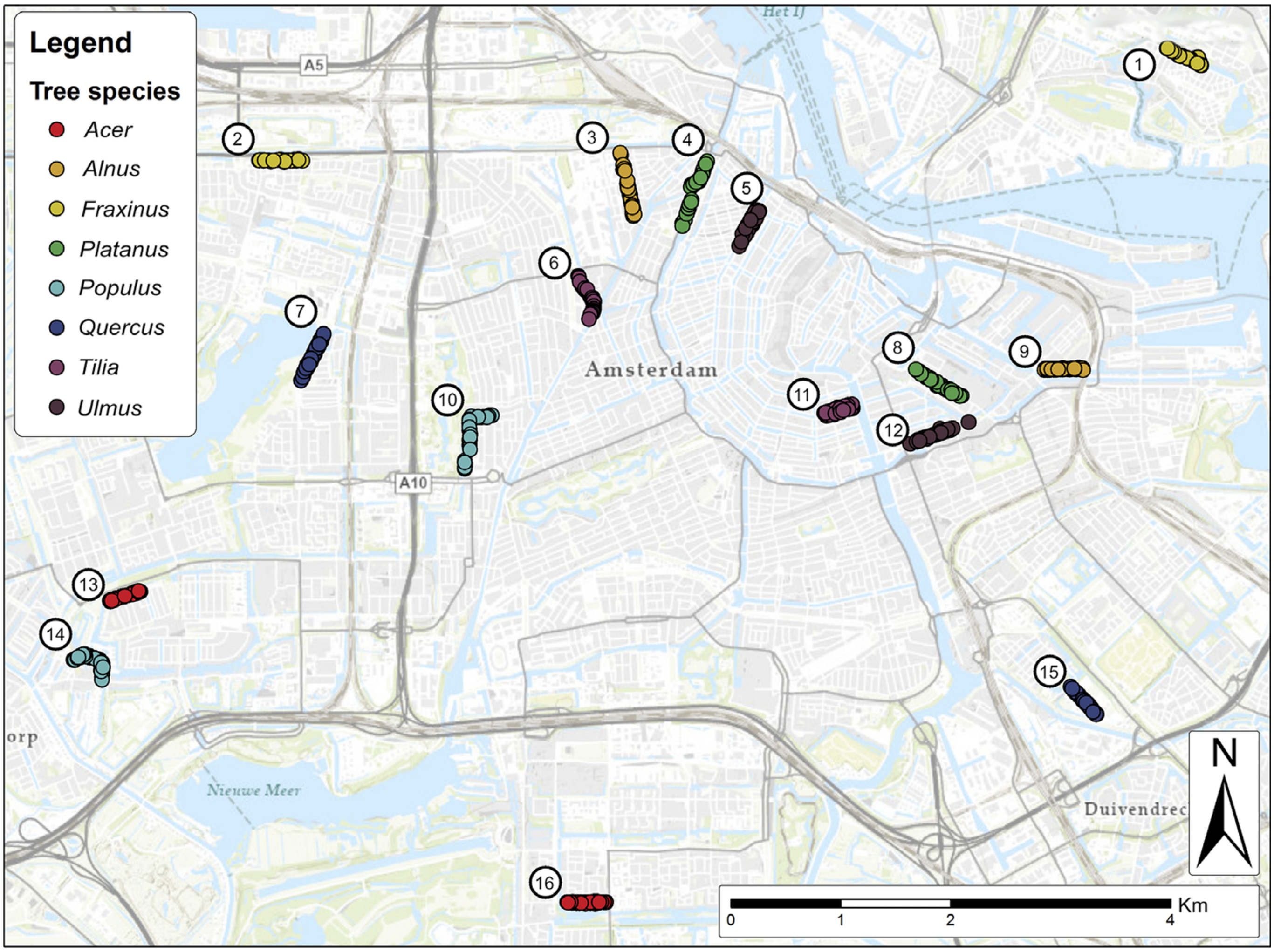

**Figure 1.** Sampling locations of eight different phorophyte species (indicated by colour and genus name) in Amsterdam. Each tree species has two sampling locations, resulting in 16 locations in total. The locations were chosen at random based on outlined criteria. 1 = Watergangseweg; 2 = Anton Struikstraat; 3 = Van Hallstraat 5; 4 = Nassaukade pointing south; 5 = Prinsengracht 2, until crossing Rozengracht; 6 = Geuzenkade 13 pointing north; 7 = Oostoever pointing south, from roundabout Jan Evertsenstraat; 8 = Plantage Middenlaan 1 pointing to Artis Zoo; 9 = Cruquiuskade pointing west, bus stop Het Funen; 10 = Postjeskade 200; 11 = Keizersgracht 1111 until crossing Vijzelstraat; 12 = Sarphatistraat 129 until Alexanderplein; 13 = Vorselaarstraat; 14 = Vrije Geer / Ditlaar; 15 = Drieburgpad; 16 = De Cuserstraat 1 pointing west. Figure by Joost de Bruijn and Harold Timans.

Bark qualities (i.e. pH, water capacity) were compared by using descriptions and data from tables II and VII in Barkman (1958), either from the same species or from other species of the same genus (Table 1) included in Barkman (1958), assuming similar qualities between species of the same genus. Only for *Platanus* were no respective values available (Table 1). The bark-quality values used have some notable constraints since they can vary due to multiple factors (see Barkman 1958), such as the proclivity for bark to have a higher water-holding capacity and lower acidity with increasing age. Barkman (1958) mentioned that acidic bark can be raised or neutralized substantially due to dust impregnation, sea salt near coastal regions or traffic-related ammonia emissions; and at that time, the neutralizing effects from ammonia in cities were outbalanced by the acidifying effect of sulphur dioxide. Lastly, some

**Table 1.** Water capacity* and pH values according to Barkman (1958) for the studied tree species or other species within the same genus if no data for the studied species was available. No values were available for *Platanus.* The values taken from a different taxon are highlighted with '*' and concern the following: *Acer pseudoplatanus* L. pH taken for *A. campestre*, *Populus nigra* L. water capacity taken for *P.* × *canadensis*, *Tilia* sp. pH with spread 4.8–6.2 taken for *T.* × *europaea*, *Tilia ulmifolia* (= synonym of *T. cordata* Mill.) water capacity taken for *T.* × *europaea*, *Ulmus campestris* L. pH and water capacity taken for *U.* × *hollandica.* Water capacity is expressed for the north-western weather side ('NW') and south-eastern lee side ('SE'); b = the substratum is bark; f = sample taken from fissures only. Acidity ranges are given in full, with an average (if available) shown in brackets.

| | *Acer campestre* | *Alnus glutinosa* | *Fraxinus excelsior* | *Platanus* × *hispanica* | *Populus* × *canadensis* | *Quercus robur* | *Tilia* × *europaea* | *Ulmus* × *hollandica* |
|---|---|---|---|---|---|---|---|---|
| Water capacity | NW 18.1b – SE 14.9b | NW 49.7b – SE 40.8b | 47 | Unavailable | NW 85.8b – SE 66.7b* | NW 44.9b – SE 32.2b | NW 45.8b – SE 38.5b* | NW 138.5b – SE 129b, 135fb* |
| pH | 6.1–6.9 (6.3)* | 4.2–5.0 (4.8) | 5.2–5.8 (5.5) | Unavailable | 5.5 | 3.7–5.0 (4.5) | 4.8–6.2 (5.6) * | 4.5–6.2 (5.4)* |

*Bark water capacity is expressed as the percent at saturation, relative to the dry weight.

values may contain errors according to Barkman (1958), since authors reporting on bark qualities failed to indicate the effect of the stated factors.

In summary, these values firstly, differentiate those trees with bark that is usually strongly to slightly alkaline (*Acer*), neutral to slightly alkaline/acidic (*Fraxinus*, *Populus*, *Tilia* and *Ulmus*) or slightly to very acidic (*Quercus*, *Alnus*). Secondly, these values characterize those trees with high (*Ulmus*), average to slightly low (*Alnus*, *Fraxinus*, *Populus*, *Quercus* and *Tilia*) or very low (*Acer)* water-holding capacity.

Fieldwork was carried out from March to May 2022. In total 576 trees were examined. On every tree, all lichen species present were recorded from the base of the trunk up to 2 m in height. Branches and twigs were disregarded. Lists of all lichen species for each individual phorophyte were compiled (*n* = 576*)* into a dataset from which could be distinguished the total individual lichen observations (*n* = 8459), epiphytic lichen species richness per individual tree, species richness per tree species (*n* = 8*)* and location (*n* = 16). Lichen community composition is determined by the specific lichen species occurring together on each individual tree. Lichen species were identified to species level where possible. All observations are stored in the Dutch digital database Nationale Database Flora and Fauna (NDFF), linked to GBIF. Lichens were identified to species level in the field with chemical spot tests using standard reagents (C, K and P). When necessary, lichens that could not be identified in the field (i.e. rare species) were collected and held in the private herbarium of the first author for microscopic identification. Digital observations of rare species were supplied with photographic evidence and identification data are available upon request from the corresponding author. Nomenclature for lichen species follows van Herk *et al.* (2022).

### *Data analysis*

The total dataset was subdivided into three sub-datasets that allowed for adequate analysis of 1) lichen observations (e.g. total species richness, occurrence frequency of species; Fig. 2, Supplementary Material Table S1, available online), 2) tree species-related species richness (e.g. species richness distribution per tree species and connected significant differences between tree species, significant species-richness differences between both locations of the same tree species; Fig. 3A & B) and how this varies per tree within one locality (e.g. species richness per tree per locality, in this case visualized with an overlayed heat-map; Fig. 4) and 3) lichen ecology (e.g. the ecological meaning of observed species and dominant communities; Figs 5A & B, 6) respectively. Data types serving as a baseline for further analysis consisted of lichen species names, total lichen species occurrence frequency (count), the tree species each lichen was observed on, species richness per tree (community), and Ellenberg ecology values taken from Sparrius *et al.* (2015).

Lichen observations (sub-dataset 1) were visualized with a bar plot using the R package *ggplot2* (Wickham 2016). To analyze sampling efficiency, an accumulation curve was calculated using a linear model through the R package *lm* in RStudio (v. 2023.12.1 +402; RStudio Team 2023), an integrated development environment for the R programming language (v. 4.3.3; R Core Team 2024).

Differences in lichen species richness between tree species (sub-dataset 2) were analyzed with a Poisson ANOVA using a Generalized Linear Mixed Model (GLMM) that takes differences in both locations of each tree species into account as a random effect. For GLMM, the R package *lmerTest* (Kuznetsova *et al.* 2017) was used. Thereafter, *P*-values were manually extracted and corrected for multiple-testing with the Bonferroni method in Microsoft Excel 2021. To analyze the potential of lichens for indicating the local UHI effect, a UHI effect map of the Netherlands utilized through the ArcGis program was used as an overlay for studied phorophytes of one location (Fig. 1; location 11), visualizing species richness for each phorophyte on a heat map of the sampling locality (Fig. 4).

For the analysis of correlations in the occurrence of lichen species (sub-dataset 3), only the species occurring on more than 10% of all sampled trees were used to avoid unreliable correlations due to rarity. Principal component analysis was conducted with the 'prcomp' function from the R base package. *P*-values for significance testing of the correlations were corrected with the Bonferroni method.

Species with one or more significant correlations were visualized in a correlogram using the R package *corrplot* (Wei & Simko 2021) and were clustered using Ward's method for hierarchical clustering. Based on the correlations, *k*-means clustering analysis was performed to find the optimal number of clusters, using the R package *cluster* (Maechler *et al.* 2023). Additional tests used for the same purpose were the Elbow Method and Silhouette Method, as well as visualizing *k*-means plots (NMDS). The optimal number of clusters served as a statistical base for assigning species to ecological groups (see also Fig. 6 and the related section in Results). Plots to visualize the results of multivariate analyses were generated using the R packages *factoextra* (Kassambara & Mundt 2020) as well as *ggplot2* for general plotting and graphical design. The full set of packages used and R codes are available upon request from the corresponding author.

Ellenberg indicator values for humidity, light, pH, eutrophic level, temperature and continentality (Sparrius *et al.* 2015) were assigned to the observed lichen species and used to characterize ecological preferences of the total lichen diversity and the ecological groups based on the field observations and clustering analysis. They were also used to characterize the urban environment as a whole, regardless of tree species. Mean Ellenberg values were calculated in Microsoft Excel and rounded to one decimal place and then visualized as bar plots in RStudio using the package *ggplot2.*

## Results

### *Epiphytic lichen biodiversity*

Fieldwork yielded 8459 lichen observations on all investigated trees. These amounted to 100 species (see Supplementary Material Table S1, available online).

The occurrence frequency of all detected species followed a skewed curve showing a small number of very common species alongside a curve of species occurring in increasing rarity (Fig. 2). Only five species occurred on more than 80% of all studied trees: *Physcia adscendens* (Fr.) H. Olivier, *Xanthoria parietina* (L.) Beltr., *Hyperphyscia adglutinata* (Flörke) H. Mayrhofer & Poelt, *Phaeophyscia orbicularis* (Neck.) Moberg and *Candelaria concolor* (Dicks.) Arnold. Of these, only *P. adscendens* and *X. parietina* occurred on more than 500 trees (> 86.8%). Twenty-four species occurred on more than 100 trees, while 65 species occurred on fewer than 10% of the trees. Of the latter, 41 species were found on fewer than 10 trees. Twenty-five species were considered as 'quite rare', 'rare' or 'very rare' on a national scale according to the Dutch national rarity index (Aptroot *et al.* 2004). The nationally very rare species included *Physciella chloantha* (Ach.) Essl., *Flavopunctelia flaventior* (Stirt.) Hale, *Ramalina canariensis* J. Steiner, *Melanelixia subargentifera* (Nyl.) O. Blanco *et al.* and *Physconia perisidiosa* (Erichsen) Moberg.

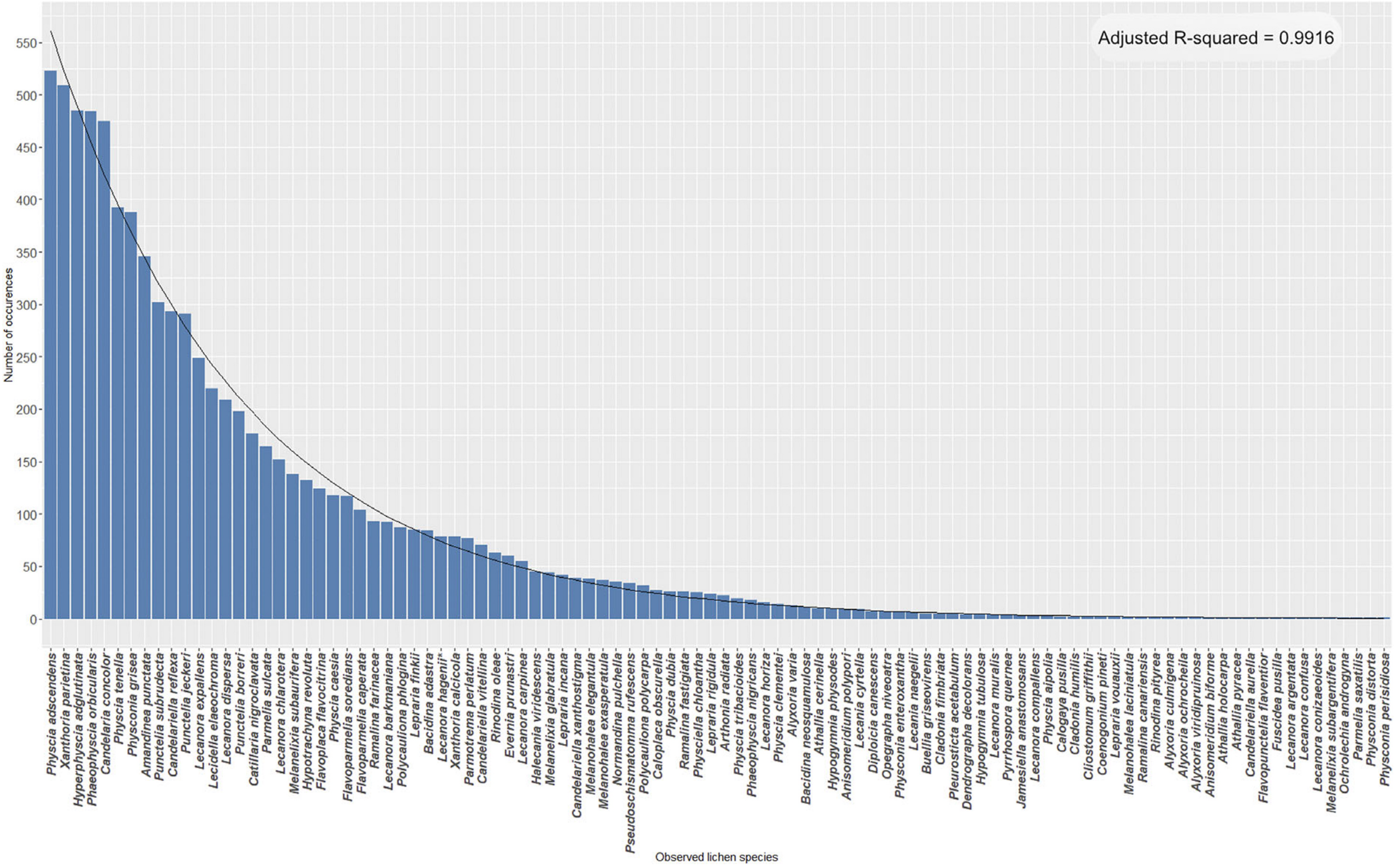

**Figure 2.** Occurrence frequency of all recorded epiphytic lichen species that were identified to species level (100 species) with fitted accumulation curve (Adjusted R-squared value = 0.9916). Xerophytic and nitrophytic species dominate the top 10 most common species. The accumulation curve demonstrated a thorough sampling of epiphytic lichen species occurring on trunks of the studied tree species. In colour online.

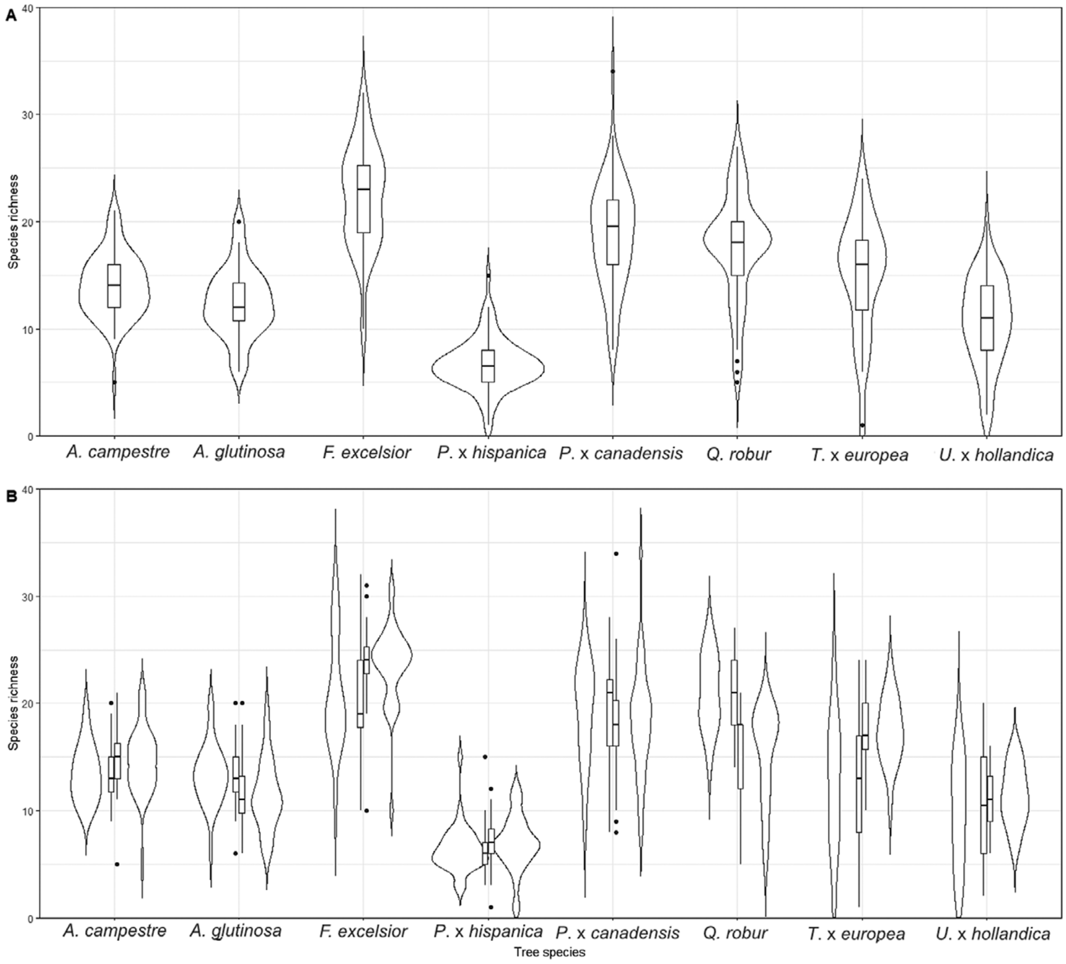

**Figure 3.** Box plot-violin plots showing epiphytic lichen species richness distributions per phorophyte species, with the two sampling locations per phorophyte species combined (A) versus separately (B). Outliers are individual trees. Tree species show a similar spread in maximum and minimum species richness between the two locations (B), but can differ relatively widely in the average species richness per location (*Fraxinus excelsior*, *Quercus robur:* species richness average difference > 5). Other tree species featured include: *Acer campestre*, *Alnus glutinosa, Platanus × hispanica*, *Populus × canadensis, Tilia × europaea* and *Ulmus × hollandica.*

### *Lichen species richness related to phorophyte species and environmental conditions*

Taking all examined tree species into consideration, the average lichen species richness consisted of 15 species per tree. *Platanus × hispanica* scored lowest with < 10 lichen species per individual tree (Fig. 3A) and was the only species that differed significantly in this respect from all the other tree species (Table 2). All other tree species typically recorded > 10 lichen species per tree. *Fraxinus excelsior* showed the highest diversity and differed significantly from the other tree species except for *P.* × *canadensis* and *Q. robur* (Table 2), exhibiting more than 20 lichen species on 46 of the 56 studied trees (82%) and even 30 or more lichen species on 5 trees.

Tree species resembling each other in terms of lichen species richness (indicated as not significant in Table 2) may still differ in terms of species composition. For example, mainly crust-forming lichen species belonging to the *Lecanoretum carpineae* (Hilitzer 1925, corrected by Barkman 1958) occurred on the smooth bark of *A. glutinosa*, but were largely absent from the rough textured bark of *U.* × *hollandica.* Nevertheless, both phorophyte species hosted a comparable lichen species richness.

Both locations of the same tree species (Fig. 3B) mostly showed a similar minimum and maximum species richness but varied in their average species richness, from narrow (e.g. *P.* × *hispanica*: difference of the mean < 3) to wide (e.g. *Q. robur*: difference of the mean > 5). This variation was most likely due to environmental factors, which seemed to have a greater influence on species richness than bark properties alone. An exception is *P.* × *hispanica*, whose frequent bark shedding kept lichen diversity at a consistently low value in both locations (Fig. 3B). Despite these differences, species richness was significantly different between tree species according to the GLMM analysis.

Species richness decreased with increasing sun exposure and decreasing humidity, but also with severe shading (observed, not measured). The most observed species were all xerophytes, indicating that the former two factors had the greatest effect on urban epiphytic lichen diversity by causing bark desiccation.

Small-scale variation of environmental factors was reflected by differences in species richness and community composition within a single street. For instance, half of the *Q. robur* trees lining the Oostoever Road (location 7; Fig. 1) received partial shade from houses and a forested park, while the other half was fully exposed to sun and wind. Species richness was lower in the exposed half than in the shaded half. This is in stark contrast to the other *Q. robur* location, which had a more stable species richness and composition, since all the trees were exposed to the same conditions. Another example was the low lichen species richness (< 8 species) on a small

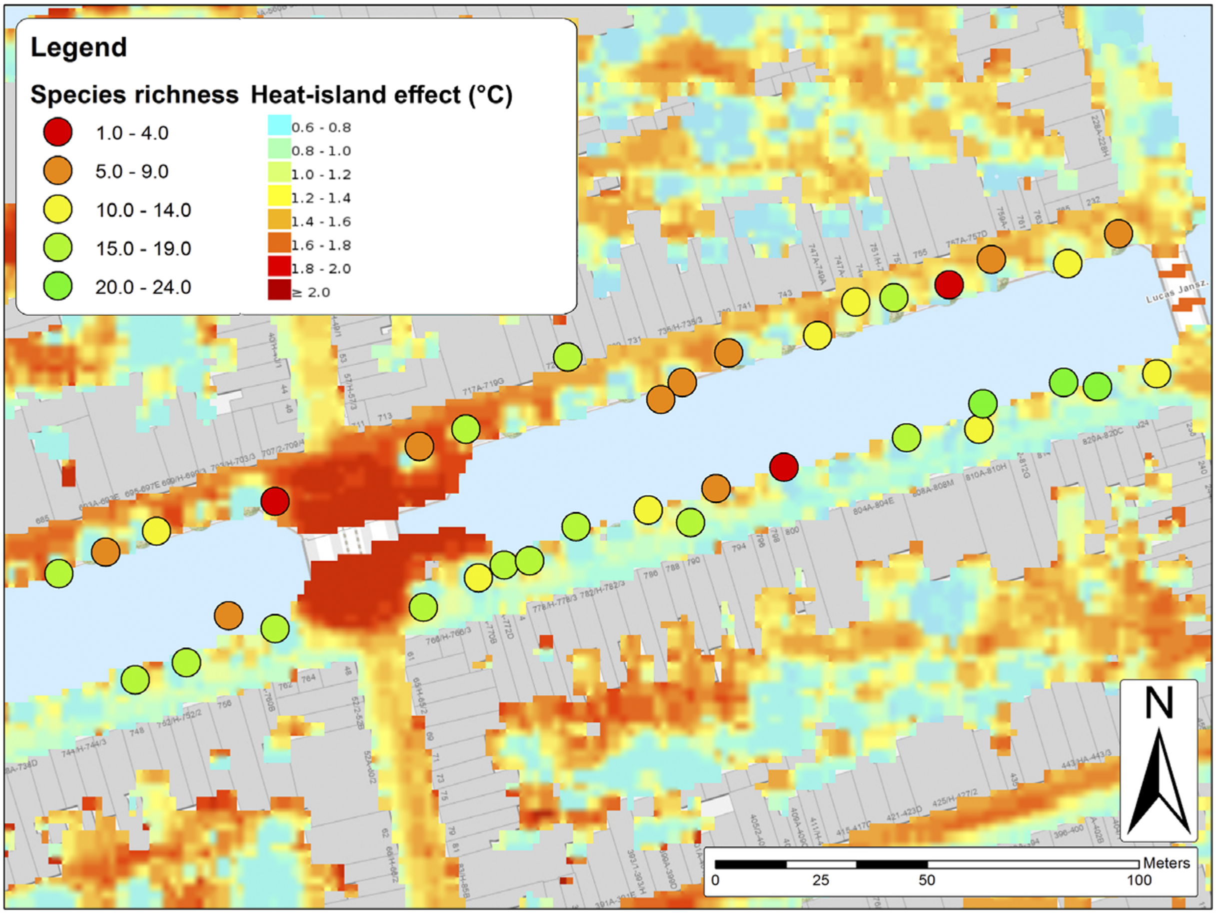

**Figure 4.** Lichen species richness on individual *Tilia* × *europaea* trees (circles) at sampling location Keizersgracht (Fig. 1, location 11), with a heat-map overlay indicating the average UHI effect in degrees Celsius (°C). This figure was made specifically as an example to indicate the local differences in the UHI effect and observed lichen species richness. Shade from canal buildings covers the southern side, but not the northern side of the canal. The exposed hotter northern side has noticeably more phorophytes with (very) low species richness (red) when compared with the shaded southern side of the canal and corresponds to hotter zones on a heat map. Xerophytes characterize the phorophytes bearing low species richness on the northern side, while bryophytes (*Syntrichia* sp.) dominate phorophytes bearing low lichen species richness on the southern side. Figure by Joost de Bruijn and Harold Timans, with assistance from Maarten van't Zelfde. UHI map based on: Rijksinstituut voor Volksgezondheid en Milieu (2020, https://www.atlasleefomgeving.nl/stedelijk-hitte-eiland-effect-uhi; for metadata see https://www.nationaalgeoregister.nl/).

number of *F. excelsior* trees whose canopy had been thoroughly pruned, causing desiccation due to increased sun exposure on lower parts of the trunks. A final example of sun exposure negatively influencing species richness was the *T.* × *europaea* trees at Keizersgracht (location 11; Fig. 1). Tall canal houses sheltered the trees at the southern end of the canal during the hottest times of the day, whilst the trees at the northern end were mostly fully exposed. The number of trees showing (very) low species richness was noticeably higher at the northern end of the canal than the southern end (Fig. 4). In addition, lichens on these trees were typically

**Table 2.** Significance levels of difference in lichen species richness between eight common lane tree species with Bonferroni correction. *Platanus* × *hispanica* is the only species significantly different from all other tree species with regards to lichen species richness. All other tree species differ significantly in lichen species richness from at least one other species. NS = not significant, * = $P$-value < 0.05, ** = $P$-value < 0.01, *** = $P$-value < 0.001.

| | *Acer campestre* | *Alnus glutinosa* | *Fraxinus excelsior* | *Platanus* × *hispanica* | *Populus* × *canadensis* | *Quercus robur* | *Tilia* × *europaea* | *Ulmus* × *hollandica* |
|---|---|---|---|---|---|---|---|---|
| *Acer campestre* | ■ | NS | *** | *** | NS | NS | NS | NS |
| *Alnus glutinosa* | | ■ | *** | *** | *** | ** | NS | NS |
| *Fraxinus excelsior* | | | ■ | *** | NS | NS | *** | *** |
| *Platanus* × *hispanica* | | | | ■ | *** | *** | *** | *** |
| *Populus* × *canadensis* | | | | | ■ | NS | NS | *** |
| *Quercus robur* | | | | | | ■ | NS | *** |
| *Tilia* × *europaea* | | | | | | | ■ | * |
| *Ulmus* × *hollandica* | | | | | | | | ■ |

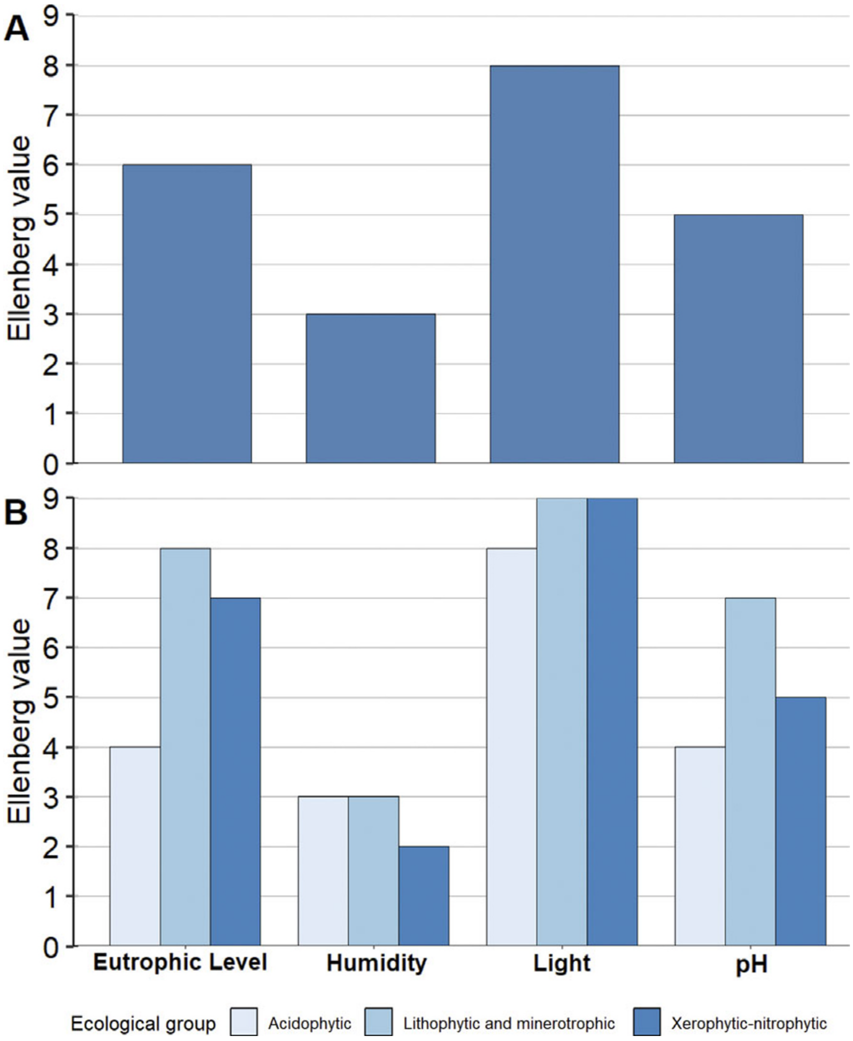

**Figure 5.** Mean Ellenberg values for four ecological parameters (eutrophic level, humidity, light and pH) for all 100 lichen species observed (A) and separate mean values for each of the three distinguished ecological groups (B). The generally high eutrophic score (nutrient-rich conditions), low humidity score (xerophytic conditions, drought-tolerant species), high light score (sun-exposed, warm conditions) and medium to high pH score (neutral to alkaline conditions) characterize the dominant urban epiphytic lichen communities.

xerophytes. This corresponds with higher heat stress associated with the UHI shown by a heat-map (Fig. 4). At this location, bryophytes (mostly *Syntrichia* sp.) dominated and outcompeted lichens at the southern end of the canal, causing a small number of trees to record low lichen species richness, whilst being absent at the northern end.

In general, species richness was lower on bark types with low water-holding capacity and greater on bark types of medium to high capacity (e.g. *F. excelsior* and *P.* × *canadensis* vs *A. campestre*) (Table 1, Fig. 3). However, *U.* × *hollandica* showed lower epiphytic species richness than *P.* × *canadensis* and *F. excelsior*, despite having the highest water-holding capacity of all sampled tree species. Textured bark, which often corresponds with higher water-holding capacity, was favoured over dry smooth bark in terms of species richness (e.g. *P.* × *canadensis* and *Q. robur* vs *A. glutinosa* and *A. campestre*). Bark pH did not display a similar pattern, although most recorded lichens indicated slightly acidic bark (Fig. 5; average Ellenberg value of all species taken together = 5.0).

### *Epiphytic lichen species and ecological groups indicative of urban environmental conditions in Amsterdam*

According to the analysis of combined Ellenberg values for all recorded species (rounded to whole numbers in Fig. 5A), urban lichens in Amsterdam indicated conditions that were mildly nutrient rich (eutrophic level: 5.8), exposed (light: 8.0), dry (humidity: 2.7), mildly acidic (pH: 5.0), in addition to mildly warm (temperature: 5.7) and temperate and sub-Atlantic (continentality: 4.3). The two most common lichen species (*X. parietina* and *P. adscendens*) belonged to the xerophytic and nitrophytic *Xanthorion parietinae* Ochsner 1928 alliance.

The correlogram of the 31 lichen species that are significantly correlated with at least one other species (Fig. 6) shows the most co-occurring lichen species. More closely associated species are also ecologically similar and allow for clustering analysis. The clustering analysis based on the significant correlations resulted in $k = 5$ clusters.

Based primarily on the clusters of the analysis (Fig. 6), secondly on the Ellenberg values (Fig. 5B) and lastly on field observations, three main ecological groups could be distinguished, namely the acidophytic, lithophytic-minerotrophic and xerophytic-nitrophytic groups. Clusters 1, 3, 4 and 5 contribute to these groups, whereas cluster 2 (*Bacidina adastra* (Sparrius & Aptroot) M. Hauck & V. Wirth and *Lepraria finkii* (de Lesd.) R.C. Harris) does not belong to any defined ecological group.

The ecological groups are described in more detail below. Field examples of the groups are shown in Fig. 7. They were highly similar in their continentality and temperature, deviating no more than 0.2 points from the mean Ellenberg score (continentality = 4.3, temperature = 5.6), but differed markedly in pH, eutrophic value,

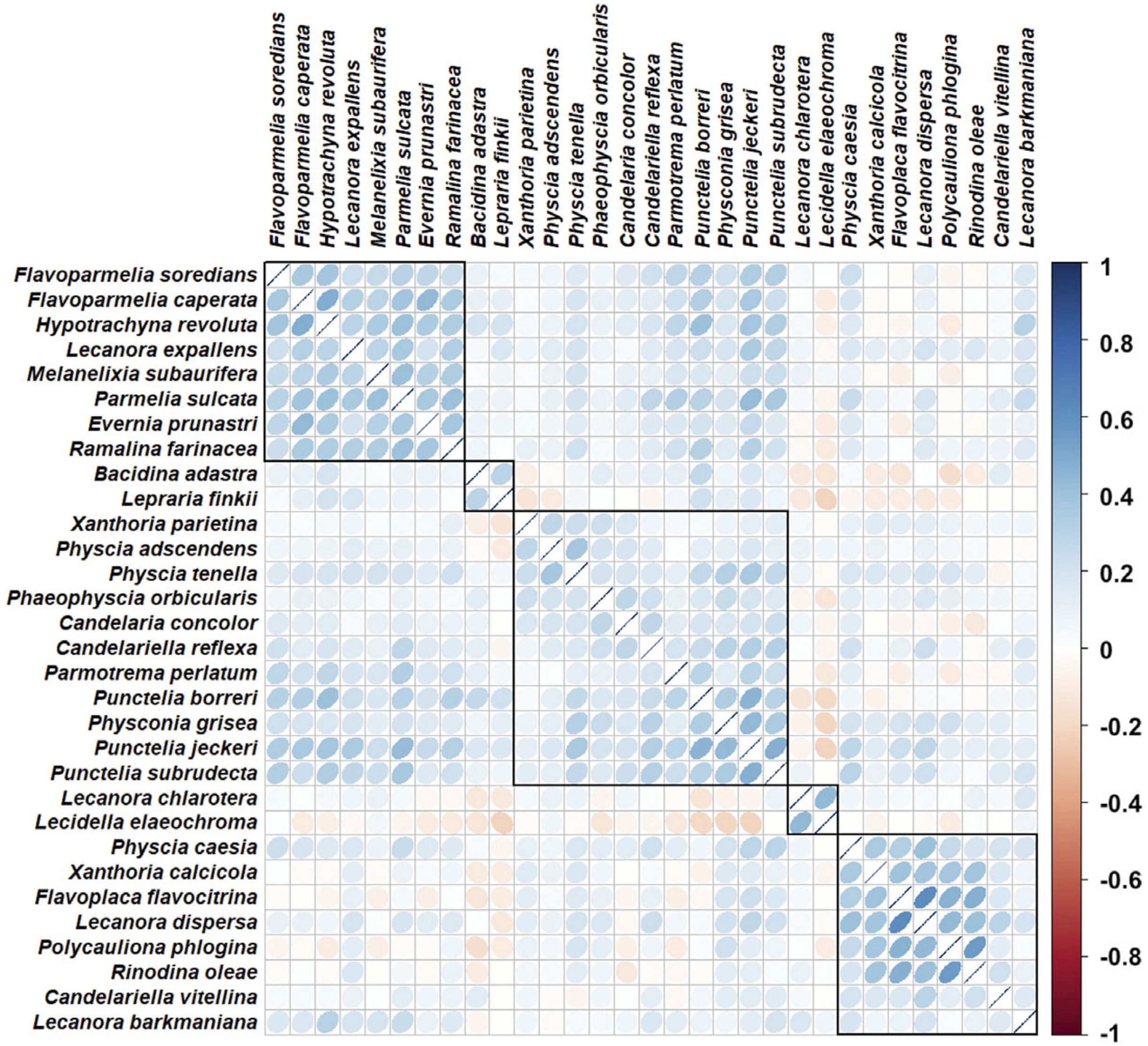

**Figure 6.** Correlogram (optimum $k = 5$ clusters) showing correlation strength between species and the clusters 1–5 (from top to bottom) that they form. Clusters 1, 3–5 are interpreted ecologically as three ecological groups: cluster 1 = acidophytic group; clusters 3 & 4 = xerophytic-nitrophytic group; cluster 5 = lithophytic-minerotrophic group. Cluster 2 is not attributed to an ecological group. Species that are ecologically similar show strong clustering and a positive correlation (dark blue = 1, meaning always co-occurring) whilst species with opposing ecology are far apart and negatively correlated (dark red = −1, meaning if one species occurs the other never does).

humidity and light exposure (Fig. 5B). Species included in ecological groups are shown in Table 3 and in Supplementary Material Table S1 (available online).

In addition to the three main groups, some rarer species were especially indicative of locally shaded and humid places (*Alyxoria varia* (Pers.) Ertz & Tehler, *Anisomeridium polypori* (Ellis & Everh.) M.E. Barr and *Normandina pulchella* (Borrer) Nyl.), and some nationally rare species seem to actively colonize new urban habitats, becoming locally common in cities (*Physcia clementei* (Turner) Lynge, *P. tribacioides* Nyl. and *Physciella chloantha*).

## Acidophytic group

A number of acidophytes, some of which are typical of the *Hypotrachynetum revolutae* Almborn ex Klement 1955 alliance (renamed by van Dort 2017), were found to be locally common in Amsterdam on acid to slightly acid bark (cluster 1 in Fig. 6). They consisted of a number of *Parmeliaceae* species (*Evernia prunastri* (L.) Ach., *Flavoparmelia soredians* (Nyl.) Hale, *F. caperata* (L.) Hale, *Parmelia sulcata* Taylor) as well as *Lecanora expallens* Ach., *Melanelixia subaurifera* (Nyl.) O. Blanco *et al.* and *Ramalina farinacea* (L.) Ach., and occurred mainly on tree species that naturally have an acidic bark (e.g. *Q. robur*) but also on trees with typically more or less neutral bark (e.g. *T.* × *europaea*). Still acidic, but more eutrophicated trees due to nitrogen deposition, typically showed a higher dominance of *Hypotrachyna revoluta* (Flörke) Hale. Eventually, eutrophication led to an increase in species of the xerophytic-nitrophytic group, such as *Parmotrema perlatum* (see below). Other species that are considered part of this ecological group but are not significantly correlated or too rare based on field observations alone, were *Hypogymnia physodes* (L.) Nyl., *Melanelixia glabratula* (Lamy) Sandler & Arup, *Melanohalea elegantula* (Zahlbr.) O. Blanco *et al.*, *M. exasperatula* (De Not.) O. Blanco *et al.* and *Ramalina fastigiata* (Pers.) Ach. The species *Hypogymnia physodes*, together with the very rarely found *H. tubulosa* (Schaer.) Hav., indicated very acidic conditions, which were rarely observed in Amsterdam.

**Table 3.** Lichen species belonging to ecological groups based on correlation significance (above) or on observational qualitative reasons (below). The latter species are not significantly correlated in their occurrence but deserve inclusion nevertheless. The species are separated based on this significance.

| | Acidophytic group | Lithophytic-minerotrophic group | Xerophytic-nitrophytic group |
|---|---|---|---|
| Significantly correlated | *Flavoparmelia soredians* | *Physcia caesia* | *Xanthoria parietina* |
| | *Flavoparmelia caperata* | *Xanthoria calcicola* | *Physcia adscendens* |
| | *Hypotrachyna revoluta* | *Flavoplaca flavocitrina* | *Physcia tenella* |
| | *Lecanora expallens* | *Lecanora dispersa* | *Phaeophyscia orbicularis* |
| | *Melanelixia subaurifera* | *Polycauliona phlogina* | *Candelaria concolor* |
| | *Parmelia sulcata* | *Rinodina oleae* | *Candelariella reflexa* |
| | *Evernia prunastri* | *Candelariella vitellina* | *Parmotrema perlatum* |
| | | *Lecanora barkmaniana* | *Punctelia borreri* |
| | | | *Physconia grisea* |
| | | | *Punctelia jeckeri* |
| | | | *Punctelia subrudecta* |
| | | | *Lecidella elaeochroma* |
| | | | *Lecanora chlarotera* |
| Insignificantly correlated | *Melanelixia glabratula* | *Phaeophyscia nigricans* | *Hyperphyscia adglutinata* |
| | *Melanohalea elegantula* | | *Amandinea punctata* |
| | *Melanohalea exasperatula* | | *Catillaria nigroclavata* |
| | *Ramalina fastigiata* | | *Lecanora hagenii* |
| | *Hypogymnia physodes* | | |

Further very rarely found acidophytes (< 1% occurrences) were not considered as part of the acidophytic group due their ecological niche (besides being acidophytes) and extreme urban rarity. These include the red-listed *Ochrolechia androgyna* (Hoffm.) Arnold (found on one *F. excelsior* tree whose bark was most likely acidified from historical $SO_2$ pollution), the mostly continental and alpine *Melanelixia subargentifera* as well as the mostly alpine *Flavopunctelia flaventior* (which were found only once in exposed locations and distant to their main distribution) and nationally more common acidophytes of different habitats (i.e. *Buellia griseovirens* (Turner & Borrer ex Sm.) Almb., *Dendrographa decolorans* (Turner & Borrer) Ertz & Tehler, *Jamesiella anastomosans* (P. James & Vezda) Lücking *et al.*, *Parmelia saxatilis* (L.) Ach., *Pleurosticta acetabulum* (Neck.) Elix & Lumbsch and *Pyrrhospora quernea* (Dicks.) Körb.).

## Lithophytic-minerotrophic group

Phorophytes with a dry, alkaline, mineralized and dusty bark showed a high presence of primarily lithophytic and minerotrophic lichen species, namely *Flavoplaca flavocitrina*, *Lecanora dispersa*, *Physcia caesia* (Hoffm.) Hampe ex Fürnr., *Polycaulionia phlogina* (Ach.) Arup *et al.*, *Rinodina oleae* Bagl. and *Xanthoria calcicola* Oxner (cluster 5 in Fig. 6), often observed together with lithophytic bryophyte species such as *Tortula muralis* Hedw. and *Grimmia pulvinata* (Hedw.) Sm. (field observations). *Lecanora barkmaniana* Aptroot & Herk and *Candellariella vitellina* (Ehrh.) Müll. were placed in the same cluster with less correlation (Fig. 6), despite being ecologically dissimilar by preferring more neutral to acidic bark (*L. barkmaniana*) or rock (*C. vitellina* occurs regularly on both). One other, usually lithophytic, less commonly recorded species (Fig. 2) that could be considered part of this ecological group but is not significantly correlated, is *Phaeophyscia nigricans* (Flörke) Moberg. The lithophytes *Calogaya pusilla* (A. Massal.) Arup *et al.*, *Candelariella aurella* (Hoffm.) Zahlbr. and *Lecanora muralis* (Schreb.) Rabenh. were not included due to their rarity (< 1% occurrences; Fig. 2).

The lithophytic-minerotrophic group can be recognized by looking for small patches with mosaics of *F. flavocitrina*, *L. dispersa*, *P. phlogina*, *R. oleae* and *X. calcicola.* On trees that were influenced only by the surrounding rocky, loamy soil, these species were restricted to the tree base, whereas alongside busy roads with more open, loamy to sandy roadsides they occurred on the entirety of the investigated trunk (up to 2 m). In such cases, some lithophytic species that grow primarily horizontally such as *F. flavocitrina* are hypothesized to be limited to the horizontal parts of the bole, regardless of mineralization higher up the trunk since their growth limits them to horizontal substrata.

The frequent observation of the lithophytic-minerotrophic group in this study is the basis for the description of the process of lithification (see Discussion). This ecological group is recognized only when multiple members are observed together. The observed abundance of each member indicates how strongly lithification takes place.

## Xerophytic-nitrophytic group

On phorophytes with desiccated bark, resulting from sun exposure in combination with low air humidity, only a small number of lichen species with a high tolerance for such extreme conditions occurred. The most commonly recorded lichens in this study were xerophytes, which most often were also nitrophytes (clusters 3 and 4 in Fig. 6). The communities formed by this group of species were often

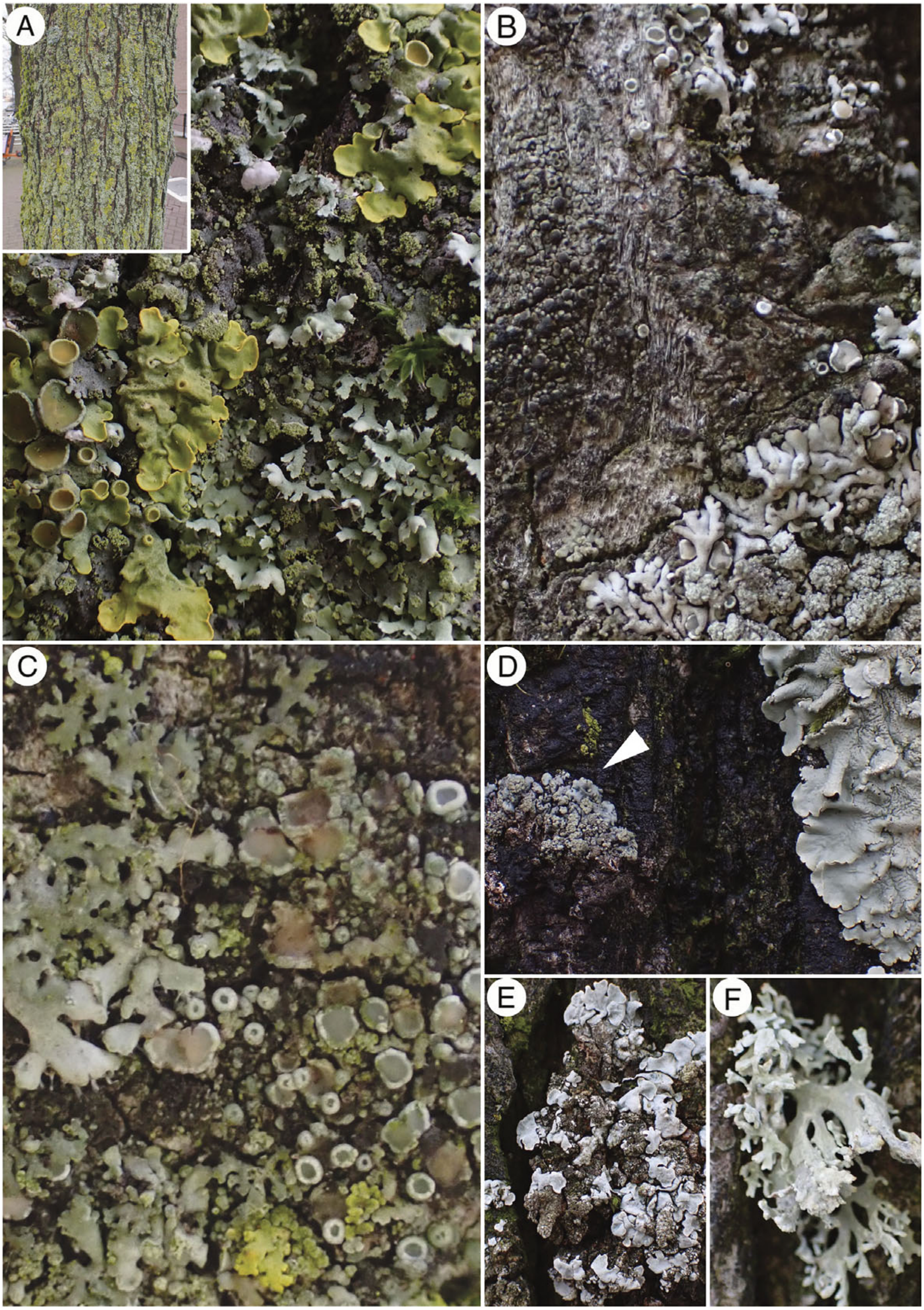

**Figure 7.** Urban ecological groups in the field. A, lush xerophytic-nitrophytic group habitus on *Ulmus* (inset) featuring mosaics of the most common urban species, *Xanthoria parietina*, *Physcia adscendens* and *Phaeophyscia orbicularis.* B, lithophytic-minerotrophic group on old *Ulmus*, with *Physcia caesia*, *Rinodina oleae* and *Lecanora dispersa.* C, micro-collection of lichen (*c.* 3 × 4 cm$^2$) with two species indicating the lithophytic-minerotrophic group amongst a mosaic of four species on *Populus*: *Lecanora dispera*, *Phaeophyscia nigricans*, *Phaeophyscia orbicularis* and *Candelaria concolor.* This group is partly characterized by small species. D–F, species from the acidophytic group growing together on two neighbouring *Ulmus* trees. The occurrence of the very acidophytic *Hypogymnia physodes* (D; arrowed), growing left of the much larger *Flavoparmelia caperata* thallus on the right, remains a rare record in Amsterdam because of a lack of very acid substrata and is therefore not included in the ecological group. When it does occur, it is very indicative and equally useful. In this case it occurs alongside two mildly acidophytic species, *Parmelia sulcata* (E) and *Evernia prunastri* (F), a combination that might occur more frequently with reducing nitrogen emissions. Images captured with an Olympus TG-6 camera with macro-settings in central Amsterdam; brightness of image A was increased to highlight the dominant yellow pigments of nitrophytic species.

recognizable as part of the *Xanthorion parietinae* Ochsner 1928 alliance. Cluster 3 comprised species that are mostly nitrophytic and xerophytic (*Physcia adscendens*, *Xanthoria parietina*), but also species of mesotrophic and slightly less arid habitats, such as members of the *Parmeliaceae* (*Physconia grisea* (Lam.) Poelt, *Punctelia subrudecta* (Nyl.) Krøg, *P. jeckeri* (Roum.) Kalb, *P. borreri* (Sm.) Krøg). Cluster 4 is differentiated only by containing two crustose species (*Lecanora chlarotera* Nyl. and *Lecidella elaeochroma* (Ach.) M. Choisy) that frequently occur together on eutrophic to mesotrophic, smooth bark instead of textured and fissured bark.

Although they did not show significant correlations with other common species, and were thus not included in the clustering analysis, the xerophytic species *Amandinea punctata* (Hoffm.) Coppins & Scheid. and *Hyperphyscia adglutinata*, as well as the two rarer species *Catillaria nigroclavata* (Nyl.) J. Steiner and *Lecanora hagenii* Rabenh., could be considered as also belonging to the xerophytic-nitrophytic group. The former two were among the only species observed consistently in the most severe cases of bark desiccation. In cases of moderate desiccation, they could cover large parts of the trunk or form monocultures; when desiccation got too severe, they were found only in small numbers. This ecological group can easily be recognized by the dominance of *Physcia adscendens, P. tenella* (Scop.) DC. and *X. parietina*, and on severely desiccated bark by the (co-)occurrence of *A. punctata* and *H. adglutinata*, and the general absence of other epiphytes.

## Discussion

### General characterization of the epiphytic lichen flora in Amsterdam

As demonstrated by the data presented here from Amsterdam, the contemporary urban environment in the Netherlands accommodates a diverse epiphytic lichen flora. The observed epiphytic lichen biodiversity represents *c.* 15.2% of the total number of species known from the Netherlands (Aptroot *et al.* 2004) and even includes some rare or very rare species, such as *Flavopunctelia flaventior*, *Melanelixia subargentifera*, *Physconia perisidiosa* and *Ramalina canariensis.* Some of the rarer species show that Amsterdam can sustain species of opposing ecology with regards to continentality. Truly Atlantic species (*Normandina pulchella*, *R. canariensis*) and continental species (*F. flaventior*, *M. subargentifera*) are found in close proximity to each other (e.g. same street or neighbourhood), possibly indicating the wide range of abiotic factors occurring in the city. However, the average of all species corresponds to the sub-Atlantic temperate climate typical of the study area. Whether the subset of these deviating rarer species reflects signs of climate change warrants further study.

The main contemporary factors determining Amsterdam's epiphytic lichen diversity are desiccation and eutrophication due to ammonia and $NO_2$ pollution, as well as lithification (see following paragraphs). Trees located in humid and partially sun-exposed (half-shaded) to fully shaded environments are rich in lichens (and bryophytes) found in humid conditions. Examples are *Normandina pulchella*, found on 35 trees (6% of all trees) in this study, *Anisomeridium polypori* and *Alyxoria varia.* Although such conditions were too infrequent in Amsterdam to be characterized as a distinctive ecological group, they may be more frequent in smaller cities or other less urbanized regions. To a lesser extent, oligotrophic conditions might also be more prevalent in some urban areas, but are expected to be rare in nearly all cases due to nitrogen pollution. This could change in the future if vehicle emissions continue to drop in cities and humidity increases (European Environment Agency 2022).

The mean species richness on all tree species studied is 15 and would be even higher if *Platanus* × *hispanica*, with its frequent bark shedding and low water-holding capacity, was excluded. According to the species accumulation curve (Fig. 2), the present sampling covered the epiphytic species richness in Amsterdam quite thoroughly (McGill 2003; McGill *et al.* 2007).

### Main changes in urban environmental conditions

Compared to when Amsterdam was an 'epiphyte desert' (Barkman 1958), the hypothesis that the urban environment hosts a low overall lichen diversity is no longer true for epiphytic species. The observed epiphytic diversity in Amsterdam testifies to long-term improvements in air quality and decreasing pollution levels, in particular $SO_2$ which was a main cause of the former 'epiphyte deserts'. This is illustrated by the infamous *Lecanora conizaeoides* Nyl. ex Cromb. ('sulphur eater', as translated from a colloquial Dutch name), which was found only once in the present study, whereas it was virtually the only common epiphytic lichen in the Amsterdam 'desert' recorded by Barkman (1958). These results correspond with Munzi *et al.* (2014) in concluding that pollution is no longer the most dominant factor determining urban lichen diversity.

The current major challenges for lichen diversity in the city are different to those in the past, and are less severe. As hypothesized, xerophytic conditions and lichen communities are prevalent throughout the city and across all tree species studied. While the average annual rainfall in Amsterdam has increased (from 800 mm in the period 1951–1980 to 897 mm in the period 1981–2010, according to data from KNMI), desiccation today is caused by higher temperatures, periods of drought and the UHI effect. These conditions, however, seem to drive diversity only sporadically and locally to near zero levels, compared to the historical impact of $SO_2$ air pollution. In addition, xerophytic species in this study were nearly all nitrophytes as well. Although levels of desiccation are thought to be the main factor in these species occurring so commonly, eutrophication due to ammonia and $NO_2$ pollution (from emissions of nitrogen compounds from traffic, industry and agriculture in rural areas surrounding the city) may also be a significant factor. It was hypothesized before that these factors would lead to a uniform and homogenous lichen flora, dominated by nitrophytes and xerophytes, as was found in other studies (e.g. Seaward 1997; Llewellyn *et al.* 2020). The observed lichen communities do indeed indicate that desiccation and eutrophication are the major factors characterizing epiphytic lichen diversity in Amsterdam. On the majority of the trees sampled, species from the *Xanthorion parietinae* Ochsner 1928 alliance were found, and more specifically the *Physcietum adscendentis* Frey & Ochsner 1926 association, both known for inhabiting this niche (van Dort *et al.* 2017). *Physcia adscendens* and *Xanthoria parietina* in particular may be considered to form the 'baseline' lichen vegetation under contemporary urban conditions. When desiccation becomes severe, *Amandinea punctata* and *Hyperphyscia adglutinata* are usually still found as remainders of the xerophytic-nitrophytic lichen communities. However, in contrast to the former air pollution, desiccation only sporadically and locally drives diversity to (near) zero levels on the investigated trees. In almost all cases, local differences in desiccation severity are thought to be the main reason for differences in mean species richness between both locations of all tree species, except *P.* × *hispanica* due to frequent bark shedding.

### Lithification

Besides the mentioned 'baseline' of xerophytic-nitrophytic species, other environmental conditions are also prevalent that seem to determine epiphytic lichen diversity in Amsterdam. The three main ecological groups inferred from our analyses indicate that, apart from desiccation-eutrophication, acidic conditions and dust deposition ('lithification') are also important factors. The presence of a considerable diversity of acidophytic lichens may show that nitrogen pollution has dropped sufficiently in urban areas, at least locally, and is no longer a limiting factor for these communities.

We know of no earlier research highlighting the frequent appearance of lithophytes on bark in urban environments (e.g. *Flavoplaca flavocitrina*, *Lecanora dispersa* and *Physcia caesia* all occurring on more than 20% of the studied phorophytes), and reason that this could be a primarily urban ecological phenomenon. The term 'lithification' is proposed here to describe the phenomenon of bark acquiring the properties of rock through deposition of dust and dirt containing minerals (not to be confused with the respective geological term describing the formation of solid rock). On strongly lithified bark, lithophytic species may be more dominant than epiphloedal ones. In an urban ecological context, lithification could signify higher local densities of dust, minerals and particulate matter deposition from the air. Thus, documenting cases of urban lithification could be a useful tool in monitoring air quality. In many instances, lithification was observed on trees standing in rocky, dusty and poorly vegetated soil around the tree base. Ellis (2012) referred to Bates (1992) and Gauslaa (1995) when stating that there may be a 'possible and confounded/interacting effect between tree species identity and soil system, on bark chemistry'. The lithification process might be regarded as one of the possible outcomes of this effect. Identifying lithification reliably requires multiple members of the ecological group to be found growing together. If only one lithophytic lichen or bryophyte species occurs in high abundance, lithification is probably the case but there is also a higher chance of making a type I error. The abundance of each member of the ecological group is a relative measure of how lithified the bark has become. The details of the mechanisms resulting in lithification, as well as recognizing lithification outside cities, require further study.

### Influence of bark qualities on epiphytic lichen diversity

Differences in species richness on trees can be attributed more to abiotic local factors than to species-specific phorophyte bark qualities. For example, tree species with markedly differing bark qualities usually housing different epiphytic communities, such as *Quercus robur* with acidic and highly textured bark and *Ulmus* × *hollandica* with more neutral and less textured bark, were found to support almost identical lichen vegetation, probably due to eutrophication and desiccation. The present data nevertheless indicate that bark properties can also have a dominant influence on epiphyte diversity. Species richness was generally higher on bark types with a medium to high water-holding capacity, probably due to its buffering against desiccation. The fact that water capacity and species richness do not correlate for all tree species, however, may be the result of urban planning. *Populus* × *canadensis* is the best example of high species richness coinciding with high water capacity and textured bark, as the locations did not have obvious large differences in overall humidity, proximate present surface water and exposure to sunlight. In contrast, *U.* × *hollandica*, with the highest water capacity of all tree species studied, scores lower than *Fraxinus excelsior*, *Q. robur* and *Populus* × *canadensis* in terms of species richness, possibly because the *U.* × *hollandica* sampling locations were situated in the centre of Amsterdam, where drought and the UHI effects are most severe. *Fraxinus excelsior* exhibits a medium water-holding capacity (Barkman 1958) but yielded the highest mean species richness in Amsterdam, possibly because it is usually planted alongside open water surfaces or humid places. Thus, it is more accurate to conclude that trees with bark with a higher water-holding capacity do not necessarily show a higher epiphytic lichen diversity in urban localities that are prone to desiccation. Rather, this quality prevents trees from severe desiccation and keeps epiphyte diversity from reaching near zero levels in otherwise arid conditions.

As far as bark pH is concerned, the naturally acid bark of *Q. robur* can locally be more effective in determining lichen diversity, for example in allowing acidophytes to prevail in urbanized areas with nitrogen pollution. In a small number of recorded instances, the naturally alkaline bark of old *F. excelsior* and *Tilia* × *europaea* lane trees also bore acidophytes. Considering that no acidifying pollutant is likely to be present in comparable quantities to the past ($SO_2$), these occurrences might represent a remnant of a long-lasting effect of historical acid rain that acidified the bark. Additional research is recommended to provide a more definitive explanation for this phenomenon.

Additional research is also recommended to validate whether the bark qualities (water-holding capacity and pH) taken from Barkman (1958) are fully justified in contemporary urban settings, since local urban factors such as traffic emissions are known to influence local bark qualities including pH (Möller *et al.* 2021).

### Considerations on ecological groups

The ecological groups distinguished here are based on the observations of this study alone and are less strictly defined than phytosociological vegetation types, but they may be used as indicators of contemporary environmental conditions in Dutch cities. While the clustering approach using only the most frequently occurring species provides a solid base for inferring the ecological groups, we acknowledge that the number of clusters may be arbitrary, depending on the method used to determine the optimum number of clusters, and needs interpretation before groups can be distinguished. Too lose clustering risks clustering species with distinctive ecology and low correlation together. Too strict clustering risks making distinctions based on only minor differences in ecology and occurrence. For the present dataset, the number $k = 5$ reflects quite well how species of similar ecology are clustered together. It is arguably too strict only for the xerophytic-nitrophytic group by clustering *Lecanora chlarotera* and *Lecidella elaeochroma* separately from cluster 3 (Fig. 6), a distinction most likely resulting from both species being especially prevalent or limited to smooth bark, but similar to cluster 3 in other aspects. Cluster 2 combines *Bacidina adastra* and *Lepraria finkii* which grow together regularly, but are not sufficiently distinctive in their ecology from other groups or accompanied by other, more closely correlated species to justify creating another ecological group or adding them to an existing one. We further acknowledge that, in addition to the statistical approach, the ecological groups may be supplemented with species that either were not significantly correlated or occurred on fewer than 10% of the trees but are still ecologically meaningful. The most notable case of frequent yet uncorrelated species concerned *Amandinea punctata* and *Hyperphyscia adglutinata.* Although occurring together with hardly any other species in the most severe cases of desiccation, this does not guarantee a strong correlation. They occurred frequently with other species, but not specifically with any of them except in the most severe cases of desiccation. The most severely desiccated trees constitute only a tiny part of the sample size, thus not allowing a strong statistical correlation (although not entirely understood, this probably explains why *H. adglutinata* is also placed opposite other species in Fig. 6). With this extra consideration, the groups more accurately describe contemporary urban conditions.

### *UHI indicator utility and concluding remarks*

The lichen species (and possibly also the ecological groups) are deemed very beneficial for their potential in characterizing and monitoring urban conditions at a very local scale. Figure 4 shows how lichen diversity is higher on the southern, shadowed side of a canal, and lower on the sun-exposed northern side, which concurs with an overlaid heat map. The lichen species on the most desiccated, exposed trees are those from the xerophytic-nitrophytic group. This shows how lichens can be used to map the effects and severity of local urban climatic factors such as the UHI effect on urban biodiversity. Klok *et al.* (2019) described local urban factors such as shade and green-spaces having an effect on local temperature. These described influences on temperature correspond well to locally observed epiphytic lichen communities.

In conclusion, although eutrophication and drought are prominent, Amsterdam is characterized by a mosaic of locally different conditions. The ecological groups distinguished here serve to more accurately describe contemporary urban conditions rather than using only the most common species (xerophytes and nitrophytes) as a means to describe urban ecology, even on a very local scale. Additional research in other (Dutch) cities should be carried out to complement the findings of this study, further evaluate the distinction of ecological groups of urban lichens, and assess the influence of contemporary environmental conditions on urban lichen biodiversity.

**Supplementary Material.** The Supplementary Material for this article can be found at http://doi.org/10.1017/S0024282925101084.

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**Competing Interests.** The authors declare none.

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