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Long-term monitoring in the Netherlands suggests that lichens respond to global warming

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Abstract: There is evidence to suggest that part of the recent changes in the lichen flora of the Netherlands is attributable to an increase in temperature. Changes which have occurred over the last 22 years were studied in detail, and were subjected to a statistical treatment by comparing the change of species to their latitudinal distribution and to ecological determinants.

All 329 epiphytic and terrestrial lichen species occurring in the Netherlands were considered in relation to their world distribution. Arctic-alpine/boreo-montane species appear to be declining, while (sub)tropical species are invading. The proportion of increasing species is by far the largest among the wide-tropical lichens (83%), and smallest among the arctic-alpine/boreo-montane lichens (14%). None of the wide-tropical species was found to decrease, while 50% of the arctic-alpine/boreo-montane species show a decline.

Long-term monitoring of the epiphytic lichen flora in the province of Utrecht from 1979 onwards shows that the total number of taxa present increased from 95 in 1979 to 172 in 2001, while the average number of taxa per site increased from 7·5 to 18·9. The rate of increase was greatest by far between 1989 and 1995. The majority of the species (152 taxa or 85%) show a gross increase, only 17 species (10%) show a decrease.

A detailed analysis of these data using multiple regression suggests global warming as an additional cause for recent changes, next to decreasing SO_2 and increasing NH_3. Changes appear to be correlated initially (1979–1995) only with toxitolerance and nutrient demand. Changes between 1995 and 2001, however, appear positively correlated to both temperature and nutrient demand, indicating a recent and significant shift towards species preferring warm circumstances, independent from, and concurrent with changes due to nutrient availability.

This is the first paper reporting long-term floristic changes for lichens that appear to be correlated significantly with increasing temperatures. We suggest that future lichen monitoring programmes also pay attention to effects of climatic change, instead of focusing on air pollution effects only.

Introduction

Since the 1950s lichens have been monitored in many countries to assess environmental changes. Monitoring has hitherto focused strongly on air pollution effects, because most lichens are highly sensitive to SO_2 (Hawksworth & Rose 1970; Seaward 1993). Classic lichen-based monitoring has generated pollution maps showing areas largely devoid of epiphytic lichens, the so-called *lichen deserts*, in and around cities in, for example, Great Britain (Hawksworth & Rose 1970), Germany (Kirschbaum *et al.* 1996) and the Netherlands (Barkman 1958). Lichens have even been shown to be useful as indicators for human health (Cislaghi & Nimis 1997).

In recent decades, air quality in most of Western Europe has improved as a result of socio-economic changes and pollution

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abatement strategies; in particular SO_2 levels have dramatically decreased. As a result, a recovery of the lichen flora became apparent in the 1980s (Hawksworth & McManus 1989; van Dobben & de Bakker 1996). Although this recovery is still in progress (van Herk & Aptroot 1998), the regenerating lichen flora appears to be different from the pre-industrial flora. A comparison with the former situation shows a number of characteristic trends:

1. Many nitrophilous species are now extremely common and spreading to substrata where they were previously absent (e.g. tree species with endogenously acid bark). An apparent explanation lies in the high levels of atmospheric NH_3 currently found in north-western Europe, as a result of intensive cattle husbandry (van Breemen *et al.* 1982; van Dobben & de Bakker 1996; van Herk 1999, 2001*a*). The nitrophilous lichens include many species with predominantly warm-temperate distributions.
2. Many acidophilous species are now decreasing in abundance. This is especially true for *Lecanora conizaeoides*, the sole species that was shown to be favoured by SO_2 (Bates *et al.* 1996). However, similar patterns are seen in a wide range of acidophilous but toxiphobous species. This category includes many boreo-alpine elements.
3. Most lichens that are increasing in frequency are warm-temperate or subtropical elements; an example is *Parmelia soredians*, which is a drought-resistant, warm temperate species which until recently had its northernmost limit in southern Scotland. It was very rare in the Netherlands before 1950, absent in 1950–1987, and recently became common all over the country (van Herk & Aptroot 1996) as well as in adjacent countries. A similar ecology and a comparable rapid increase holds for *P. borreri* (Spier & van Herk 1997). Similar changes have been observed in the distribution of some bryophytes in Central Europe (Frahm & Klaus 2001).
4. The newly established lichens include species with a mainly tropical distribution which are usually recorded as single specimens, for example *Physcia tribacioides* and *Heterodermia obscurata* (Wolfskeel & van Herk 2000). The latter, originally described from Colombia, has a pantropical distribution, extending into the subtropics and reaching northwards to southern Europe. This phenomenon was not seen in surveys prior to 1995.
5. Newly established lichens also include species which were previously unknown. Seven epiphytic species new to science have been described recently from the Netherlands (Aptroot *et al.* 1997, 1998; Aptroot & van Herk 1999*a*, *b*; van Herk & Aptroot 1999; Sparrius & Aptroot 2000). It is improbable that they have been overlooked in the past, as most of them are common now, and tree bark has been intensively studied for lichens since the 1950s (Barkman 1958; de Wit 1976). At present, these species, which are still spreading rapidly, are known only from Western Europe and their origin is unclear. However, several of them have close relatives in warm-temperate to wide-tropical regions (Lücking *et al.* 1994), and some of the new species may occur there.

In this paper we provide evidence to support the hypothesis that climatic change could be an additional factor for the observed changes in the distribution pattern of lichens, besides increasing NH_3 and decreasing SO_2. In the Netherlands the annual average temperature has increased by 0·3°C since 1980 (Houghton *et al.* 1996), while the mean precipitation increased from *c.* 700 mm year^{-1} to *c.* 800 mm year^{-1} over the past 100 years. According to the most recent reports from the Dutch meteorological institute, K.N.M.I., the annual average temperatures in the Netherlands were *c.* 0·8°C higher during 1991–2000 compared to 1961–1990. During recent years, many temperature records were set in the Netherlands, for example, the mean temperature for October 2001 was the warmest since regular measurements began in 1706.

Materials and Methods

Three different analyses were carried out to test the hypothesis that lichen populations have changed in response to climate change. First, the estimated increase or decrease in lichen species in the Netherlands was compared to the latitudinal distribution patterns of these species. Second, these changes were related to seven major determinants of species' ecology as delineated by Wirth (1991), the so-called 'Ellenberg-values', using multiple regression. Third, changes in epiphytic lichen composition that have occurred since 1979 in the central part of the Netherlands were quantified and analysed, and related again by means of multiple regression to Wirth's determinants.

The latitudinal distribution of species was derived from a wide range of lichen checklists and floras, for example Purvis *et al.* (1992) and Wirth (1995). Five categories were distinguished:

1. predominantly wide-tropical species, often extending into (warm-) temperate areas;
2. species with a warm-temperate to (sub)tropical distribution, i.e. with the majority of the distribution well south of the Netherlands;
3. predominantly (or only) cool-temperate species, often very widespread over all vegetation zones in at least the northern hemisphere;
4. boreo-montane/arctic-alpine species, the majority of the distribution well north of the Netherlands or at altitudes well above sea level, mainly in the montane and/or alpine belt;
5. species for which insufficient distribution data are available (these usually rare species are excluded from the calculations).

Estimates of the change in the occurrence in the Netherlands of epiphytic and terricolous lichen species were obtained by assigning them to six change classes, ranging from 'strong decrease' to 'very strong increase' (see below). All six classes relate the present (2000) occurrence of species with their occurrence in the 1980s. Change class values were derived from checklists (Brand *et al.* 1988; Aptroot *et al.* 1999), field meetings organized by the Dutch Lichenological Society (BLWG), herbarium material, and long-term monitoring data. Reports of most of the field meetings, complete with species lists per site, are recorded in the journal *Buxbaumiella* (1973 onwards). Herbarium material in all institutional and private herbaria has been consulted, as well as all data from mapping and long-term monitoring programmes (de Wit 1976; van Dobben & de Bakker 1996; van Herk & Aptroot 1998; van Herk 1999, 2001*a*). The predominantly saxicolous species were not considered, as data about these are generally too incomplete.

Six change classes were distinguished, defined as follows:

1. A species was considered to have a 'strong decrease' when it had disappeared from more than 50% of its known stations, while the remaining populations had diminished as well.
2. A species was considered to show a 'slight decrease' when it had disappeared from 20 to 50% of its stations; the remaining populations usually became smaller.
3. 'No change' is used when only small changes (-20% to $+25\%$) in the numbers of stations were found; often the sizes of the populations remained about the same.
4. Species were considered to have had a 'slight increase' when they had established at 25 to 100% new stations; the sizes of the populations often became larger.
5. A 'strong increase' was used for species which occurred at 100 to 500% new stations; the size of the original populations often became considerably larger.
6. A 'very strong increase' is valid for species which had increased more than 500%, often with large new populations.

If a very rare species became extinct, the change was counted as a 'slight decrease'. Alternatively, if a species was newly established, it was not automatically counted as showing a 'very strong increase', but was rated according to the abundance of the new species, for example, where a new species was very rare, it was counted as showing only a 'slight increase', although the increase was technically over 500%.

A detailed analysis was carried out of the changes in epiphytic lichen composition that have occurred since 1979 in the province of Utrecht in the central part of the Netherlands. This area of *c.* 1500 km^2 has been monitored intensively since the 1970s and a database with *c.* 70 000 lichen records was available to analyse the changes in the occurrences of species. In contrast to the previous change class estimates, all changes presented are based on 'hard' field observations at stations that were revisited in subsequent periods. Data collected during lichen surveys in 1979 (van der Knaap 1980), 1984 (van der Knaap 1984; fieldwork partly carried out by A. Aptroot), 1989 (Aptroot 1990), 1995 (van Herk 1996) and 2001 (van Herk 2001*b*) were used, all based on monitoring sites with usually 10 trees of the same species. For all species recorded, their frequency (based on absence/presence per site) was calculated for the five survey periods from 1979 onwards. Changes were derived in a stepwise manner for 5 or 6 year intervals by calculating the increase or decrease in frequency at sites monitored in both periods only. Frequencies of species in 1995 (the most extensive survey) were taken as the starting-point, and frequencies in 2001, 1989, 1984 and 1979 were related to that period by calculating the frequency for the whole set based on the differences at the sites which were monitored during the two survey periods concerned. In

TABLE 1. *Relationship between increase or decrease of lichen species in the Netherlands since 1980 and the latitudinal world distribution of these species*

Change class		Latitudinal world distribution				
		1 wide-tropical	2 warm-temperate/ subtropical	3 cool-temperate	4 boreo-montane/ arctic-alpine	Total
−2	strong decrease	0	3	2	7	12
−1	slight decrease	0	33	8	26	67
0	no change	2	56	31	24	113
+1	slight increase	5	57	27	9	98
+2	strong increase	2	22	7	0	31
+3	very strong increase	3	4	1	0	8
	Total	12	175	76	66	329

The values in the body of the table are the numbers of species concerned. The numbers in the column and row headings are class numbers used in the correlation analysis.

this way, all changes due to termination of sites (e.g. tree felling, etc.), new sites or changed scope of the survey could be excluded. More than 20 tree species were involved, mainly *Quercus robur*, *Populus × canadensis*, *Salix alba*, *Fraxinus excelsior*, *Ulmus* spp., *Tilia* spp., *Fagus sylvatica*, *Betula* spp. and *Pinus sylvestris*.

Wirth's seven major ecological determinants of species are estimates of the species' responses to 'light demand', 'temperature preference', 'continentality', 'moisture-dependence', 'pH preference', 'nutrient demand' and 'toxitolerance', scored on a nine-point scale (1=preferring deep shade, very cool, hyper-oceanic, very dry, very acid, nutrient-poor, and clean circumstances, respectively). In the fitted models changes were regressed on the seven determinants following $C=\alpha+\Sigma_{i=1\ldots7}(\beta_i D_i)$, with α=constant (intercept), β_i=regression coefficient for determinant i, D_i=value of determinant i, and C=change class (Table 2) or changes during 1979–1989, 1989–1995 and 1995–2001 in Utrecht (Table 4). The models presented were derived by stepwise exclusion of non-significant terms from the full model, i.e. the model including all seven determinants. For some species Wirth does not give values for all seven ecological determinants. All regression models were constructed using the maximum number of species possible for that combination of predictors.

Results

Estimated change related to latitudinal distribution

In total, 329 species were used to relate their change in the Netherlands since 1980 to their latitudinal world distribution (Table 1). Many more species have increased (42%) than decreased (24%), while some 34% of the species remained approximately constant. Many of the species (57%) have a southern, warm-temperate to tropical distribution, fewer (20%) have a boreo-montane and/or arctic-alpine distribution and 23% are typically cool-temperate. The relative proportion of species which have increased appears to be greatest among the wide-tropical lichens (83%), and least among the arctic-alpine/boreo-montane lichens (14%). The opposite holds for the species which have decreased; none of the wide-tropical species was found to have decreased, while 50% of the arctic-alpine/boreo-montane category showed a decrease. Thus, arctic-alpine/boreo-montane species are declining, while (sub)tropical species are invading the Netherlands. Warm- and cool-temperate species are increasing as well (both *c.* 46%). The correlation of the change class number with the distribution class number per species (as given in Table 1) is statistically highly significant ($r=-0{\cdot}345$, $n=329$, $P<0{\cdot}0001$).

Three wide-tropical species, viz. *Anisomeridium polypori*, *Hyperphyscia adglutinata* and *Parmelia perlata* show a 'very strong increase'. A 'strong increase' in this category holds true for *Candelaria concolor*

Table 2. *Regression coefficients and significance resulting from multiple regression of the change class per species on Wirth's (1991) ecological determinants*

Term	Regression coefficient	*t*-value	*P*-value
Constant	− 0·51	− 1·16	0·25
Light demand	− 0·13	− 2·73	0·0072
Temperature	+0·18	+2·50	0·0135
Nutrient demand	+0·21	+3·56	0·0005

Number of species considered (n) = 146 (34 species with missing values excluded), degrees of freedom = 142, explained variance = 18·3%. Not significant (r and P values refer to t values of terms excluded from the model): continentality ($r = +0{\cdot}05$, $P = 0{\cdot}55$, $n = 127$), moisture dependence ($r = -0{\cdot}11$, $P = 0{\cdot}22$, $n = 127$), pH-preference ($r = -0{\cdot}12$, $P = 0{\cdot}17$, $n = 127$), toxitolerance ($r = -0{\cdot}08$, $P = 0{\cdot}42$, $n = 103$).

and *Fellhanera bouteillei*. Warm-temperate species showing a 'very strong increase' are *Candelariella reflexa*, *Lecidella flavosorediata*, *Parmelia borreri* and *P. soredians*. The boreo-montane/arctic-alpine lichens include seven species with a 'strong decrease' viz. *Baeomyces roseus*, *Cetraria chlorophylla*, *C. islandica*, *Cladonia cornuta*, *C. squamosa*, *Pseudevernia furfuracea* and *Pycnothelia papillaria*. Warm-temperate and tropical species found to be increasing are most often epiphytic, while terrestrial species with this distribution are nearly absent in the Netherlands. The decreasing arctic-alpine/boreo-montane species, on the other hand, are mostly terricolous.

Estimated change related to ecological determinants

The most parsimonious model resulting from a multiple regression of the change class numbers on Wirth's ecological determinants is shown in Table 2. These determinants are available for 180 species out of the original 329 species with change class estimates, but because of missing values in Wirth's determinants, 34 species were excluded from the calculation.

The terms for 'light demand', 'temperature preference' and 'nutrient demand' contribute significantly to the fit of the model. Change class is correlated positively to 'temperature preference' and 'nutrient demand', and negatively to 'light demand'. Thus, three independent trends have occurred: 1, species preferring warm conditions have increased proportionally more than species preferring cool conditions; 2, species preferring nutrient-rich habitats have increased proportionally more than species preferring nutrient-poor conditions; 3, species preferring shade have increased proportionally more than species preferring direct sunlight.

The multiple regression confirms that these three trends are independent factors. No significant effect was found for 'pH preference'; the significant simple correlation between 'pH preference' and change class ($r = +0{\cdot}25$, $P = 0{\cdot}0007$) disappeared when 'nutrient demand' was included in multiple regression. Similarly, the simple correlation between 'moisture-dependence' and change class ($r = -0{\cdot}21$, $P = 0{\cdot}0088$) appeared to be due to 'temperature preference'.

Observed changes in epiphyte frequency related to ecological determinants

Long-term changes of the 178 epiphytic lichen species present in the monitoring programme carried out in the province of Utrecht from 1979 onwards are presented in Table 3. It can be seen that species diversity as well as the frequency of many species has increased considerably. The total number of taxa present increased from 95 in 1979 to 172 in 2001 while the average number of taxa per site increased from 7·5 to 18·9. The

TABLE 3. *Long-term changes in epiphytic lichens at monitoring sites in the province of Utrecht, the Netherlands, 1979–2001*

	Frequency (%)‡				
Species*	1979	1984	1989	1995	2001
Anisomeridium biforme	0·1	0·1	0·1	0·1	0·1
A. polypori	0·0	0·6	0·2	5·7	6·3
Arthonia muscigena	0·0	0·4	0·2	0·2	0·2
A. pruinata	0·0	0·0	0·2	0·2	0·2
A. radiata	0·9	1·4	1·8	2·0	4·7
A. spadicea	0·7	0·7	0·9	4·7	6·7
Bacidia arnoldiana s.l.§	0·0	3·9	12·2	53·8	78·6
B. chloroticula	0·0	0·0	0·2	0·5	0·5
B. neosquamulosa	0·0	0·0	0·0	0·2	10·2
B. subfuscula	0·0	0·0	0·0	0·0	0·8
Buellia griseovirens	1·4	5·1	5·3	9·9	14·1
B. punctata	62·3	68·1	71·4	79·2	81·4
Calicium viride	1·8	2·1	1·0	0·6	1·0
Caloplaca chlorina	0·0	0·0	0·0	0·1	0·1
C. citrina	1·5	2·4	1·7	6·3	9·4
C. decipiens	0·0	0·0	0·0	0·2	0·0
C. flavocitrina	0·0	0·0	0·0	2·2	2·9
C. holocarpa	0·0	0·0	0·0	0·9	0·5
C. obscurella	0·0	0·4	1·1	2·2	3·1
Candelaria concolor	1·1	1·1	1·1	7·4	32·1
Candelariella aurella	0·0	0·6	0·3	3·4	2·5
C. reflexa	4·1	3·9	4·8	37·2	61·9
C. vitellina	2·3	6·7	9·3	20·2	28·6
C. xanthostigma	1·1	3·5	1·6	5·3	13·1
Catillaria nigroclavata	0·0	0·0	0·0	0·0	0·7
Cetraria chlorophylla	1·3	1·0	1·0	0·7	0·2
Chaenotheca brachypoda	0·0	0·0	0·0	0·5	0·5
C. chlorella	0·0	0·0	0·0	0·4	0·6
C. chrysocephala	0·0	0·0	0·0	0·4	0·2
C. ferruginea	4·3	5·1	4·6	9·2	10·5
C. furfuracea	0·0	0·1	0·1	0·3	0·5
C. stemonea	0·0	0·0	0·0	0·5	0·7
C. trichialis	0·4	0·3	0·2	2·4	3·7
Chrysothrix candelaris	0·0	0·0	0·0	0·5	0·5
Cladina portentosa	0·0	0·3	0·1	0·3	0·1
Cladonia caespiticia	0·0	0·0	0·0	0·0	0·7
C. chlorophaea	7·1	2·6	2·4	11·1	15·1
C. coccifera	0·0	0·0	0·0	0·3	0·5
C. digitata	1·1	0·6	0·4	0·2	0·4
C. floerkeana	0·0	0·0	0·0	0·9	0·7
C. glauca	0·5	1·1	3·5	3·1	3·1
C. grayi	0·1	0·1	0·1	0·1	0·1
C. humilis	0·0	0·0	0·0	0·0	0·2
C. incrassata	0·0	0·0	0·0	0·2	0·9
C. macilenta	1·5	0·2	0·3	2·4	6·8
C. polydactyla	0·0	0·0	0·0	0·2	0·1
C. ramulosa	0·0	0·0	0·0	0·6	1·0
C. squamosa	0·1	0·0	0·0	0·0	0·0
C. sp.§	19·2	22·1	22·9	23·8	22·4
Cliostomum griffithii	2·8	3·9	4·5	9·0	9·2
Dimerella pineti	0·5	2·0	3·0	16·3	19·4
Diploicia canescens	7·2	9·1	8·3	14·1	23·7

Table 3. *Continued*

	Frequency (%)‡				
Species*	1979	1984	1989	1995	2001
Enterographa crassa	0·1	0·1	0·1	0·2	0·2
Evernia prunastri	41·8	40·2	28·4	28·9	24·7
Fellhanera bouteillei	0·0	0·0	0·0	0·1	0·9
F. subtilis	0·0	0·0	0·0	0·2	0·6
F. viridisorediata	0·0	0·0	0·0	0·5	7·3
Graphis elegans	0·0	0·0	0·1	0·1	0·1
G. scripta	0·1	0·1	0·2	0·2	0·2
Gyalideopsis anastomosans	0·5	0·9	1·1	7·6	12·5
Haematomma ochroleucum	0·8	3·2	1·8	1·3	1·3
Halecania viridescens	0·0	0·0	0·0	0·3	2·5
Hyperphyscia adglutinata	0·0	0·6	0·6	3·7	22·6
Hypocenomyce scalaris	5·4	6·4	5·7	10·2	11·3
Hypogymnia physodes	43·3	37·5	33·2	22·5	16·5
H. tubulosa	7·9	4·5	2·9	8·0	6·9
Imshaugia aleurites	0·4	0·4	0·3	0·3	0·3
Lecania cyrtella	0·2	0·3	0·6	1·6	1·4
L. erysibe	0·0	0·0	0·0	0·2	0·0
L. naegelii	0·1	0·1	0·1	0·1	0·1
L. rabenhorstii	0·0	0·0	0·0	0·0	1·1
Lecanora aitema	3·3	2·5	2·4	1·2	0·8
L. argentata	0·3	0·3	0·4	0·2	0·1
L. barkmaniana	0·0	0·0	0·0	1·5	17·5
L. carpinea	3·1	4·7	4·2	9·1	14·4
L. chlarotera	19·2	23·4	24·4	37·5	43·9
L. confusa	0·0	0·0	0·0	0·0	0·7
L. conizaeoides	80·7	88·8	91·3	35·3	12·4
L. dispersa	9·5	9·8	11·2	23·5	29·5
L. expallens s.l.§	56·8	58·5	64·0	81·6	85·8
L. hageni	0·2	0·2	0·8	24·8	37·2
L. horiza	0·0	0·1	0·1	0·3	2·7
L. muralis	0·2	0·5	0·0	1·2	1·4
L. pulicaris	0·8	0·5	0·5	3·0	2·6
L. saligna	0·0	0·0	0·2	2·3	1·2
L. subcarpinea	0·0	0·0	0·0	0·1	0·3
L. symmicta	1·2	2·8	2·9	8·2	7·3
Lecidella elaeochroma	18·9	19·8	22·1	42·7	54·7
L. flavosorediata	0·0	0·0	0·0	4·2	7·3
L. scabra	0·0	0·0	0·0	1·1	12·7
L. stigmatea	0·0	0·0	0·0	0·0	0·4
Lepraria incana	55·8	64·0	68·1	61·9	64·3
L. lobificans	0·0	0·0	0·3	0·9	4·2
L. umbricola	0·0	0·0	0·0	0·0	0·4
Leproloma vouauxii	0·0	0·0	0·0	0·0	0·2
Micarea denigrata	0·0	0·0	0·0	1·0	0·8
M. nitschkeana	0·0	0·2	0·2	2·0	1·6
M. peliocarpa	0·0	0·1	0·0	0·8	1·5
M. prasina	0·8	1·1	2·6	7·3	18·4
M. viridileprosa	0·0	0·0	0·0	0·0	0·2
Mycoblastus fucatus	0·0	0·2	0·4	1·4	1·4
Ochrolechia androgyna	0·0	0·0	0·0	1·1	1·5
O. microstictoides	0·0	0·0	0·0	0·6	0·2
O. turneri	0·0	0·0	0·0	0·1	0·5
Opegrapha atra	0·5	1·6	1·8	3·0	3·0

TABLE 3. *Continued*

	Frequency (%)‡				
Species*	1979	1984	1989	1995	2001
O. herbarum	0·0	0·0	0·0	0·8	1·0
O. niveoatra	0·4	0·2	0·2	5·0	6·6
O. rufescens	0·0	0·2	0·2	1·5	1·5
O. varia	0·0	0·0	0·0	0·1	0·5
O. vermicellifera	1·0	1·9	1·9	3·4	3·4
O. vulgata	0·9	0·9	0·9	3·4	3·6
Parmelia acetabulum	9·6	8·6	6·6	6·0	5·8
P. borreri	0·0	0·0	0·0	4·0	10·0
P. caperata	1·1	4·3	5·7	13·4	20·3
P. elegantula	0·5	0·5	0·5	1·0	2·8
P. exasperatula	1·4	5·0	4·4	2·2	3·1
P. glabratula	0·3	1·2	1·4	2·7	4·0
P. laciniatula	0·4	0·4	0·2	0·4	1·7
P. pastillifera	0·0	0·0	0·0	0·0	0·2
P. perlata	0·0	0·1	0·0	7·5	19·3
P. revoluta	5·3	6·8	4·2	11·2	20·8
P. saxatilis	5·3	4·0	2·6	4·9	4·9
P. soredians	0·0	0·0	0·0	7·8	15·4
P. subaurifera	23·2	27·1	19·7	43·0	47·2
P. subrudecta s.l.§	15·2	20·0	19·1	32·9	45·3
P. sulcata	45·0	49·9	47·3	61·3	64·9
P. tiliacea	0·0	0·3	0·1	0·4	0·3
P. verruculifera	0·0	0·0	0·0	0·1	0·1
Parmeliopsis ambigua	0·8	2·5	1·5	2·7	1·8
Pertusaria albescens	2·0	0·4	0·4	1·3	1·1
P. amara	2·0	2·9	2·0	3·4	2·6
P. coccodes	0·8	1·5	1·3	3·0	3·7
P. leioplaca	0·0	0·0	0·0	0·1	0·1
P. pertusa	0·7	1·3	1·0	1·4	1·6
Phaeophyscia nigricans	0·0	1·2	0·3	3·1	1·2
P. orbicularis	4·2	13·7	16·2	43·1	53·1
Phlyctis argena	1·8	4·5	5·1	6·7	6·9
Physcia adscendens	5·4	10·0	17·8	56·8	73·7
P. aipolia	0·0	0·0	0·0	0·1	0·0
P. caesia	6·5	16·8	13·8	32·3	33·0
P. clementei	0·0	0·0	0·0	0·0	0·9
P. dubia	2·0	7·1	9·1	14·9	16·7
P. semipinnata	0·0	0·0	0·0	0·1	0·0
P. stellaris	0·3	0·3	0·0	0·8	0·6
P. tenella	44·8	51·7	55·9	72·6	73·3
P. tribacia	0·0	0·0	0·0	0·0	0·2
P. tribacioides	0·0	0·0	0·0	0·0	0·2
Physconia distorta	0·0	0·0	0·0	0·2	0·4
P. enteroxantha	0·1	0·1	0·2	0·8	1·2
P. grisea	3·3	7·6	8·2	15·6	27·4
Placynthiella icmalea	0·3	0·1	2·1	13·9	6·6
Platismatia glauca	8·8	6·8	5·0	3·5	1·7
Porina aenea	1·5	0·8	1·5	3·5	3·5
Protoparmelia hypotremella	0·4	0·5	0·8	2·7	3·6
P. oleagina	0·0	0·0	0·0	0·4	0·6
Pseudevernia furfuracea	1·8	2·3	1·5	2·7	1·1
Psilolechia lucida	0·0	0·1	0·0	0·2	0·2
Pyrenula nitida	0·1	0·1	0·1	0·1	0·1

Table 3. *Continued*

Species*	Frequency (%)‡ 1979	1984	1989	1995	2001
Pyrrhospora quernea	0·3	0·3	1·3	5·7	8·4
Ramalina canariensis	0·0	0·0	0·0	0·0	0·2
R. farinacea	19·5	22·0	14·5	29·3	37·3
R. fastigiata	3·0	3·7	2·0	5·2	8·5
R. fraxinea	0·0	0·1	0·1	0·0	0·2
R. lacera	0·0	0·0	0·0	0·1	0·1
Rinodina gennarii	0·8	0·8	0·5	6·2	8·2
R. pityrea	0·0	0·0	0·3	3·5	7·1
Schismatomma decolorans	1·2	2·6	2·6	3·2	4·1
Scoliciosporum gallurae	0·0	0·0	0·0	0·0	0·9
Stereocaulon vesuvianum	0·0	0·0	0·0	0·1	0·0
Strangospora pinicola	0·0	0·0	0·3	1·5	2·8
Trapeliopsis flexuosa	0·0	0·2	2·0	1·6	0·4
T. granulosa	5·4	7·5	8·7	5·1	4·2
T. pseudogranulosa	0·0	0·0	0·0	0·1	0·8
Usnea spp.§	0·1	0·1	0·2	1·7	1·0
Xanthoria calcicola	0·5	0·1	0·6	2·7	4·0
X. candelaria	22·0	31·0	34·6	51·2	53·4
X. parietina	8·7	18·6	22·8	63·1	74·9
X. polycarpa	19·0	21·6	23·6	55·8	54·5
Number of species (total)	95	113	115	160	172
Number of species (per site)	7·5	8·9	9·1	15·2	18·9

*Nomenclature follows Aptroot *et al.* (1999); species for which Wirth's (1991) ecological determinants are available in **bold**.

‡Frequencies vary between 0·0% (not found) and 100·0% (always present), and are based on observations from *c.* 10 trees at each monitoring site.

§No data are available for *Lecanora compallens*, *L. expallens* s.str. and *L. leuckertiana* Zedda (taken together as *L. expallens* s.lat.), *Parmelia subrudecta* s.str. and *P. ulophylla* (taken together as *P. subrudecta* s.lat.), *Cladonia coniocraea* and *C. fimbriata* (taken together as *Cladonia* sp.), *Bacidia arnoldiana* and *B. delicata* (taken together as *B. arnoldiana* s.lat.), *Usnea* species (taken together as *Usnea* spp.) and *Lecanora sinuosa* (omitted), because these species have not been recognized in all periods.

increase was greatest between 1989 and 1995 (+45 taxa, +6·1 site^{-1}), followed by 1995–2001 (+12 taxa, +3·7 site^{-1}) and 1979–1984 (+18 taxa, +2·4 site^{-1}). Increases were practically absent between 1984 and 1989 (+2 taxa, +0·2 site^{-1}).

Most species (152 taxa, 85%) show a gross increase, most notably *Bacidia arnoldiana* s.l. (+786%; Table 3; values are absolute differences in frequency percentages), *Physcia adscendens* (+68·3%), *Xanthoria parietina* (+66·2%), *Candelariella reflexa* (+57·8%), *Phaeophyscia orbicularis* (+48·9%), *Lecidella elaeochroma* (+35·8%), *Lecanora hageni* (+37·0%), *Xanthoria polycarpa* (+35·5%), *X. candelaria* (+31·4%), *Candelaria concolor* (+31·0%), *Parmelia subrudecta* s.l. (+30·1%), *Lecanora expallens* s.l. (+29·0%), *Physcia tenella* (+28·5%), *P. caesia* (+26·5%), *Candelariella vitellina* (+26·3%), *Lecanora chlarotera* (+24·7%), *Physconia grisea* (+24·1%), *Parmelia subaurifera* (+24·0%), *Hyperphyscia adglutinata* (+22·6%), *Lecanora dispersa* (+20·0%), *Parmelia sulcata* (+19·9%), *P. perlata* (+19·3%), *P. caperata* (+19·2%), *Buellia punctata* (+19·1%), *Dimerella pineti* (+18·9%), *Ramalina farinacea* (+17·8%), *Micarea prasina* (+17·6%) and *Lecanora barkmaniana* (+17·5%). The last species was described only recently (Aptroot & van Herk 1999*a*). The following species

TABLE 4. *Regression coefficients and significance resulting from multiple regression of the changes in occurrence per species in Utrecht (Table 3) on Wirth's (1991) ecological determinants for the years 1979–1989, 1989–1995 and 1995–2001*

Years	Term	Regression coefficient	t-value	P-value
1979–1989*	Constant	−6·41	−4·35	<0·0001
	Nutrient demand	+1·25	+4·79	<0·0001
	Toxitolerance	+0·59	+2·83	0·0059
1989–1995‡	Constant	−12·59	−4·08	0·0001
	Nutrient demand	+3·26	+5·97	<0·0001
	Toxitolerance	+1·16	+2·64	0·0099
1995–2001§	Constant	−8·93	−3·31	0·0014
	Temperature	+1·63	+2·91	0·0046
	Nutrient demand	+1·02	+2·55	0·0126

*Number of species considered (n)=87 (19 species with missing values excluded), degrees of freedom=84, explained variance=2·79%. Not significant (all at n=74; r and P values refer to t values of terms excluded from the model): continentality (r= −0·05, P=0·68), moisture dependence (r=+0·03, P=0·78), light demand (r= −0·21, P=0·08), temperature (r=+0·00, P=0·98), pH-preference (r=+0·04, P=0·75).

‡Number of species considered (n)=87 (19 species with missing values excluded), degrees of freedom=84, explained variance=34·5%. Not significant (all at n=74): continentality (r= −0·02, P=0·87), moisture dependence (r=+0·07, P=0·56), light demand (r=+0·03, P=0·82), temperature (r= −0·06, P=0·63), pH-preference (r= −0·03, P=0·82).

§Number of species considered (n)=88 (18 species with missing values excluded), degrees of freedom=85, explained variance=22·7%. Not significant (all at n=74): continentality (r=+0·14, P=0·23), moisture dependence (r=+0·07, P=0·55), light demand (r=+0·03, P=0·83), pH-preference (r= −0·09, P=0·46), toxitolerance (r= −0·00, P=0·98).

expanded rapidly (>5·0%, absolute) and increasingly during the most recent period (1995–2001): *Candelaria concolor* (+24·7%), *Hyperphyscia adglutinata* (+18·9%), *Lecanora barkmaniana* (+16·0%), *Parmelia perlata* (+11·8%), *Physconia grisea* (+11·8%), *Lecidella scabra* (+11·6%), *Micarea prasina* (+11·1%), *Bacidia neosquamulosa* (+10·0%), *Diploicia canescens* (+9·6%), *Candelariella xanthostigma* (+7·8%), *Fellhanera viridisorediata* (+6·8%), and *Parmelia borreri* (+6·0%). Three of these were recently described (Aptroot *et al.* 1998; Aptroot & van Herk 1999*a*, 1999*b*).

Only 17 species (10%) showed a decrease: *Lecanora conizaeoides* (−68·3%), *Hypogymnia physodes* (−26·8%), *Evernia prunastri* (−17·1%), *Platismatia glauca* (−7·1%), *Parmelia acetabulum* (−3·8%), *Lecanora aitema* (−2·5%), *Trapeliopsis granulosa* (−1·2%), *Cetraria chlorophylla* (−1·1%), *Hypogymnia tubulosa* (−1·0%), *Pertusaria albescens* (−0·9%), *Calicium viride* (−0·8%), *Cladonia digitata* (−0·7%), *Pseudevernia furfuracea* (−0·7%), *Parmelia saxatilis* (−0·4%), *Lecanora argentata* (−0·2%), *Cladonia squamosa* (−0·1%) and *Imshaugia aleurites* (−0·1%). The course of *L. conizaeoides* shows a gradual increase up to 1989, and an extremely rapid decrease after that date. None of the declining species became rapidly and increasingly rare during the most recent period.

Models resulting from multiple regression of the changes on Wirth's determinants were calculated for three periods.These determinants were available for 106 epiphytic species out of the 178 for which changes were calculated (Table 3), but because of missing values, another 18 species were excluded from the models, leaving *c.* 88 observations for regression (Table 4).

Changes over the periods 1979–1989 and 1989–1995 are positively correlated to both 'nutrient demand' and 'toxitolerance' (Table 4). These changes indicate that a shift occurred towards species preferring nutrient-rich circumstances; such species have increased proportionally more than species preferring nutrient-poor circumstances. The significant fit with 'toxitolerance' shows that species with low toxitolerance increased proportionally more than species with high toxitolerance. It is impossible to reduce these two fits to each other or to one of the other five determinants.

Changes between 1995–2001 are positively correlated to both 'temperature preference' and 'nutrient demand' (Table 4), indicating a recent and significant shift towards species preferring warm circumstances. Thus, species preferring warm conditions have increased proportionally much more than species preferring cool conditions, independent of, and concurrent with, changes due to nutrient availability. Over this period, no correlation was found with 'toxitolerance'.

In all three calculations (Table 4) it can be observed that single positive correlations with 'pH preference' have given way to correlations with 'nutrient demand', similar to previous calculations with change class. After regression, 'pH preference' no longer showed a significant fit.

Discussion

The changes in the terricolous and especially the epiphytic lichen flora of the Netherlands have been dramatic over the past two decades. Interestingly, many more species (137, see Table 1) have increased than decreased (79) in abundance, and it might seem that the Netherlands is regaining its original lichen flora, which was largely lost due to heavy air pollution. However, a close examination of the changes in lichen communities reveals some trends that deviate from the general pattern expected in response to eutrophication and decreasing SO_2 concentrations alone. For example, some wide-tropical epiphytes (e.g. *Anisomeridium polypori*, *Fellhanera* spp., *Parmelia borreri*, *P. perlata* and *P. soredians)* are among the fastest spreading species and most boreo-alpine terrestrial species (e.g. *Cetraria islandica*, *Cladina rangiferina*) are declining or have even disappeared from heathlands with otherwise intact or barely changed *Cladonia* rich lichen communities. An explanation for these changes has eluded us for some years, as they could not be explained by altered air quality alone.

The epiphytic lichen flora of the Netherlands might be expected to show an increase in abundance of southern species due to its western suboceanic position in Europe. There is, however, no reason to assume that southern suboceanic elements should increase proportionally faster simply due to the decreased levels of SO_2: indicator values for 'toxitolerance' and 'temperature preference' are not intercorrelated ($r = +0{\cdot}08$, $n = 108$, $P = 0{\cdot}4035$), thus species with a high sensitivity to SO_2 do not particularly prefer warm circumstances. Furthermore, no change was found for the terms 'continentality' and 'moisture dependence'. If the observed changes were ascribed erroneously to 'temperature' instead of 'toxitolerance', then a significant fit with 'temperature' would be expected in the regressions over the periods 1979–1989 and 1989–1995 as well, instead of over 1995–2001 only. Major reductions in Dutch SO_2 emission and concentration levels were achieved mainly before 1989; lichen changes due to decreased SO_2 levels were found primarily over 1979–1995 (Tables 3 & 4).

Lichen floras of boreo-montane regions are particularly rich in acidophytic species, while southern floras have proportionally more species typical of eutrophic habitats. As a consequence, indicator values for 'nutrient demand' and 'temperature' are intercorrelated ($r = +0{\cdot}40$, $n = 88$, $P = 0{\cdot}0001$), and it may be expected that eutrophication, which is severe in the Netherlands, will attract proportionally more southern species. However, eutrophication has occurred during the whole period 1979–2001 (Table 4), while recent nitrophytic species responding to eutrophication are quite different from the species responding before 1995; see for instance *Hyperphyscia adglutinata*, *Lecanora barkmaniana* and *Lecidella scabra* (epiphytic!) in Table 3. Furthermore, multiple regression (Table 4) shows recent changes attributable to 'temperature' preference as significantly distinct from concurrent changes due to 'nutrient demand', i.e. species indicating increased temperatures are not just nitrophytes, but can be found throughout other ecological groups as well.

Lichens are known to respond to environmental changes. They can do so by dispersing over long distances through large numbers of minute diaspores. Their common biotopes such as tree bark or sparsely vegetated soil usually provide enough open space to permit colonization. Numerous studies have shown that new equilibria may easily evolve as a result of changes in, for example, atmospheric quality (positive or negative), pH of the substratum or nutrient availability. Insarov & Schroeter (2002) have predicted a response of lichens to changes in mean annual temperatures. Gignac (2001) discussed possible implications of climate change for bryophytes. The significant positive effect of 'temperature preference' in the regressions, together with the changes in distribution pattern, provide strong support for our hypothesis that lichens in the Netherlands are responding to global warming. This change is additional to other (simultaneous or previous) changes attributable to changed nutrient availability, SO_2 concentration, and light conditions, and has only become apparent since 1995.

The significant positive effect of 'nutrient demand' can be explained from an increase in atmospheric NH_3. Our correlations with pH-preference could probably also be accounted for in terms of nutrient availability. The reverse was found in earlier work based on real measurements: changes in species composition due to high levels of NH_3 were found to be governed by high bark pH rather than increased availability of nitrogen (de Bakker & van Dobben 1988; van Herk 2001*a*). Wirth's indicator values for 'pH preference' and 'nutrient demand' are strongly intercorrelated ($r=+0{\cdot}86$, $n=107$, $P<0{\cdot}0001$); as a consequence the present calculations do not indicate properly whether pH or nitrogen is more important.

'Toxitolerance' only showed a significant fit in the change regression with epiphytic data from the period 1979–1995. Afterwards 'toxitolerance' was no longer significant. This may be explained as follows: decreasing SO_2 concentrations were initially beneficial only to species with high toxitolerance; with further reduced SO_2 levels, species with low toxitolerance also benefited. The negative effect of the 'light demand' determinant (Table 2) could be an effect of increased forest growth (McMurtrie *et al.* 2000) and increased dominance of vascular plants in heathland (Berendse & Elberse 1990), both probably as a result of generally increased N input. This may have led to a reduced light availability for, and competitive exclusion of lichens (Makipaa 1995).

The results in Table 3 may partly reflect increasing experience and taxonomic knowledge of resident lichenologists. We do not believe that this is the case for several reasons. First, from the initial period (van der Knaap 1980) field work was carried out by experienced workers who gained their knowledge during a previous intensive mapping programme (de Wit 1976). Second, all three field workers routinely collected inconspicuous species that could not be identified in the field. Third, it is evident from Table 3, that even inconspicuous crusts such as *Anisomeridium polypori* and *Gyalideopsis anastomosans*, which apparently increased rapidly, were recognized from the beginning. Inconspicuous crusts such as *Anisomeridium biforme* and *Lecania naegelii*, which remained rare, were also found from the very beginning. Fourth, re-examination of herbarium samples, collected during previous survey periods, has revealed no records of species that had been unrecorded, with the exception of the taxa marked with a § in Table 3, the records of which are aggregated with related species for all periods.

The present application of Wirth's determinants fulfils all requirements for treatment of independent variables in multiple regression. It should be stressed that neither the discrete units of Wirth's scale, nor the unequal ecological distances between these units, prevent a valid application of multiple regression (Sokal & Rohlf 1969). Since lichen species tend to be widespread, it is to be assumed that ecological determinants based on a neighbouring country (Germany) are largely applicable. In fact, using Wirth's determinants is likely to give an underestimate of the effects of global warming, since many of the southern species that have increased rapidly (e.g. *Parmelia borreri, P. soredians* and all recently described species) are not treated by him and therefore had to be omitted from the calculations.

Although our data suggest that generally the most warmth-tolerant lichens are the fastest increasing species, we do not know whether the upper or lower temperature threshold (e.g. frost) or the average temperatures (yearly/summer/winter) underlie the biological explanation. The climatic effects of global warming as they are now recognized in the Netherlands largely apply to average temperatures for periods of one month up to 10 years, not to extreme values. Frost is surely an important threshold for lichens, and many species will remain confined to the tropics for this reason, although the definition for a tropical climate is a mean annual temperature of >25°C.

To our knowledge, this is the first paper reporting long-term floristic changes for lichens that appear to be correlated significantly with increasing temperatures. We suggest that future lichen monitoring programmes also pay attention to effects of climatic change, instead of focusing only on the effects of air pollution.

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