

Changes in the distributions of epiphytic lichens in southern Sweden using a new statistical method

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Past studies on changes in species distribution have mainly been based on analysis of range boundaries. In contrast, the method used here evaluates shifts in species' geographic centroids within a predefined area. We used presence/absence data on epiphytic lichens collected 1986 and 2003 from 64 sites in southern Sweden. A centroid was calculated each year, for each lichen species and substrate. The distance of centroid movement was evaluated in a permutation procedure. In total, 56 lichen species on 22 tree species were involved in the analyses, yielding 30 cases that had sufficient sample sizes both years to be evaluated. Out of these, three exhibited a significant movement of their centroid. The shift of lichen centroids of *Hypogymnia physodes* (L.) Nyl. and *Vulpicida pinastri* (Scop.) J.-E. Mattsson & M. J. Lai on the tree species *Juniperus communis* L. was 50 and 151 km with the direction 27° and 48°, respectively. For *Hypogymnia physodes* on *Pinus sylvestris* L., corresponding values were 41 km and 30°. The northnortheast shifts of these species in Sweden could be a response to a warming climate.

Large-scale environmental changes, such as global warming, are likely to affect several organisms in a similar way, e.g. by range shifts in similar directions, and also through a change in the density of individuals within populations. So far, most studies of distributional changes attributed to global warming in the northern hemisphere have been examined as the northward expansion of the studied organism (Thomas and Lennon 1999, Warren et al. 2001, Parmesan and Yohe 2003, Root et al. 2003, Hickling et al. 2005). The number of studies based on population densities within a species distribution (Thomas and Lennon 1999, Warren et al. 2001, Hickling et al. 2005), or to the likelihood of encountering a species (Bridle and Vines 2007) is much lower. As the appropriate spatial and temporal scales involved are large, relatively few data sets exist. Further, available data are often not straightforward and rarely detailed; for example field notes from sites with long time gaps, data not collected under a uniform protocol, or data with low information content (e.g. presence/absence only). Data of this type, however, still provide opportunities for interesting questions to be addressed. Thus, simple methods for analysis of uneven-quality data would be valuable.

Epiphytic lichens on trees, and other transient substrates, are likely to respond relatively quickly to broad-scale changes in the climate. van Herk et al. (2002) used checklists, data from field meetings, herbarium material and long-term monitoring data to study large-scale changes of lichens in the Netherlands. Based on the documentation

of 329 lichen species collected in 1979, 1984, 1989, 1995 and 2001, they conclude that lichens can respond to global warming over a time frame of only a few decades. Lichens with a northern distribution and a southern border in the Netherlands have declined. On the other hand, species with a southern distribution and a northern border are at present invading the Netherlands.

In the present study, we illustrate an approach using presence/absence data to compare calculated centroids of geographic location, within the area studied (also known as 'centre of occurrence', La Sorte and Thompson 2007), from investigations at two points in time (1986 and 2003). The changes of distance and direction of the centroid was easily calculated and for distance, significance (null hypothesis of no change in centroid) can be tested with a permutation procedure. One advantage is that no assumption is needed about the direction (most analyses so far test for changes in northern and southern borders). Another is that our focus is on the general distribution of the species within any predefined area of any shape, not just on the boundaries. The latter might be a poor representation of a large-scale change in abundance, is sensitive to grid size, might be highly influenced by single observations and be very sensitive to data deficiencies (Dormann 2007). Furthermore, data for most species are not available to determine clear distribution boundaries. We apply the method to a data set on epiphytic lichens, a group likely to respond relatively quickly, as both the lichen and its host might

respond to environmental changes on temporal and spatial scales relevant for the data at hand. The data come from 64 sites in southern Sweden visited in 1986 and 2003.

Material and methods

Sampling

Epiphytic lichens on 64 sites in southern Sweden were sampled in 1986 and 2003 (Fig. 1a). One of the authors Jan-Eric Mattsson, (JEM) originally selected and visited the sites for a study to which the extent *Vulpicida juniperinus* (L.) J.-E. Mattsson and M. J. Lai and *Vulpicida pinastri* (Scop.) J.-E. Mattsson and M. J. Lai were still present at former localities (Mattsson 1988). The identification of species and selection of the sites, from the first study, were based on herbarium specimens of the genus *Vulpicida* collected over a period of about one hundred years. Hence, the sites are not a random selection but follow a previously known occurrence of these target species. The sites span over a wide range of ecological habitats with no apparent bias towards a particular tree diameter (successional stage). The sites were of different sizes ranging from a single tree to one hectare and often delimited by natural boundaries such as creeks or ridges, or by man-made borders such as fences,

or different land use. Different habitats common to southern Sweden are represented at the sites, i.e. coniferous, deciduous and mixed forests, wooded pastures, parks, and on occasion single trees in towns, villages and farms.

Tree trunks, branches and twigs were examined to a height of 2 m above the ground in search of all epiphytic macrolichens. And on each site, all epiphytic lichen species were collected on all substrates present. The number of tree species per site varied from one to eleven and the aim was to investigate approximately 50 trees with lichens at each site. Tree trunks without visual lichens were observed, but were not included in the study. Most of the lichen species recorded are widespread and abundant with some exceptions, e.g. the redlisted *Melanelia laciniatula* (Flagey ex H. Olivier) Essl. and *Usnea barbata* (L.) Weber ex F. H. Wigg. (Thor and Arvidsson 1999). The species are, with a few exceptions, easy to identify based on macro-characters only. Most of the lichen species are foliose or fruticose. Some of the species are habitat generalists and may occur on several of the tree species surveyed, as well as on rock. One observer (JEM) investigated the sites in 1986 and two observers JEM and Håkan Lättman (HL) in 2003. Total time, spent to record all species present, per site was similar both times and the search method was identical. In 1986, JEM used 40 minutes on each site and in 2003, JEM and

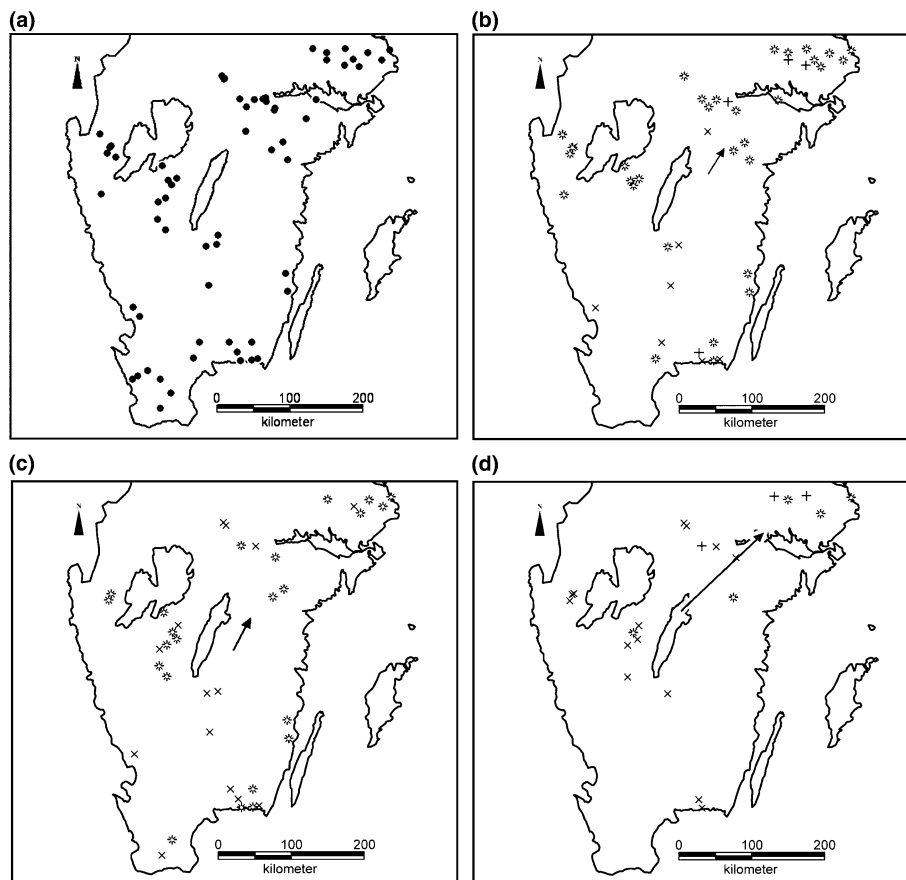


Figure 1. (a)–(d) distribution of 64 sites in southern Sweden where collection of epiphytic lichen species were recorded 1986 and 2003, and the results of the three significant cases of centroid movement (arrows) (Table 1). (a) the 64 investigated sites. The centroid shift of (b) *Hypogymnia physodes* on *Pinus sylvestris*, (c) *Hypogymnia physodes* on *Juniperus communis* and (d) *Vulpicida pinastri* on *Juniperus communis*. A cross indicates a site occupied by the lichen species 1986, a plus indicate a site occupied by the lichen species 2003 and the star indicate a site occupied by the lichen species both years. The arrows indicate length and direction of centroid movements.

HL used 20 minutes each per site. Tree and lichen species nomenclature follows Karlsson (1997) and Santesson et al. (2004) respectively.

In total, the data included 64 sites, 22 tree species and standing dead wood and 56 lichen species. Longitude and latitude were recorded in field and converted to WGS 84 before analysis.

Analysis

We developed a permutation procedure to assess whether the distance moved by the distributional centroid (the arithmetic mean of coordinates of sites) was greater than expected due to chance. Each combination of lichen and tree species was analyzed separately. For a site to be included for a particular combination of lichen and tree species analysis, the tree species had to be recorded at the site both years and the lichen species in at least one of the years. From the information included per combination of lichen and tree, we calculated the geographic centroid of the lichen species in 1986 and 2003, and then the distance between these centroids. We then randomly permuted the status (present both times, present in 1986 only, and present in 2003 only) for all those sites in which the lichen occurred on that tree species at least once (Table 1). Thirty combination of trees and lichen species were possible to analyze, involving eight and 17 tree and lichens species, respectively (Table 1).

We calculated the centroids and associated distance for each of 5000 permutations, and compared these distances to our measured value to obtain a p-value. This analysis was performed using an Excel visual basic macro written by MWP.

Although it may seem that a reasonable null hypothesis for direction of movement is that all compass directions are equally likely, irregularities in the distribution of samples as well as the elongated shape of the study area in Sweden (Fig. 1) mean that this is not the case. Therefore, we stored the directions generated by the permuted data to compile an expected distribution of directions. In addition, we calculated the directions between all possible pair-wise combinations of sites. The cumulative distribution of these two data sets were compared with the corresponding of the observed changes of directions of centroids (including those whose distance had scored NS), using the Kolmogorov–Smirnov (KS) test.

Results

Centroid movements of lichen species

We recorded a significant change ($p < 0.05$) in distance between the centroids calculated for 1986 and 2003 for three of the 30 analysis possible to conduct (Table 1). Centroid movements of the lichens *Hypogymnia physodes* and *Vulpicida pinastri* on the tree species *Juniperus communis* were 50 and 151 km, respectively, and corresponding movement of *Hypogymnia physodes* on *Pinus sylvestris* was 41 km (Table 1). The direction of centroid movements of these three significant cases were in a northeast direction

(Fig. 1). Furthermore, in these three cases there was a general decrease in occurrence. *Hypogymnia physodes* and *Vulpicida pinastri* on *Juniperus communis* decreased from 14 to 6 and from 14 to 3 observations, respectively. For *Hypogymnia physodes* on *Pinus sylvestris*, the corresponding values were 8 to 4 (Table 1).

If applying a control for false discovery rates (following Benjamini and Hochberg 1995), due to multiple testing ($n = 30$), one of the three cases remained significant (i.e. *Vulpicida pinastri* on *Juniperus communis*: $p = 0.0002$). It can be argued, however, whether the 30 tests conducted actually belong to the same family of tests (cf. Perneger 1998, Proschan and Waclawiw 2000).

The cumulative distribution of all possible directions and of all permuted directions were similar, with two soft bumps (Fig. 2); a consequence of the elongated shape of the study area (Fig. 1a). The observed distribution of the 30 analyses, that were possible to conduct (Fig. 2), deviated from both of the above-mentioned in the KS tests ($p < 0.025$, $p < 0.005$). Overall, the direction of movement was, for the 30 evaluated cases, dominated by 16 in northeast and 9 in southwest (Fig. 2).

Discussion

Movements and directions as judged by centroids

There are two main results in this study. First, it provides evidence that movement of centroids (representing the probability of finding a species, within an area), of epiphytic lichens can be detected over a time frame of less than two decades. The strength of the evidence is further discussed below. This conclusion corroborates the findings of van Herk et al. (2002); a study that was conducted on comparable spatial and temporal scales which suggested that epiphytic lichens can respond very quickly to climatic changes. It is easy to speculate on the cause for shifts in distribution but more difficult to disentangle the possible contributions of trends in, e.g. temperature, precipitation and pollution. Yearly average temperature and precipitation at sites within the investigated area increased slightly over the study period ($0.056^{\circ}\text{C year}^{-1}$ (29 sites) and 5.0 mm year^{-1} (28 sites), respectively; SMHI 1987–2003). During the same period air pollution decreased strongly and, e.g. NO_2 (14 sites) and SO_2 (6 sites) in the air dropped by approximately 50 and 90%, respectively (IVL 2009). Other studies of epiphytes in southern Sweden have documented a local ‘reinvansion/recolonisation’ of lichens attributed to the improved air quality (Hultengren et al. 2004). The three significant cases documented in the present study involved two lichens (*Hypogymnia physodes* and *Vulpicida pinastri*) that both have mainly a northerly distribution in Sweden, and that were shown to be generally on the retreat (Table 1), and specifically so in the southwest (Fig. 1). This region was also the one with the poorest air quality at the onset of our study, so unless air pollutant concentrations recorded in the 1980s turn out to be beneficial to the lichens in question, it is difficult to see how the documented patterns could be driven by a decrease in air pollution. Hence, our tentative interpretation is that the shifts seen are climate-driven.

Table 1. Presence/absence of epiphytic lichens were recorded on 64 sites in southern Sweden in 1986 and 2003. The shift in centroid (Distance) was calculated and its direction could be calculated for 30 cases (lichen species on tree species). The statistical significance of the shift in centroid was evaluated in a permutation test. *p-value <0.05, **p-value highly significant also after adjusting for false discovery rate.

Lichen species	Tree species	Occurrences 1986 only/both years/2003 only	Total occurrences (max 128)	Distance (km)	Direction (0–360°)	p-value
<i>Hypogymnia physodes</i> L.	<i>Betula</i> spp.	9/35/15	94	23	44.3	0.2126
<i>Hypogymnia physodes</i>	<i>Pinus sylvestris</i> L.	8/31/4	74	41	30.5	0.0066*
<i>Hypogymnia physodes</i>	<i>Picea abies</i> (L.) H. Karst	9/29/3	70	13	348.4	0.5594
<i>Hypogymnia physodes</i>	<i>Juniperus communis</i> L.	14/23/6	66	50	26.9	0.0258*
<i>Hypocenomyce scalaris</i> (Ach.) M. Choisy	<i>Pinus sylvestris</i>	6/10/15	41	31	41.7	0.5262
<i>Pseudevernia furfuracea</i> (L.) Zopf	<i>Betula</i> spp.	16/6/12	40	71	43.2	0.1028
<i>Pseudevernia furfuracea</i>	<i>Picea abies</i>	9/9/13	40	70	93.2	0.0688
<i>Platismatia glauca</i> (L.) W. L. Culb. & C. F. Culb.	<i>Betula</i> spp.	10/7/9	33	70	35.8	0.0808
<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.	<i>Betula</i> spp.	5/3/19	30	106	45.0	0.1160
<i>Vulpicida pinastri</i> (Scop.) J.-E. Mattsson & M. J. Lai	<i>Juniperus communis</i>	14/5/3	27	151	47.7	0.0002**
<i>Parmelia sulcata</i> Taylor	<i>Betula</i> spp.	7/1/14	23	106	51.6	0.1132
<i>Vulpicida pinastri</i>	<i>Pinus sylvestris</i>	8/3/2	16	43	27.2	0.4002
<i>Tuckermanopsis chlorophylla</i> (Willd.) Hale	<i>Picea abies</i>	6/1/7	15	101	71.2	0.2192
<i>Hypogymnia tubulosa</i> (Schaer.) Hav.	<i>Juniperus communis</i>	2/1/10	14	100	16.6	0.4590
<i>Usnea hirta</i> (L.) Weber ex F. H. Wigg.	<i>Pinus sylvestris</i>	8/2/2	14	70	212.8	0.4262
<i>Vulpicida pinastri</i>	<i>Picea abies</i>	13/0/1	14	106	44.6	0.6408
<i>Xanthoria parietina</i> (L.) Th. Fr.	<i>Populus tremula</i> L.	1/2/8	13	35	94.7	0.6994
<i>Ramalina farinacea</i> (L.) Ach.	<i>Acer platanoides</i> L.	0/4/4	12	92	222.9	0.0882
<i>Evernia prunastri</i> (L.) Ach.	<i>Populus tremula</i>	5/1/4	11	111	197.9	0.0604
<i>Bryoria fuscescens</i> (Gyeln.) Brodo & D. Hawskw.	<i>Betula</i> spp.	6/2/0	10	97	59.0	0.3570
<i>Parmelia sulcata</i> Taylor	<i>Picea abies</i>	1/2/5	10	19	224.8	0.9146
<i>Usnea hirta</i>	<i>Betula</i> spp.	7/1/1	10	48	195.5	0.5198
<i>Evernia prunastri</i>	<i>Picea abies</i>	2/1/5	9	42	222.6	0.8922
<i>Usnea hirta</i>	<i>Juniperus communis</i>	5/2/0	9	70	189.0	0.7186
<i>Usnea subfloridana</i> Stirt.	<i>Betula</i> spp.	8/0/1	9	258	53.7	0.2196
<i>Ramalina farinacea</i>	<i>Fraxinus excelsior</i> L.	1/0/6	7	322	16.3	0.2768
<i>Calicium viride</i> Pers.	<i>Quercus robur</i> L.	1/1/2	5	211	169.3	0.3292
<i>Ramalina fastigiata</i> (Pers.) Ach.	<i>Fraxinus excelsior</i>	1/0/4	5	149	302.1	0.8000
<i>Tuckermanopsis chlorophylla</i>	<i>Pinus sylvestris</i>	0/1/3	5	115	223.4	0.7524
<i>Usnea subfloridana</i> Stirt.	<i>Picea abies</i>	3/0/2	5	169	204.0	0.0958

The estimates of shift of the centroids presented, 3–10 km year⁻¹, is in range with the weighted centroids of counts of wintering shorebirds in western Europe (1.5–6.0, MacLean et al. 2008). Although not comparable, it might be noted that published estimates of northward movement show an average of 6.1 km per decade (Parmesan and Yohe 2003, several organisms), 9.5 km per decade (Thomas et al. 1999, birds) and 98.8 km per decade (Perry et al. 2005, marine fishes). Further, simulations on the range expansions needed for different organism groups to keep track with expected climate warming, suggest less than 1 km in most cases, and rarely longer than 10 km per annum (Malcolm et al. 2002).

Second, our study also showed that the prevailing direction of movements of lichens is likely to be in a northeast direction, rather than north, in southern Scandinavia. Most studies of species evaluating range shifts assume a northward movement of organisms in the Northern Hemisphere (Parmesan 2006). It is not easy to justify this particular direction when considering the global air circulation; the prevailing northeast direction documented in the present study are more in line with the global atmospheric circulations (de Blij and Muller 1996) and the gradients in temperature and rainfall in the study area (SMHI 1987–2003).

Methodological considerations

The current lichen data set and its low power

All data sets suffer from shortcomings. In our case, field sampling was designed to be quick, recording only presence/absence of lichens that, in most cases, did not require a specialist for identification. Consequently, we were able to include more sites than if including, e.g. assessment of abundance or demographic data. Future power analyses would be welcome to strike an appropriate compromise between data quality and quantity when setting up monitoring studies in general.

We lacked information about trees without lichens and were therefore unable to discriminate between actual losses of lichens on specific substrates and the loss of the substrate on a site. An additional consequence of this is that it prevented us from evaluating a possible change in substrate preference (e.g. a species might, over time, occur on a wider range of tree species).

Another drawback of the simple field method is that the age or size of the tree species, and where the lichen was found (trunk or branches), were not recorded. Although most of the epiphytic species sampled are not sensitive to tree species or tree size, some may, e.g. prefer thin branches over trunks and thus suffer a bias due to tree size composition.

Three out of 30 tests turned out to be significant, which might be interpreted as negligible change. It must be remembered, though, that many of the tests were based on very few occurrences (Table 1). Thus, the statistical power was, in most cases, low or very low and only large movements would be possible to detect.

The relatively large number of tests conducted (n = 30) might imply a need for adjusting for the family-wise type-I error (rejecting a true null hypothesis). Only one of three significant tests was found significant after applying the adjustment for false discovery rate (Benjamini and Hochberg 1995). It is mainly a matter of opinion

whether the current analyses should be considered to belong to the same family of tests or not (i.e. a justified need for correction or none), so we present both. But we focus on the uncorrected p-values for two reasons. Firstly, as generally in monitoring, type-II errors (accepting a true null hypothesis) might be equally, or more, harmful than type-I errors (Legg and Nagy 2006). Secondly, we were interested in including all species to be able to consider the directions – several cases, each with a weak signal, might together indicate a trend. This was, in fact, the outcome – also non-significant cases contributed to the evidence suggesting a prevailing northeast direction (Fig. 2, Table 1).

In conclusion, despite the low power of the data our new method proved to work well, and there were significant case(s) of centroid movements with a discernable prevailing northeast direction.

The versatile permutation procedure

The above-mentioned shortcomings are mainly related to this particular data set and its small sample size, and the method of analysis has some general advantages and might be useful in a broader range of analyses. First of all, it is possible to study changes within distribution areas without any knowledge of distribution boundaries. These are often difficult to determine and also probably have poor statistical properties (Dormann 2007). Some species do not have their outermost localities within an area studied, severely reducing the data sets available for boundary analysis. With the current method, many more types of data set could be analyzed.

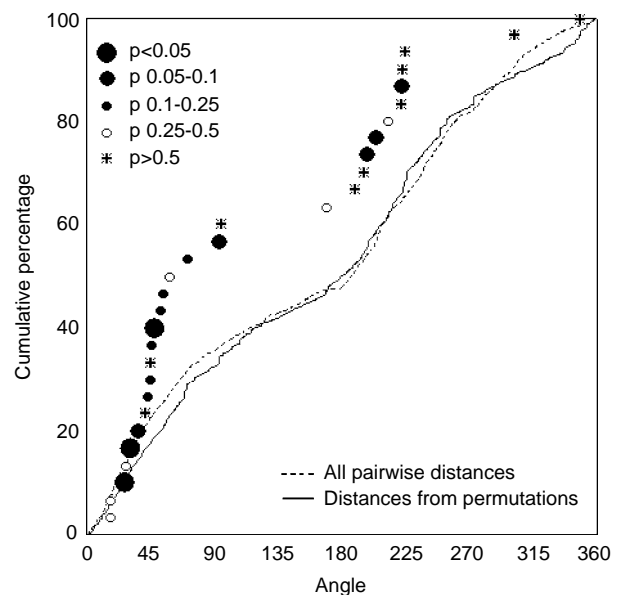


Figure 2. The cumulative distribution of the calculated directions of centroid movement (Table 1), that were based on inventories of epiphytic lichens on trees at 64 sites in southern Sweden in 1986 and 2003. The size of the mark shows the probability of a movement of centroid between the two years. The dotted line show the angles of all possible pair-wise combinations of sites and the unbroken line show the angles generated in the 30 permutation tests. The two soft bumps are due to the slightly elongated shape of the study area (Fig. 1a).

With presence/absence data, power decreases when approaching both zero and 100% frequency of the phenomenon under study. Hence, species with intermediate abundance, occurring in ca 50% of sample points, would have the strongest power in the present analysis. Basing centroids on abundance data, would allow a strong analysis also of very frequent species (cf. the weighted centroids used by MacLean et al. 2008).

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