During the last few decades there appears to have been a general increase in the range and abundance of a number of epiphytic bryophytes in much of the UK, as will be evident from a comparison of distributions reported in Hill et al. (1994) with recent data available on NBN Gateway (http://data.nbn.org.uk/). In South Lancashire (v.-c. 59) marked colonization appears (subjectively) to have coincided with intensive recording, during the years 1995–2005, towards a vice-county flora. We therefore have a possibility of a quantitative analysis of the progress of various epiphytes.

When detailed and reasonably complete surveys of an area are carried out at widely different times, increases in species densities are readily apparent. However, if an area has not been intensively recorded in the recent past (as was the case for South Lancashire in 1995), one can only hope to determine whether a species is currently increasing. One reliable approach is to record thoroughly at a number of sites over a number of years, but this is time-consuming and can only give information about changes which occur after the decision to investigate them. Here, we consider the possibility of a retrospective and objective assessment of such changes, using data from a normal program of tetrads, e.g. for a vice-county Flora, during which the number of records for all species increases steadily. One might hope to see whether the number of records for a particular species is increasing more quickly than those of some common species known to be stable, but ‘more quickly’ needs careful consideration; records of scarcer species must of course increase more slowly than those for common species. We will consider the possibility of an analysis along these lines, with the v.-c. records as a test case.

First, consider an idealized recording scheme in which tetrads are visited one-by-one at a constant rate of $R$ tetrads per year, with equal recording effort in each visit. If a particular species is present in a constant fraction $F$ of the tetrads, the number of tetrads $N$ in which that species has been recorded after $Y$ years will be:

$$N = RYF/P$$

where we have included a factor $P$, assumed to be constant, representing the probability that the species will be detected in a visit to a tetrad in which it is present; this will depend on the degree of prominence of the species and the diligence of recording. This expression is valid until all tetrads have been visited, if it is supposed that no tetrad is visited twice until all have been visited once.

Epiphyte colonization in v.-c. 59

Epiphytic bryophytes appear to be on the increase in Britain, but how can we measure changes in their abundance and distribution? John Lowell describes a model to assess such changes objectively based on tetrads recording data.
When all tetrads have been visited, the total number of tetrads $N_t$ within which the species has been recorded will be:

$$N_t = FPN_0$$

$N_t$ being the number of tetrads in the vice-county. So:

$$N/N_t = R Y/F N_0$$

Thus, in this idealized case, a plot of $N/N_t$ against time (1) in years should be a universal straight line for any species (for $Y < N_t / R$). Note that this is true whether the species is common or scarce ($N/N_t$ is independent of $F$). Furthermore, since $N/N_t$ is also independent of $P$, it is not necessary to suppose that recording is ‘complete’, i.e. that a species is recorded for all tetrads in which it actually occurs. This is significant in view of the analysis of Callaghan & Ashton (2008), which suggests that the v.-c. 59 records are probably far from complete.

It is important to review the assumptions behind the conclusion that $N/N_t$ should increase linearly with time:

1. The rate of recording $R$ is constant, and tetrads are not revisited.
2. The recording effort is uniform, equal time and attention being given to each tetrad visited.
3. The detection probability $P$ does not change with time.
4. The species density is not changing (i.e. $F$ is constant).

Assumption 4 reflects the question we are testing; i.e. are species increasing or diminishing? Such changes can be detected by deviations from linearity of a plot of $N/N_t$, providing that assumptions 1–3 hold; we propose that this can be tested by examining the plots for species believed to be stable.

Assumptions 1 and 2 are stringent, and unlikely to be met exactly in any real survey – they certainly do not apply to our recording in South Lancashire. The rate of recording was probably roughly constant, but the recording effort was not, visits varying from intensive to more or less casual. However, this may not be important, given that the recording effort averaged over all the tetrads visited in any particular year was probably similar from year to year, i.e. independent of $Y$. The assumption that tetrads were not revisited is also invalid for our survey: in the later stages, considerable effort was put into tetrads visited previously, resulting in fewer visits to new tetrads; this implies, in effect, a reduction in $R$ at later values of $Y$. We can expect this to result in the rate of increase of $N/N_t$ falling off in the later years, rather than increasing at a steady rate until coverage becomes complete. All of these problems refer to recording procedure and should be equally apparent for all species. Therefore, we can assess their influence by checking whether an $N/N_t$ versus $Y$ plot has the expected universal linear form for species which can be assumed to be stable in their distribution – in particular common and widespread species.

Assumption 3 is more problematical; unless recorders are very expert from the start of recording, the detection probability $F$ may well be dependent on time for some species. Indeed, we were aware in the v.-c. 59 survey of a ‘learning curve’ for several species, the detection rate increasing either because we learned to identify the species accurately or gained experience in seeking it out in obscure habitats. Accordingly, in the analysis below we have restricted attention to species which we feel are prominent and easily recognized. Nevertheless, it must be admitted that an apparent time dependence of $F$, revealed by the $N/N_t$ versus $Y$ plot, might in principle be due to an unsuspected learning curve rather than a genuine increase in species density, though we think this is unlikely for the species considered here.

In retrospect, it is unfortunate that recording was not more regular and uniform (we strongly endorse the recommendations of Rich (1998)). However, there is evidence that irregularities are not too important (probably because of the ‘averaging’ discussed above). Thus, Fig. 1(a) shows a plot of $N/N_t$ versus $Y$ for several species which we believe to be stable in distribution (this is undoubtedly the case for the commoner species). The species chosen include Brachythecium rutabulum, which is ubiquitous, three species (Dicranoweisia cirrata, Hypnum cupressiforme and Orthotrichum affine) which are very frequent and largely epiphytic, and several others chosen to provide a range of frequency from common to quite scarce. Note that plots are initially close to linear, though they level off in the later years (probably because of revisiting, see above). Also, the plots for all species are roughly coincident as expected. This is true not only for widely distributed species, but also for Scapania undulata, for example, which is frequent in the hillier one-third or so of v.-c. 59, but scarce elsewhere. There is considerable scatter, which is probably at least partly due to irregular recording procedures, and also to statistical fluctuations in the case of scarcer species with fewer records. Nevertheless, it is clear that the plots are close to the prediction based on assumptions 1–4, apart from the deviation in later years. As we noted above, assumptions 1 and 2 are determined solely by recording procedure; if they are (in effect) valid for the species in Fig. 1(a), they must be valid for all species. Therefore, as long as we restrict ourselves to easily recognized species, i.e. as long as assumption 3 is valid, the plot of $N/N_t$ versus $Y$ for any species should be of the form apparent in Fig. 1(a), provided that assumption 4 applies. Any gross difference can be attributed to failure of assumption 4, i.e. to a variation in $F$, reflecting changes in species density.

![Graph showing variation with time (years) of the number of records](image-url)
Fig. 1(b) shows plots for a number of epiphytic species, for all of which we have had a subjective impression of increasing density. The plots for all of these species are very different to those of Fig. 1(a). In particular, it is clear that $N/N_0$ increases much more slowly in the earlier years, and continues rising at an increasing rate towards the end of the recording period, rather than levelling off. We regard all of these species as prominent and easily recognizable, so we consider the marked differences between the plots of Fig. 1(a) and (b) to be objective evidence that densities of these epiphytic species are increasing with time. A rough measure of the rate of increase is given by the discrepancy between the plotted points and the straight line in Fig. 1(b) (which represents, roughly in view of the scatter, the expected fraction of tetrads occupied by a species which later in time). Thus in 1997 (for example) $N/N_0$ (present in 0.9% of tetrads by 2005) and Microlejeunea ulicina (0.8%) are still too scarce for a meaningful analysis along the above lines; the same is true for $O. affine$ and Metzgeria violacea (1.7%), which also fails to satisfy the requirement that species be ‘prominent’: $M. conanguinea$, though prominent in itself, is easily passed over for the much commoner $M. violacea$, and in that sense may be said to be an ‘obscure’ species. It is also relevant to mention Cololejeunea minutissima and Colura calyptrifolia which were not detected during the recording period, but have been noted subsequently to 2005.

Fig. 1(c) shows plots for a number of epiphytic species which also appear to be colonizing South Lancashire; Orthotrichum lyellii (present in 0.8%) and $O. pulchellum$ (and also $O. affine$) are still too scarce for a meaningful analysis along the above lines; the same is true for $M. conanguinea$, though prominent in itself, is easily passed over for the much commoner $M. violacea$, and in that sense may be said to be an ‘obscure’ species. It is also relevant to mention Cololejeunea minutissima and Colura calyptrifolia which were not detected during the recording period, but have been noted subsequently to 2005.

Finally, we consider two species (Fig. 1c) for which the plots are somewhat intermediate between those of (a) and (b). We selected these particular species because our subjective impression during recording was that one of them, Radula complanata, was becoming more frequent, whereas the other, Orthotrichum affine, was more or less stable. In fact, Fig. 1(c) shows that our impression was quite wrong; there is little difference between the two plots. For both species, the initial slope of the plot is rather less than for the species in Fig. 1(a), indicating that both species were increasing their range somewhat during the recording period. The increase is less spectacular than for the epiphytes of Fig. 1(b) [and in view of the scatter in (a) may just possibly be spurious]. Our interest here stems from the implication that subjective impressions may easily be mistaken. It is not difficult to suggest reasons for this. When a species is already frequent (Orthotrichum affine) a modest rate of increase may be difficult to discern among the steadily increasing tetrad records of a conventional vice-county survey, so it is easy to understand why the increase of $O. affine$ (if indeed it is real) was overlooked.

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