

Using data from local floras for ecological research

M. O. HILL

CEH Monks Wood, Abbots Ripton, Huntingdon PE28 2LS

ABSTRACT

Ecology has been variously defined ‘the scientific study of the interactions between organisms and their environment’ or ‘the scientific study of the interactions that determine the distribution and abundance of organisms’. Many local floras contain accounts of the environment; all give information on the distribution and abundance of plants. In spite of this, there is rather little flow of information between ecologists and flora writers. Among possible explanations are the disparity in the spatial scale of interest, the subtlety of plant life histories, the obscurity of key environmental factors, and the emphasis of floras on rarities rather than on the ‘ecosystem engineers’. Nevertheless, some interesting analysis of flora data is possible, both of spatial patterns and of temporal change.

KEYWORDS: biogeography, ecology, autecology, vegetation, life cycle

INTRODUCTION

ECOLOGY

We all have a vague idea of what we mean by ecology, but the word has acquired new significance in an age of environmentalism. Ecologists, so it is supposed, are people who want to save the planet. They have a green message. The reality is more mundane. The authors of a well known ecology textbook (Begon, Harper & Townsend 1986) give two definitions: ‘the scientific study of the interactions between organisms and their environment’ and ‘the scientific study of the interactions that determine the distribution and abundance of organisms’.

Definitions are not always the best way to find out what a subject is about. It is often prudent to see what subjects appear in a textbook. The most suitable for this purpose is *Plant Ecology*, edited and largely written by the BSBI vice-county recorder for Berkshire (Crawley 1997). Most of the topics are ‘plant-centred’ (Table 1), that is to say that they relate to how a plant can survive and reproduce in an often hostile world. The later topics in *Plant Ecology* shade into biogeography, the study of organisms at larger scales of time and space.

An aspect of ecology that is implicit but not prominent in *Plant Ecology* is autecology, the species-centred view of the world. Autecological accounts of species can be mini-monographs such as the Biological Flora of the British Isles (Table 2; e.g. Blackman & Rutter 1954; Carey & Farrell 2002), databases such as the Ecological Flora Database (Fitter & Peat 1994) or books combining a database with verbal accounts (Grime, Hodgson & Hunt 1988). Grime *et al.* (1988), for example, categorize *Hyacinthoides non-scripta* as a woodland bulb-forming monocotyledonous herb with a vernal phenology, pointing out that it is sensitive to grazing by cattle and sheep but avoided by rabbits. They describe how the bulbs are buried deeply by the action of contractile roots and how the species normally reproduces by seed, taking at least 5 years to reach flowering size. These facts tell us much about the life of *H. non-scripta* and together indicate where it should be expected to occur.

LOCAL FLORAS

Local floras differ among each other but there is a general pattern followed by many. I categorized the contents of 30 local floras dating from Deering (1738) through to Evans, Evans & Rothero (2002), dividing them into four headings (Table 3). In several floras, chapters categorized as ‘interpretation of distributions and change’ are basically a travelogue, giving the interesting features of sub-regions or catchments. Some of these travelogues are a complex blend of floristics

TABLE 1. TOPICS INCLUDED IN CRAWLEY'S *PLANT ECOLOGY* (1997)

General topic	Examples
Physiology	Photosynthesis, water relations, nutrient acquisition
Life history	Growth, longevity, reproduction, dispersal, seed dormancy
Interactions	Competition, herbivory, diseases, plant defences
Population biology	Genetics, population dynamics, plant-herbivore dynamics
Plant communities	Physiognomy, succession, diversity, species-area relations
Large-scale factors	Pollution, climate change
Biodiversity	Hotspots, islands, aliens

TABLE 2. HEADINGS IN BIOLOGICAL FLORA OF THE BRITISH ISLES

Main heading	Details
Geographical and altitudinal distribution	British, Irish, European and world range, altitudinal limits in Britain and Europe
Habitat	Climatic and topographic limitations, substratum
Communities	Nowadays classified by NVC types (Rodwell 1991–2000)
Response to biotic factors	Effects of disease, insects, mammalian grazing
Response to environment	Gregariousness, response to various factors, effect of frost, drought etc.
Structure and physiology	Morphology, mycorrhiza, perennation, reproduction, chromosomes, physiological data, biochemical data
Phenology	Timing of germination, flower and fruit production, tuber initiation etc.
Floral and seed characters	Floral biology, hybrids, seed production and dispersal, germination, seedling morphology
Herbivory and disease	Animal feeders, parasites, diseases
History	Quaternary and archaeological data, first records

TABLE 3. CHAPTERS IN AN AVERAGE LOCAL FLORA

No.	Chapter	No. of pages
1	Environmental background	18
2	Interpretation of distributions & change	27
3	History of recording	9
4	Flora enumerated by species	226
	Length of chapters 1 and 2 as a percentage of the total	16%

and physical background. Other floras, such as my own account of North Wales bryophytes (Hill 1988), enumerate the interesting plants mainly by habitat. The distinction in Table 3 between environmental description and interpretation is not sharp.

The earliest local floras lacked almost all information about the physical background, but by the late 19th century, they sometimes contained lengthy descriptions. These did not necessarily relate strongly to the accounts of individual species; Mansel-Pleydell's (1895) description of Dorset geology is gloriously irrelevant to his flora. Much the same applies to more recent floras where there are lengthy descriptions of the vegetation. For example, in the Natural History Museum's account of the Island of Mull (Jermy & Crabbe 1978), there is a chapter entitled 'Terrestrial Ecosystems', much of which is devoted to the vegetation. In this chapter, we learn that *Trichophorum cespitosum* is sometimes a dominant component of lowland bog vegetation and that the conditions for its dominance are quite specific. All of this detail is lost in the species account, which states merely 'In damp peaty areas, a common associate of *E. tetralix* on the Ross. Can withstand some grazing and burning. Frequent to abundant; widespread'.

Clearly, the two chapters, one on vegetation and another on flora, are aimed at describing the plants and their environment from different perspectives. The flora is plant-centred and brief. The account of vegetation is concerned mainly with the dominants, the big plants, 'ecosystem engineers' that help to define the environment as well as being merely a part of it.

INFORMATION FLOW BETWEEN LOCAL FLORAS AND ECOLOGISTS

Much early ecology was descriptive, showing how plants in general and vegetation in particular can be related to the environment. Ecologists (e.g. Aber & Melillo 1991; Walter 1979) have recently devoted much attention to the physiological factors that determine vegetation types, driven especially by the need to understand the potential response of ecosystems to climate change (Sykes *et al.* 2001; Woodward 1992). Such work is global and generic, though the factors determining the changes in individual species have also attracted some attention (Huntley *et al.* 1995; Walther 2000).

In these grand matters, the place of the local flora has not been large. Likewise, Tansley (1939) and Rodwell (1991–2000) made little use of information from local floras in describing the vegetation of our islands.

A glance at the accounts written for the Biological Flora of the British Isles shows that they make extensive use of descriptions of vegetation, but that local floras are little cited. For example, neither Blackman & Rutter (1954) nor Carey & Farrell (2002) cited local floras in their accounts of *Hyacinthoides non-scripta* and *Himantoglossum hircinum* (Carey & Farrell did, however, consult local floras as part of their study of *H. hircinum*). Gilbert (1995) cited Grose (1957) and Wolley-Dod (1937) for the habitat and spread of *Symphoricarpos albus*. Watkinson, Newsham & Forrester (1998) cited Hind (1889), Petch & Swann (1968) and Trist (1979) for the history of *Vulpia ciliata* ssp. *ambigua*; and Rose, Bannister & Chapman (1996) cited Brewis *et al.* (1996) and Mansel-Pleydell (1895) for the history of *Erica ciliaris*.

The reverse flow, of ecological information to local floras, is hugely variable. At one extreme, Burton (1983) gives a 12-page analysis of factors affecting the distribution of plant species in the London area but refers to only two published sources, both of them papers in the *London Naturalist* and neither of them ecological. The excellent flora of West Lancashire by Wheldon & Wilson (1907) includes a 61-page disquisition on the factors affecting plant distribution, including some material that would now be categorized as physiological plant ecology. The authors explicitly cite only six papers, of which two are physiological and one ecological; but then there was almost no British literature on plant ecology at the time. In Hertfordshire, there was also an early ecological influence, dating from 1910 when E.J. Salisbury was most active in the county (Dony 1967). Some of the grander modern floras, such as those of Cumbria (Halliday 1997), Oxfordshire (Killick, Perry & Woodell 1998) and Assynt (Evans *et al.* 2002), include extensive ecological and historical sections. They present a broad view of the environment and floristics of their regions but, unlike the West Lancashire flora, mainly ignore physiology.

In summary, local floras are used by ecologists to a small extent, mainly to provide information on distributional change, and ecological information is included as background in some local floras but not in others.

ECOLOGICAL ANALYSES OF LOCAL FLORA DATA

If local floras have limited use to ecologists, what about the distributional data that they contain? One of the most extensive analyses of distributional data in a local flora was that of Good (1948) for the English county of Dorset. Good was particularly interested in the effects of climate. Climate is by far the largest influence on flora at the global scale but becomes less significant than soil and topography at smaller scales (Cain 1944). According to Good (1948, p.52) 'Climate primarily determines what species constitute the flora of Dorset, but edaphic conditions chiefly determine how those species are distributed individually within the county, that is to say, which are widespread, which are abundant, which are local, and which are rare'.

Good recognized two types of climatically-determined distributions, the marginal type (species at the edge of their range) and the gradient type (species which are widespread in the county but

are more frequent in one climatic zone). Some species' ranges were determined by rainfall, others by proximity to the sea, which is a complex climatic response depending on temperature and humidity. In addition, he recognized 40 species for which Dorset offers optimal climatic conditions. In enumerating edaphic factors, he distinguished a variety of soil types, such as saline, calcareous, medium, acid, clayey and sandy. Additional important factors were the presence of special habitats, notably water and woodland.

Even when all these factors were taken into account, patterns of distribution were not simple. There were compound distributions such as that of *Iris foetidissima*, which was found in woods, hedges and undercliffs on the coast, but inland was more or less confined to woods on the north-eastern chalk and adjacent Tertiary clays. Good was completely unable to explain this pattern, though other complex patterns such as that of *Phragmites communis* could be understood as the sum of the coast and the larger rivers. Other species such as *Achillea ptarmica* and *Viola palustris* had strangely disjunct distributions within the county. Good called these simply 'anomalous distributions'.

Good was hampered in his statistical analysis by the magnitude of his dataset. He made many of his inferences by 'eyeballing' the distribution maps and applying his extensive knowledge of Dorset plants in the field. His dataset, based on 7,500 sampling stations, would be easy to analyse on a modern computer, but would have been a large computational problem as little as 10 years ago. Such an analysis may soon be forthcoming because, thanks to a grant from the Heritage Lottery Fund, all of his stand data have now been computerized, geo-referenced and checked. They are a valuable resource for the future.

With the advent of electronic computing came habitat-based distribution maps (Cadbury, Hawkes & Readett 1971). There was also the possibility of more organized analysis of plant distributions. Several methods were explored by the authors of the Shropshire flora (Sinker *et al.* 1985). These included classifications of quadrat data, composite maps ('coincidence maps') of groups of species, and attractive small distribution maps fitted into the text. For the adjacent county of Montgomeryshire (Trueman, Morton & Wainwright 1995), a wider range of figures and analyses was possible, including satellite images of land-cover types, a scatter diagram of species richness in relation to altitude, and ordination and classification of tetrads based on their species, using the programs DECORANA and TWINSpan (Hill 1979a; Hill 1979b). Particularly impressive is the agreement between the coincidence map for 23 ancient woodland species (Fig. 1) and a distribution map of ancient woodland sites (Fig. 2). The TWINSpan classification (Fig. 3) divides the tetrads into two (and then four and eight), separating tetrads with the moorland species *Erica tetralix*, *Juncus squarrosus*, *Molinia caerulea* and *Nardus stricta* from those with *Ribes uva-crispa*, which is frequent in hedgerows and woods, especially near human habitation.

An additional method of analysis, Canonical Correspondence Analysis (ter Braak 1986) explicitly seeks correlations between environmental attributes and species lists. Canonical Correspondence Analysis was used by Bates (1995a) to make an analysis of bryophyte distributions in 5 km squares of Berkshire (Bates 1995b). This demonstrated a major axis of variation distinguishing heathland and bogs on the one hand from eutrophic and calcareous countryside on the other. A secondary axis distinguished eutrophic lowlands with rivers from countryside containing specialists of nutrient-poor chalk. The other two axes of variation found by this method were hard to interpret, though one axis had some relation to ancient woodland.

Bates, like Good before him, contrasted the strongly edaphic basis of variation within the county with the climatic basis found when 10 km squares were analysed at the scale of Great Britain (Hill & Domínguez Lozano 1994). Overall, the result of the county analysis was a little disappointing, in that the gradients revealed were obvious without complex analysis or, if not obvious, were hard to interpret. Even those that were obvious did not necessarily reflect single controlling factors but instead showed complex patterns of variation, such as that between relatively upland parts of the county (with higher rainfall, lacking major watercourses, often well wooded) and the major river valleys (with lower rainfall, intensively agricultural, largely unwooded, with rich riparian floras). Interestingly, some specialists of tree bark and rotting wood showed strong correlations with soil acidity, even though they did not themselves grow on soil.

Using the same methods of analysis on 1 km square data from an intensively-recorded area of northern Finland, Heikkinen, Birks & Kalliola (1998) came to rather a similar conclusion. All numerical techniques revealed a major gradient from alpine areas at one extreme to lowland sites with rivers and rocky outcrops at the other; a secondary gradient was correlated with the

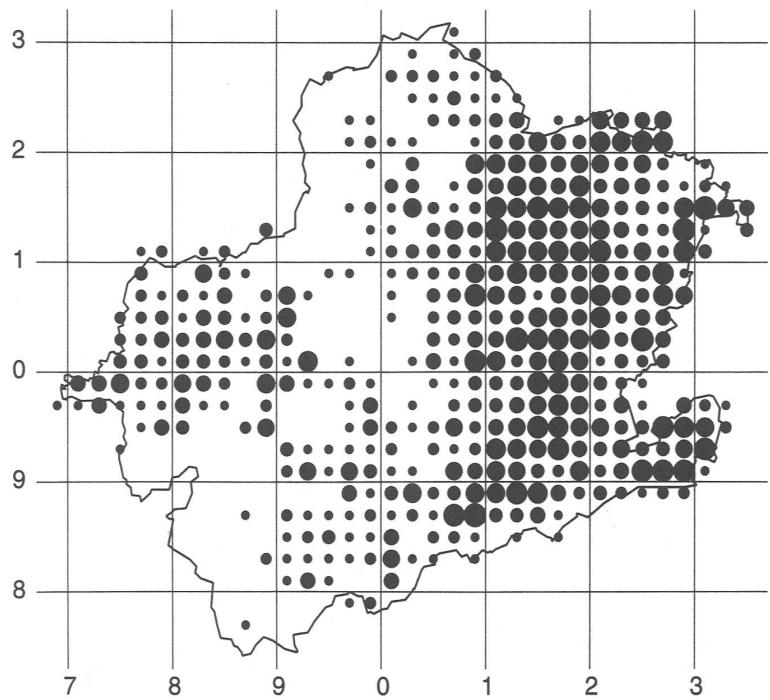


FIGURE 1: Coincidence map of ancient woodland species in Montgomeryshire (from Trueman *et al.* 1995).

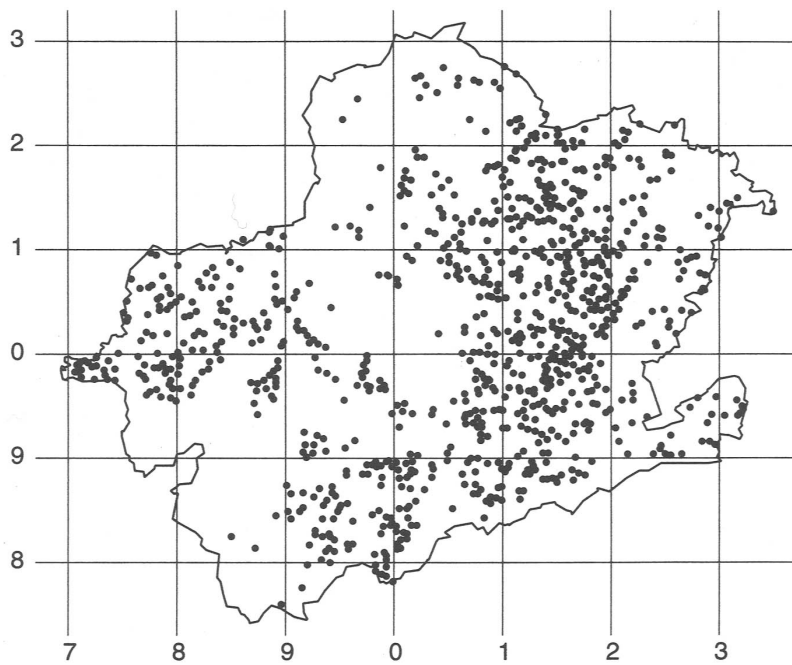


FIGURE 2: Distribution of ancient woodland sites in Montgomeryshire (from Trueman *et al.* 1995).

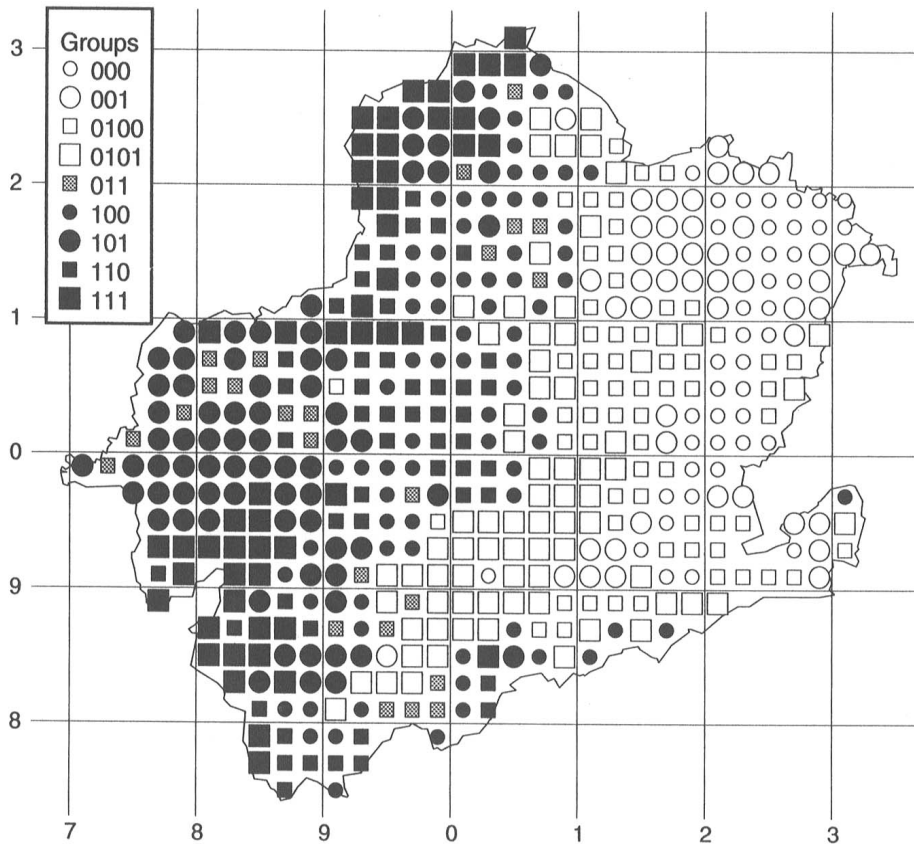


FIGURE 3: Tetrads of Montgomeryshire classified into groups on the basis of their flora (from Trueman *et al.* 1995).

abundance of mires. However, much of the floristic variation was determined mainly by small-scale factors, which were not readily detected at the 1 km square scale. Richness of rare species was likewise not easy to predict from environmental variables (Heikkinen 1998). Local hotspots were mainly in topographically heterogeneous grid squares, where high cliffs occur in deep gorges. Again, small-scale variation was important.

DISCUSSION AND CONCLUSIONS

It is clear that data from local floras are used rather little in ecological research. What are the reasons?

DISPARITY OF SCALE

Most ecological phenomena are studied at the ecosystem scale, which is smaller than the 1 km square scale or 2 km square scale used in many local floras. Ecological processes can of course be used to explain some of the phenomena that are observed. But it is the landscape scale that matters for local floras, with broader phenomena such as eutrophication, pasture abandonment, loss of burning, winter cropping of arable etc. acting as the great drivers of change. The ecological basis of calcium tolerance or of adaptation to high-nutrient or low-nutrient environments is fascinating for a plant ecologist but the ecology is just a little too detailed for understanding distributions. For a local flora, it is normally sufficient to know whether a plant thrives under particular conditions and where those conditions can be found.

A key factor that is often expressed at an inconveniently small scale for distribution maps is the topographic roughness of the terrain. Just as Heikkinen (1998) found small-scale terrain factors to be important in northern Finland, so may gullies and ravines be important as plant habitats in many parts of Britain. Likewise, the presence of grazed flushes with mineral enrichment of the ground water may be crucial for the survival of various marsh plants on extensive moorland, but small flushes are not mapped by cartographers nor are they easily recognized in satellite images.

The timescales of ecological phenomena, especially those of soil processes such as peat formation, may also be incompatible with those of a local flora; but this is less common. Many plants live for decades or even as clones for hundreds of years. Most, however, complete their life cycles within a human generation.

OBSCURITY OF KEY ENVIRONMENTAL FACTORS

Recurrent patterns of distribution are apparent when the key factors controlling the presence of species are similar. However, key factors for particular species may not be correlated with those for others, at least at the scale of recording, so that an appearance of randomness results. One formerly obscure factor is the presence of ancient woodland. Since the pioneering work of Peterken (1974) and Rackham (1976), the importance of ancient woodland has been well understood. Its presence can now be mapped as an environmental factor to aid interpretation of distribution patterns (Spencer & Kirby 1992).

Biotic factors such as susceptibility to slug grazing (Bruehlheide & Scheidel 1999) are much more troublesome. Slug densities depend on a variety of factors, including the moisture of the season and the abundance of predators that eat them. Deer grazing and its effect on woods is often all too obvious (Crampton *et al.* 1998), but the effects of herbivory by many invertebrates, especially those that eat roots, are still largely unknown even to ecologists.

Equally unknown for many species is the extent to which they depend on dispersal vectors. Poschod *et al.* (1998) were of the opinion that, in former times, sheep movements between and around farms transported propagules between patches of calcareous grassland. Thus species could become locally extinct for a few years and then be reintroduced. Modern farming prevents such reintroductions. If this theory is true, then long-term declines of calcareous grassland plants could be expected even if the physical condition of the habitat is maintained.

SUBTLETY OF PLANT LIFE HISTORIES

The dependence of some species such as *Lobelia urens* on intermittent disturbance (Dinsdale, Dale & Kent 1997) cannot be appreciated without a detailed ecological understanding of its life cycle. At the present time, many of these peculiarities are being discovered in the process of devising species action plans (UK Biodiversity Group 1998). There are many such peculiarities. Plants that depend on rare events such as occasional fires or droughts may seem to be particularly unpredictable. Sometimes the key life-history factor may no longer be operative. *Tilia cordata* survives in Cumbria without effective reproduction; it is a relict of warmer times in the past (Halliday 1997).

EMPHASIS OF FLORAS ON RARE SPECIES

Much ecological study is devoted to finding out how the commoner species perform in the landscape. Large, abundant plants determine how most ecosystems work. They are the ecosystem engineers. Likewise, most types of vegetation are defined by common and widespread species. Plants such as *Paris quadrifolia* that were found in less than 10% of samples of any vegetation type were not even mentioned by Rodwell (1991–2000). Writers of local floras all take pleasure in the unusual, even if, like Good (1948), their species accounts do not show it. Good's frontispiece shows *Himantoglossum hircinum*, extremely rare in Dorset, where only two isolated plants had at that time been found.

Large numbers of ecologists are in fact concerned with rare species, as well as with common ones. Rarity is the subject of a well known ecological textbook (Gaston 1994). Most local floras say little of interest about their common plants. *Galium aparine*, for example, receives a dull notice in almost all floras. Even the authors of the excellent Shropshire flora (Sinker *et al.* 1985), cannot say much for it. Their most notable comment is 'Difficult to clear when brushing hedges'. Maybe *G. aparine* is just too much part of the furniture (or dross, depending on one's point of view) of our everyday lives.

CONCLUSIONS

In extreme cases, the authors of local floras provide distributional data almost without interpretation. At the other extreme, some ecologists are fixated on life cycles and physiological responses and ignore distributions. In the centre, there is much common ground. To write a local flora is inspiring for an ecologically-minded botanist, who is thereby forced to think about the distribution and abundance of plants in the locality. Ecological studies can feed into local floras where they help to explain remarkable phenomena such as the survival of *Tilia cordata* in Cumbria. But the fact remains that distributional data from local floras remain rather intractable and difficult to use. Probably this is because the standard methods of analysis seek general patterns. Plant distributions are interesting at all scales, from the continent to patches in a field. At the scale of the local flora, distributional data are often hard to interpret, being the result of diverse historical processes and biotic factors, which produce complex patterns. It is to be hoped that improved methods of analysis will in future allow ecologists to solve some of the problems that Good (1948) found so intractable. Present methods of numerical analysis are inadequate. Much remains to be done.

ACKNOWLEDGMENTS

I am grateful to David Pearman for information about Dorset, to Chris Preston for help in selecting local floras, and to Alan Morton and Ian Trueman for permission to reproduce their figures.

REFERENCES

- ABER, J. D. & MELILLO, J. M. (1991). *Terrestrial Ecosystems*. Saunders College Publishing.
- BATES, J. W. (1995a). Numerical analysis of bryophyte-environment relationships in a lowland English flora. *Fragmenta Floristica et Geobotanica* 40: 471–490.
- BATES, J. W. (1995b). A bryophyte flora of Berkshire. *Journal of Bryology* 18: 503–620.
- BEGON, M., HARPER, J. L. & TOWNSEND, C. R. (1986). *Ecology – Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford.
- BLACKMAN, G. E. & RUTTER, A. J. (1954). Biological Flora of the British Isles. *Endymion nanscriptus* (L.) Garke. *Journal of Ecology* 42: 629–638.
- BREWIS, A., BOWMAN, P. & ROSE, F. (1996). *The flora of Hampshire*. Harley Books, Colchester.
- BRUELHEIDE, H. & SCHEIDEL, U. (1999). Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *Journal of Ecology* 87: 839–848.
- BURTON, R. M. (1983). *Flora of the London Area*. London Natural History Society, London.
- CADBURY, D. A., HAWKES, J. G. & READETT, R. C. (1971). *A computer-mapped flora: a study of the county of Warwickshire*. Academic Press, London.
- CAIN, S. A. (1944). *Foundations of plant geography*. Harper & Bros, New York.
- CAREY, P. D. & FARRELL, L. (2002). Biological Flora of the British Isles. *Himantoglossum hircinum* (L.) Sprengel. *Journal of Ecology* 90: 206–218.
- CRAMPTON, A. B., STUTTER, O., KIRBY, K. J. & WELCH, R. C. (1998). Changes in the composition of Monks Wood National Nature Reserve (Cambridgeshire, UK) 1964–1996. *Arboricultural Journal* 22: 229–245.
- CRAWLEY, M. J. (1997). *Plant ecology*. Blackwell Science, Oxford.
- DEERING, C. (1738). *A catalogue of plants naturally growing and commonly cultivated in divers parts of England, more especially about Nottingham*. C. Rivington, London.
- DINSDALE, J., DALE, P. & KENT, M. (1997). The biogeography and historical ecology of *Lobelia urens* L. (the heath lobelia) in southern England. *Journal of Biogeography* 24: 153–175.
- DONY, J. G. (1967). *Flora of Hertfordshire*. Hitchin Museum, Hitchin.
- EVANS, P. A., EVANS, I. M. & ROTHERO, G. P. (2002). *Flora of Assynt*. Privately published.
- FITTER, A. H. & PEAT, H. J. (1994). The Ecological Flora Database. *Journal of Ecology* 82: 415–425.
- GASTON, K. J. (1994). *Rarity*. Chapman & Hall, London.
- GILBERT, O. L. (1995). Biological Flora of the British Isles. *Symphoricarpos albus* (L.) S.F. Blake (*S. rivularis* Suksd., *S. racemosus* Michaux). *Journal of Ecology* 83: 159–166.
- GOOD, R. (1948). *A geographical handbook of the Dorset flora*. The Dorset Natural History and Archaeological Society, Dorchester.
- GRIME, J. P., HODGSON, J. G. & HUNT, R. (1988). *Comparative plant ecology: a functional approach to common British species*. Unwin Hyman, London.
- GROSE, D. (1957). *The flora of Wiltshire*. Wiltshire Archaeological and Natural History Society, Devizes.

- HALLIDAY, G. (1997). *A Flora of Cumbria*. Centre for North-West Regional Studies, Lancaster.
- HEIKKINEN, R. K. (1998). Can richness patterns of rarities be predicted from mesoscale atlas data? A case study of vascular plants in the Kevo Reserve. *Biological Conservation* **83**: 133–143.
- HEIKKINEN, R. K., BIRKS, H. J. B. & KALLIOLA, R. J. (1998). A numerical analysis of the mesoscale distribution patterns of vascular plants in the subarctic Kevo Nature Reserve, northern Finland. *Journal of Biogeography* **25**: 123–146.
- HILL, M. O. (1979a). *DECORANA – a FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Section of Ecology and Systematics, Cornell University, Ithaca, N.Y.
- HILL, M. O. (1979b). *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Section of Ecology and Systematics, Cornell University, Ithaca, N.Y.
- HILL, M. O. (1988). A bryophyte flora of North Wales. *Journal of Bryology* **15**: 377–491.
- HILL, M. O. & DOMÍNGUEZ LOZANO, F. (1994). A numerical analysis of the distribution of liverworts in Great Britain, pp. 11–20 in HILL, M. O., PRESTON, C. D. & SMITH, A. J. E., eds. *Atlas of the bryophytes of Britain and Ireland, Vol. 3, Mosses (Diplolepidae)*. Harley Books, Colchester.
- HIND, W. M. (1889). *The flora of Suffolk*. Gurney & Jackson, London.
- HUNTLEY, B., BERRY, P. M., CRAMER, W. & McDONALD, A. P. (1995). Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography* **22**: 967–1001.
- JERMY, A. C. & CRABBE, J. A., eds. (1978). *The island of Mull: a survey of its flora and environment*. British Museum (Natural History), London.
- KILLICK, J., PERRY, R. & WOODILL, S. (1998). *The Flora of Oxfordshire*. Pisces Publications.
- MANSEL-PLEYDELL, J. C. (1895). *The flora of Dorsetshire*, 2nd ed. Privately published, Dorchester.
- PETCH, C. P. & SWANN, E. L. (1968). *Flora of Norfolk*. Jarrold & Sons, Norwich.
- PETERKEN, G. F. (1974). A method for assessing woodland flora for conservation using indicator species. *Biological Conservation* **6**: 239–45.
- POSCHLOD, P., KIEFER, S., TRÄNKLE, U., FISCHER, S. & BONN, S. (1998). Plant species richness in calcareous grasslands as affected by dispersibility in space and time. *Applied Vegetation Science* **1**: 75–90.
- RACKHAM, O. (1976). *Trees and Woodland in the British Landscape*. J.M. Dent & Sons Ltd, London.
- RODWELL, J. S. (1991–2000). *British plant communities*. 5 volumes. Cambridge University Press, Cambridge.
- ROSE, R. J., BANNISTER, P. & CHAPMAN, S. B. (1996). Biological Flora of the British Isles: *Erica ciliaris* L. *Journal of Ecology* **84**: 617–628.
- SINKER, C. A., PACKHAM, J. R., TRUEMAN, I. C., OSWALD, P. H., PERRING, F. H. & PRESTWOOD, W. V. (1985). *Ecological flora of the Shropshire region*. Shropshire Trust for Nature Conservation, Shrewsbury.
- SPENCER, J. W. & KIRBY, K. J. (1992). An inventory of ancient woodland for England and Wales. *Biological Conservation* **62**: 77–93.
- SYKES, M. T., PRENTICE, I. C., SMITH, B., CRAMER, W. & VENEVSKY, S. (2001). An introduction to the European Terrestrial Ecosystem Modelling Activity. *Global Ecology and Biogeography* **10**: 581–593.
- TANSLEY, A. G. (1939). *The British islands and their vegetation*. Cambridge University Press, Cambridge.
- TER BRAAK, C. J. F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167–1179.
- TRIST, P. J. O. (1979). *An ecological flora of Breckland*. EP Publishing, Wakefield.
- TRUEMAN, I., MORTON, A. & WAINWRIGHT, M. (1995). *The Flora of Montgomeryshire*. The Montgomeryshire Field Society, Welshpool.
- UK BIODIVERSITY GROUP. (1998). *Action Plan Volume 2: Vertebrates and vascular plants*. English Nature, Peterborough.
- WALTER, H. (1979). *Vegetation of the earth and ecological systems of the geo-biosphere*, 2nd ed. Springer-Verlag, New York.
- WALTHER, G.-R. (2000). Climatic forcing on the dispersal of exotic species. *Phytocoenologia* **30**: 409–430.
- WATKINSON, A. R., NEWSHAM, K. K. & FORRESTER, L. (1998). Biological Flora of the British Isles. *Vulpia ciliata* Dumort. ssp. *ambigua* (Le Gall) Stace & Auquier (*Vulpia ambigua* (Le Gall) More, *Festuca ambigua* Le Gall). *Journal of Ecology* **86**: 690–705.
- WHELDON, J. A. & WILSON, A. (1907). *The flora of West Lancashire*. Henry Young & Sons, Liverpool.
- WOLLEY-DOD, A. H. (1937). *Flora of Sussex*. K. Saville, Hastings.
- WOODWARD, F. I., ed. (1992). The ecological consequences of global climate change. *Advances in Ecological Research* **22**. Academic Press, London.

(Accepted October 2002)