Vegetation Description and Data Analysis

A Practical Approach

MARTIN KENT

SECOND EDITION

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VEGETATION DESCRIPTION AND DATA ANALYSIS

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A PRACTICAL APPROACH

Second Edition

Martin Kent

University of Plymouth

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This second edition is dedicated to my dear friend, academic colleague and former co-author, Paddy Coker, who sadly died in July 2005. His enthusiasm for and enjoyment of the subjects of plant ecology, vegetation science and computing are greatly missed.

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Preface to the second edition

The success of the first edition of this text was as much of a surprise to the authors as it was to both the publishers and its academic and scientific audience. The enthusiastic response demonstrated that there was a very clear need for a book that sought to simplify the complexities of vegetation description and multivariate analysis in the context of vegetation data and plant ecology. The first edition went through eight reprints and only went out of print in 2005. A second edition has been at the proposal stage for over ten years and it is only now, following retirement from mainstream academic life, that the author has found the time to develop the project further. Nevertheless, the need for such a text appears to be as great as ever.

In the 19 years since the publication of the first edition, a great deal has changed in the world of vegetation science and plant ecology. What is now one of the key journals in the subject, *Journal of Vegetation Science,* was only founded in 1990, two years before the publication of the first edition of this book in 1992. The sister journal *Applied Vegetation Science* only appeared in 1997. Numerous other journals relevant to the subject have evolved during the intervening years and the whole field of multivariate analysis has extended its application across the full range of ecological sciences. While actual methods and techniques have evolved only relatively slowly over this time, far more significant changes have occurred in the world of computer hardware and software. As the review of software in Chapter 9 of this new edition demonstrates, there are now numerous quite sophisticated packages available for vegetation data analysis, and a whole new approach has emerged at the research frontier using the R language and related packages.

Over the past 20 years, the use of methods of vegetation description and analysis has extended globally. Originally the province of a relatively small group of academics in the United Kingdom, Europe, North America and Australia, examination of the range of research locations of scientific papers published in *Journal of Vegetation Science* and *Applied Vegetation Science* clearly demonstrates that the scope and application of vegetation description and analysis by scientists and academics is now truly worldwide. One of the paradoxes of this is that during that same period, both plant ecology and vegetation science can only be described as having taken a back seat in the author's home country of the UK. This is partly because many of the most exciting avenues for research and exploration in vegetation science lie elsewhere on the globe, particularly in the tropics. A key theme of the new edition is to demonstrate and foster this worldwide perspective of the subject. This is a perspective that is all the more important because of the universal threats to biodiversity and the limited success of the numerous valiant efforts at biological conservation across the globe in the face of human exploitation and so-called development.

Lastly, the author would like to thank all those students, particularly those who have completed his Masters course in ecology and multivariate analysis at the University of Plymouth over the past 12 years, for their enthusiasm for and commitment to this subject. While the greater range and complexity of methods and of computer software today means that this text cannot possibly cover every aspect of the subject of vegetation science at the research level, ultimately, the purpose of this book is to introduce, simplify and explain quite complex things for the improvement of understanding and to assist with learning. I have never forgotten the comment of a very well-known vegetation research scientist, who came up to me at a conference after the publication of the first edition and told me in no uncertain terms that '*you should never have published that book – it makes things too easy for students and removes the mystique*'!! I knew from that moment onwards that the book had every potential to achieve its objectives and it is my fervent hope that this second edition manages to build even more successfully upon that achievement.

Martin Kent
Plymouth, UK
March 2011

Acknowledgements

Many people assisted in writing the first edition of this book. In particular Martin Kent would once again like to thank Dr Tom Dargie (private ecological consultant, Boreas Ecology – http://www.boreasecology.com/), who has always shared his enthusiasm and interest for the subject, Professor David Gilbertson (School of Geography, Earth and Environmental Sciences, University of Plymouth), Dr Ken Thompson (formerly of the Department of Biological Sciences, University of Sheffield) and Dr Peter Wathern (formerly of the Department of Biological Sciences, University of Aberystwyth, Wales), all of whom gave their support and encouragement. A good number of years ago, Dr Nicholas J. Cox of the Department of Geography at the University of Durham read the first edition of the text with an exceptionally trained and critical eye, noting the many small errors therein, and his corrections have helped greatly with this revision. I thank him for his efforts.

Martin Kent wishes to offer very special thanks to Professor Robin Pakeman of The James Hutton Research Institute (formerly the Macaulay Land Use Research Institute), Craigiebuckler, Aberdeen, Scotland, for his kindness and patience in carefully reading and correcting the manuscript of this new edition and making a number of very helpful suggestions for its improvement. Very particular thanks also go to Jamie Quinn of the Cartographic Resources Unit in the School of Geography, Earth and Environmental Sciences at the University of Plymouth, who redrew most of the original figures and diagrams, as well as many new ones. The volume of work became far more than either of us originally realised but, as the quality of the diagrams demonstrate, he has succeeded admirably. Dr Rana Moyeed of the Department of Statistics, Computing and Mathematics at the University of Plymouth deserves special mention for his tolerance of my many questions concerning statistical analysis relevant to the writing of the revision.

My very good friends, Professor Liquan Zhang of the State Key Laboratory for Estuarine and Coastal Research (SKLEC) and Dr Xihua Wang of the Department of Environmental Science, both from East China Normal University, Shanghai, kindly funded a study visit to China in September–October 2010, which acted as a catalyst for embarking on this second edition. I thank them both very warmly indeed. The University of Plymouth and particularly the School of Geography, Earth and Environmental Science have also provided invaluable support throughout the revision and in particular I would wish to thank my colleague Dr Ruth Weaver.

In truth, this edition would never have appeared at all, were it not for the dogged perseverance of a succession of editors at John Wiley and Sons (now Wiley-Blackwell), Keily Larkins, Rachael Ballard and most especially Fiona Woods. Fiona was the one who finally succeeded, and I offer very grateful thanks to you, Izzy Canning, Sarah Karim and your colleagues for all your hard work in seeing this second edition through to publication.

Finally, I owe an enormous debt of gratitude to my wife Gay for her infinite patience and support during the writing and revision of the book. It is also dedicated to our children Jonathan, Joseph, Holly and Kitty and her husband Ben, and to our grandchildren Sam and Tom.

Copyright and authorship of all figures and tables are acknowledged in the appropriate captions. The authors are grateful to Routledge publishers for permission to include diagrams from P. Gould and R. White (1986) *Mental Maps* in Chapter 6.

The author also wishes to thank Professors Bruce McCune and James Grace and MjM Software Design for permission to include material from McCune, B. and Grace, J.B. (2002) *Analysis of Ecological Communities*, MjM Software Design in Figures 4.1 and 6.23 and the 'Landscape Analogy' text for non-metric multidimensional scaling in Chapter 6. Dr. Peter Henderson of Pisces Conservation Ltd. is thanked for permission to present the data in Table 6.5. Dr. Jane Robbins (School of Animal, Rural and Environmental Sciences, Nottingham Trent University, UK) and Professor John Matthews (Department of Environment and Society, Swansea University, UK) kindly gave permission to use their research published in *Journal of Vegetation Science* and in *Arctic, Antarctic and Alpine Research* as a case study and Plate 1.2.

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School of Geography, Earth and Environmental Sciences
University of Plymouth, UK
March 2011

Safety in the field

All fieldwork is potentially dangerous, even when carried out in local, well-known areas. Precautions should always be taken and local safety codes adhered to. The following recommendations are important:

(1) Always obtain an up-to-date weather forecast.
(2) Take advice from local experts if in doubt.
(3) Be aware of potential health problems of any members of the party.
(4) Collect the addresses and telephone numbers of family or friends of every member of the party.
(5) Leave this information and details of the route to be followed with a responsible person at the base and an expected time of return.
(6) If possible, carry a mobile phone and a geographical positioning system (GPS) device but bear in mind that signals and reception may be weak or non-existent in remote areas.
(7) Never, ever, carry out fieldwork alone: a group of three or four leaves one or two people free to go for help, while a second person can stay with an injured or ill colleague.
(8) All members of the party should have had a tetanus injection. Always take note of travel advice relating to preventative inoculations and medicines in the fieldwork locality.
(9) Be extra careful in certain habitats such as wetlands, bogs and swamps. Working in the tropics carries special potential dangers.
(10) Be prepared for the worst that can happen in terms of bad weather or an accident. Responsible members of the party must be familiar with basic first aid and safety procedures. The following equipment is essential, depending on environment:

> suitable footwear (usually stout boots), appropriate clothing, waterproofs with hood, over-trousers, warm hat and gloves, sunhat and sunscreen, water, first aid kit, insect repellent, torch with batteries, whistle, emergency rations including glucose sweets, spare warm clothing and socks, survival blanket or lightweight tent, map and compass.

(11) The standard SOS signal for torches or whistles is three short signals, three long and three short.

In the United Kingdom, all those responsible for organising fieldwork and research overseas should be aware of the British Standard 8848 (2007) + Amendment 1 (2009) which provides clear guidelines for good practice. Similar documents and information exist in many other countries.

ACCESS

Always obtain permission from landowners, farmers and other relevant agencies before carrying out fieldwork on their land. By far the majority will gladly give permission provided it is requested before going onto their land.

DISCLAIMER

While every reasonable care has been taken, neither the author nor the publisher accept any liability for any injury, accident, loss or consequent damage, however caused, arising from this book or any information contained therein.

Chapter 1

The nature of quantitative plant ecology and vegetation science

THE NATURE OF VEGETATION

Dictionary definitions usually describe vegetation as ‘plants collectively’ or ‘plant growth in the mass’. To the plant ecologist and vegetation scientist, this definition is completely inadequate and perhaps conforms to the view of many students (and teachers and lecturers!), who see it as ‘a frightening and unknown mass of green, shrouded in technical terms and Latin Names’ (Randall, 1978: p. 3). This book is concerned with the techniques for both collecting and analysing data on vegetation with the primary aim of making sense of the ‘frightening and unknown mass of green’. As such, it is a text on quantitative plant ecology, which is a clearly recognisable subdiscipline of ecology and biogeography. The field of quantitative plant ecology is also related to an area of research known as vegetation science, which in addition to vegetation description and analysis, also includes plant population biology, species strategies and vegetation dynamics (successional processes and vegetation change) (van der Maarel, 1984a, 2005a,b). Most researchers and students take the phrase ‘vegetation description and data analysis’ to mean the collection of vegetation data, followed by analysis, usually using complex mathematical methods. However, in the 1980s and 1990s, there was a distinct tendency for the processes of analysis to become an end in themselves. An important aim of the previous edition of this book was to show that quantitative plant ecology and vegetation description and data analysis can and perhaps should be primarily ecological rather than mathematical in emphasis. The only way that variations in vegetation and plant species distributions can be properly understood and explained is within an ecological framework. This introduces the fundamental point that vegetation is always an integral part of an ecosystem (Tansley, 1935; Waring, 1989; Willis, 1997; Dickinson and Murphy, 1998; Leuschner, 2005) and can only be studied by fully exploring its role within that ecosystem. Vegetation cannot be isolated as a separate entity from the ecosystem within which it exists.

The building blocks of vegetation are individual plants. Each plant is classified according to a hierarchical system of identification and nomenclature using carefully selected criteria of physiognomy and growth form. The individuals of a species, taken together, form a species

Vegetation Description and Data Analysis: A Practical Approach, Second Edition. Martin Kent.

population, and within the local area of a few square metres to perhaps as much as a square kilometre, groups of plant species populations that are found growing together are known as plant communities or plant species assemblages. Much more will be said of plant communities and species assemblages later in Chapter 2, but within plant communities, the presence or absence of particular species is of primary importance. After this, the amount or abundance of each species present is of interest. Although most vegetation data are still collected at the species level, one of the more interesting developments of the past 20 years has been in alternative methods of describing vegetation, such as plant functional types and taxonomic, morphological and structural surrogates (Ramsay *et al*., 2006). This book is concerned with reasons and methods for collecting data of these kinds, and with techniques for their analysis.

The importance of vegetation within ecology is three-fold. Firstly, in most terrestrial parts of the world, with the exception of the hot and cold deserts, vegetation is the most obvious physical representation of an ecosystem. When ecologists talk about different ecosystem types, they usually equate these with different vegetation types and the dominant species life-forms within them. Secondly, most vegetation is the result of primary production, where solar energy is transformed through photosynthesis by different plant species into green plant tissue. The net primary production, which is the amount of green plant tissue accumulated within the area of a particular vegetation type over a given period of time, represents the base of the trophic pyramid. All other organisms in both the grazing and detrital food webs are ultimately dependent upon that base for their food supply. Thirdly, vegetation also acts as the habitat within which the organisms live, grow, reproduce and die. In the case of the grazing food web, it is among the above-ground parts of plants. With the detrital web, it is on the surface and below ground among the roots. Taken together, these three points show the central importance of vegetation to ecology and demonstrate the need for methods to assist with both description and data analysis (Anderson and Kikkawa, 1986; Cherrett, 1989; Barbour *et al*., 1999; van der Maarel, 2005a,b).

WHY STUDY VEGETATION?

There are many situations where vegetation merits study. The commonest examples of the use of vegetation description are in the recognition and definition of different vegetation types and plant communities, which is known as the science of phytosociology, the mapping of vegetation communities and types, the study of relationships between plant species distributions, environmental controls and their interactions with humans and animals, and the study of vegetation as a habitat for animals, birds and insects. Change in vegetation over time may also need to be described using concepts of succession and climax.

Information on vegetation may be required to help to solve an ecological problem, for biological conservation and management purposes, as an input to environmental impact statements, to monitor management practices, or to provide the basis for prediction of possible future changes in plant species distributions and linked to both human impacts on habitats via land use practices and also climate.

A useful distinction is into aspects of study that are academic, as opposed to those which can be termed applied. In the academic case, vegetation may be described and data analysed largely for their own sake. Applied studies are where vegetation data are collected and analysed with the aim of providing information of relevance to some ecological problem, often to do with environmental conservation and ecosystem management or the prediction of future environmental and ecological change. Many examples of research include elements of both.

CASE STUDIES

Throughout this book, many different examples of the application of methods for the description and analysis of vegetation will be presented. A brief introduction to four contrasted case studies serves to demonstrate the diversity of situations where vegetation may need to be surveyed and data collected and analysed.

Case Study 1: Evergreen broad-leaved forest in Eastern China: its ecology and conservation and the importance of resprouting in forest restoration (Wang **et al.***, 2007)*

Evergreen broad-leaved forest (EBLF) is now recognised as an important global vegetation formation type that contributes to both the biodiversity and the sustainable development of the subtropical regions of China. Discussion of the forests is omitted in Archibold (1995), although they are mapped as EBLF in the more recent overview of world vegetation types by Box and Fujiwara (2005). While its biogeographical status in China still remains a matter of debate, unfortunately, the extent of the EBLF has decreased very significantly due to long-term anthropogenic disturbance, including deforestation, logging and fire, and much of the forest is now degraded to plantation, secondary forests, shrub and grassland communities. Song (1988, 1995) provided the most valuable review in English of both the position of the Chinese EBLF within the world vegetation formation types and the overall characteristics of the forest. In China, it occurs between 24°–32°N and 99°–123°E and formerly covered around 25% of the area of the country (Figure 1.1). It lies within areas dominated by a subtropical monsoon climate and the forests occupy mountainous and hilly areas across the south and east of China (Plate 1.1). The forests are extremely diverse, particularly in terms of tree and shrub species (phanerophytes 50–80% of species – see Chapter 3), ranging from over 100 vascular plant species/400 m^2 in the south, to 30–45 species in the north of its distribution (Song, 1988). The dominant species of the EBLF come from only a few genera, together with some ancient coniferous species, many of which have ‘broad leaves’.

To inform forest conservation and management, Wang *et al*. (2007) described research into major plant community types and underlying environmental gradients (see Chapter 2) of degraded EBLF around Tiantong and Dongqian Lake near Ningbo in Eastern China (Figure 1.1; Plate 1.1), and examined the importance of vegetative resprouting as a key mechanism in secondary succession following forest clearance. Species composition was described from 199 10 m × 10 m plots (Chapter 3) and analysed using various methods presented later in this book (Two-Way Indicator Species Analysis [TWINSPAN] – Chapter 8; and canonical correspondence analysis [CCA] ordination – Chapter 6). Some 22 degraded and mature forest community types were identified, while CCA indicated that a primary vegetation gradient was related to the distance of sample plot from mature forest, which was closely linked to altitude and slope. The secondary gradient corresponded to successional stage and disturbance. The roles of resprouting and reseeding characteristics in forest regeneration were researched firstly by 10 m × 10 m plots taken from selected TWINSPAN groups, and secondly by 20 m × 20 m plots in representative areas of forest at different ages – 1, 20, 43 and 60 years, and in an area of mature forest – 100+ years.

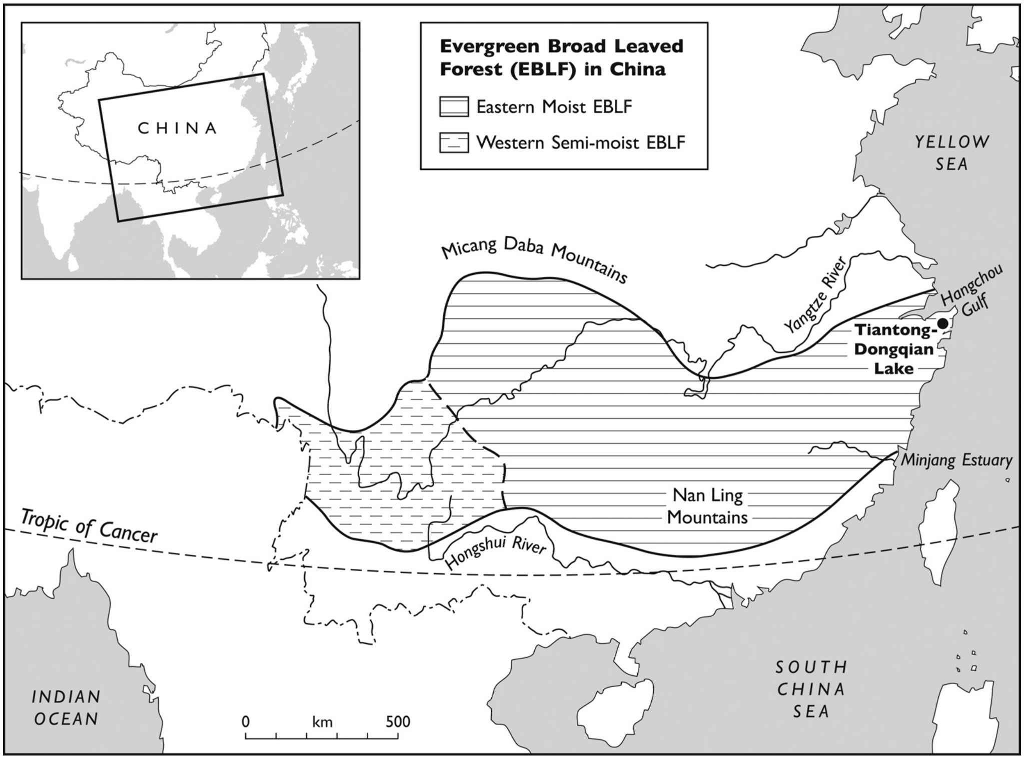

Figure 1.1 The distribution of evergreen broad-leaved forest (EBLF) in China and the separation of forest into the Western semi-moist and Eastern moist forest types (after Song, 1988; Wang *et al*., 2007: reproduced with kind permission of Elsevier).

The importance of resprouting in the regeneration of many EBLF tree and shrub species was demonstrated, a process linked to ideas of the persistence niche – resprouting from stumps is an important means of persistence for many species. Existing remnant forests should be conserved, but forest restoration is also essential and will benefit from understanding of the importance of tree/shrub resprouting, as well as seedling recruitment in forest regeneration. Further work is in progress on seedbanks, germination success and both inter- and intra-specific competition within Chinese EBLF to assist with successful conservation and management of this rare forest type (Chapter 6 – Case studies).

Case Study 2: Pioneer vegetation on glacier forelands in southern Norway (Robbins and Matthews, 2009, 2010)

Climate change and its ecological impact is one of the most important and also controversial environmental topics at the present time. A widely observed phenomenon in Europe and Scandinavia over the past 100 years has been the retreat of mountain glaciers in response to increased summer temperatures and relatively low winter precipitation, and Nesje *et al*. (2008) have predicted that up to 98% of Norwegian glaciers may have disappeared by 2100. Robbins and Matthews (2009) saw the retreat of such glaciers as a valuable opportunity to study the earliest stages of vegetation colonisation (primary succession) and the manner in which plant species are responding the availability of new terrain on glacier forelands (Plate 1.2). They were concerned firstly to examine the species composition of early pioneer stages, and secondly to see whether these highly disturbed sites are colonised by consistent sets of species or whether species composition is more dependent on chance (stochastic) factors that tend to produce more random and variable collections of species. McCook (1994), Walker and del Moral (2003), Pickett and Cadenasso (2005) and Pickett *et al.* (2008) present the most recent reviews of processes of primary succession.

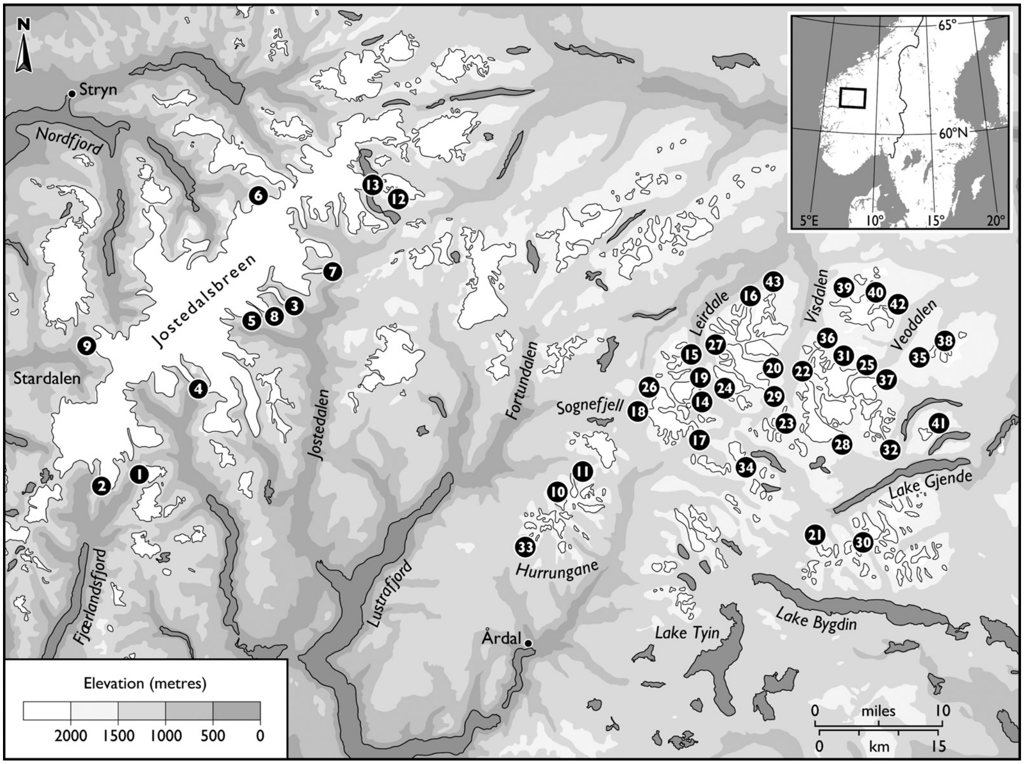

Figure 1.2 The locations of the 43 glacier forelands in southern Norway studied by Robbins and Matthews (2009, 2010). Redrawn and reproduced with kind permission from Wiley-Blackwell.

A total of 43 glacier forelands in the Jotunheim and Jostedalsbreen regions of southern Norway, with an altitudinal range of 80–1860 m, were sampled (Figure 1.2). The vegetation data were collected in a particularly interesting manner, using rectangular quadrats for contiguous (adjacent) sampling along transects away from the glacier snout in each case. The detail of this is presented in a case study at the end of Chapter 3. In addition to the vegetation data, two regional explanatory environmental variables were collected at each quadrat, altitude and distance eastwards from a fixed reference point, representing a continentality index. Earlier surveys had also examined more local habitat factors, such as snow distribution, microsite conditions, and measures of the randomness of points of initial colonisation (stochasticity) (Whittaker, 1989, 1991).

As with the Chinese case study above, data analysis involved techniques of multivariate analysis – numerical classification using a form of similarity analysis known as flexible-β followed by use of a multi-response permutation procedure (MRPP) (see Chapter 8) and ordination using non-metric multidimensional scaling (NMS) (McCune and Grace, 2002) (see Chapter 6). An example NMS ordination plot, displaying the results for 42 sites, with four classification groups superimposed is shown in Figure 1.3. This type of plot is fully explained in Chapter 6.

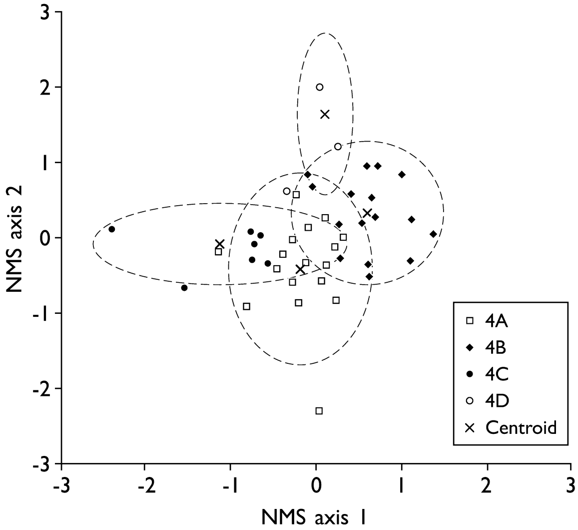

Figure 1.3 Non-metric multidimensional scaling (NMS) ordination plot of the 42 glacier foreland sample sites with four numerical classification groups superimposed. One site was removed due to a complete absence of vegetation in the pioneer zone. Redrawn and reproduced with kind permission from Wiley-Blackwell.

The key result of the research was that the vegetation could be seen as one broad vegetation type characterised by *Poa alpina* (Alpine meadow grass) and *Oxyria digyna* (Mountain sorrel), indicated in general terms by the overlapping of the classification group circles on Figure 1.3 (see Chapter 8). Nevertheless, within this overall group, there was a high degree of variability, but two emerging subcommunities could be identified and these were shown to be linked to both site altitude and continentality. Whereas the very earliest stages of colonisation could be said to be highly stochastically determined (i.e. by randomness and chance), the beginnings of the organisation of changes in species composition into two successional pathways could be observed. There are many interesting features to this work, including the regional scale of vegetation description, the underlying model of vegetation change and dynamics, the sampling design and its relevance to the topic of vegetation response to climate change.

Case Study 3: Vegetation description and data analysis to inform the conservation of a rare plant species – **Lobelia urens** *L. (the heath lobelia) in southern England (Dinsdale* **et al.***, 1997, 2000)*

The successful conservation of rare plant species usually requires a range of information and scientific research linked to both the autecology (the study of a single species in relation to its ecology and environment) and synecology (the study of a community of species in relation to their ecology and environment) of the species involved in order to assist with management practice. *Lobelia urens* L. (the heath lobelia) (Plate 1.3) is a perennial rhizomatous herb that shows a Lusitanian distribution in Europe and North Africa extending from Morocco, Madeira and the Azores in the south, along the Atlantic coast through Portugal, Spain and France, as far north as Belgium. However, in the UK, at the extreme north of its range, *L. urens* is today limited to six locations in the southern coastal counties of England, although historical records indicate that it may have been found on 19 sites altogether. Dinsdale *et al*. (1997) surveyed the historical and documentary evidence for its distribution and completed extensive botanical surveys to try to understand the plant communities and species assemblages within which it grows (its phytosociology) and to assess both environmental controls and limitations on the species.

At the six remaining sites in southern England, a total of 95 0.5 m × 0.5 m quadrats, containing 122 plant species, were recorded, using a Domin abundance scale and a carefully devised sampling strategy (see Chapter 3). Data on 16 environmental variables were also collected (Table 1.1) in order to summarise the environmental variability and the factors possibly limiting its distribution. Analysis of the data for phytosociological purposes involved using the numerical classification method called Two-Way Indicator Species Analysis (TWINSPAN: Hill, 1979b) (see Chapter 8), while the floristic variation and correlations with the environmental variables in the 95 quadrats were assessed using the method of ordination known as canonical correspondence analysis (CCA) (ter Braak, 1986a, 1987, 1988a,b) (see Chapter 6).

Table 1.1 The 16 environmental variables measured in the survey of *Lobelia urens* L. (the heath lobelia) at six sites in southern England (Dinsdale *et al.*, 1997). Reproduced with kind permission of Wiley-Blackwell.

Microclimate and habitat	Soil variables
1. Height of dominant vegetation (cm)	8. Soil texture (6-point ordinal scale)
2. Slope (degrees)	9. Soil structure (4-point ordinal scale)
3. Bare ground (% cover; 5-point Domin scale)	10. Soil calcium (mg/cm^3)
4. Litter cover (% cover; 5-point Domin scale)	11. Soil sodium (mg/cm^3)
5. Litter type (5-point ordinal scale)	12. Soil magnesium (mg/cm^3)
6. Microtopography (5-point ordinal scale)	13. Soil phosphorus (mg/cm^3)
7. Exposure (5-point ordinal scale)	14. Soil pH
	15. Organic matter (g/cm^3)
	16. Moisture content (g/cm^3)

This research, as with the previous two case studies, demonstrates a common feature of vegetation and ecological survey, in that very large quantities of data on both vegetation and associated environmental variables are often collected. Such data are described as *multivariate*, because they contain information on many species and many environmental factors or variables. Most of the methods of data analysis described later in this book are designed to look for order and pattern within these types of data.

The first part of the data analysis involved numerical classification of the 95 quadrats using TWINSPAN and resulted in six groups of quadrats (A–F) that were each characterised in terms of their within-group species composition and were taken as representing the range of plant community types within which *L. urens* occurs (Table 1.2). The important next step, however, was to enter the quadrats into another computer program, TABLEFIT (Hill, 1989, 1991), which compares the species composition of the quadrats within each of the groups with a large database of sample quadrats from recognised key vegetation types in the British Isles, as defined in the National Vegetation Classification (NVC) (Rodwell, 1991, 1992a,b, 1995a, 2000, 2006). The NVC is described in more detail in the case studies of Chapters 3 and 8. Use of the NVC enabled each of the six groups A–F to be matched with their nearest key vegetation types in Britain, each of which is characterised by a code, such as M25, W25 or H3.

Table 1.2 The six Two-Way Indicator Species Analysis (TWINSPAN) groups (A–F) resulting from numerical classification of the 95 quadrats in the *L. urens* survey matched with their nearest vegetation types in the British National Vegetation Classification (NVC) (Dinsdale *et al.*, 1997). Reproduced with kind permission of Wiley-Blackwell.

TWINSPAN group	NVC group
A	M25 – *Molinia caerulea–Potentilla erecta* mire
B	M25c – *Molinia caerulea–Potentilla erecta* mire
C	W23 – *Ulex europaeus–Rubus fruticosus* scrub W25 – *Pteridium aquilinum–Rubus fruticosus* under scrub
D	M25 – *Molinia caerulea–Potentilla erecta* mire H3 – *Ulex minor–Agrostis curtisii* heath
E	W23 – *Ulex europaeus–Rubus fruticosus* scrub W25 – *Pteridium aquilinum–Rubus fruticosus* under scrub
F	W23 – *Ulex europaeus–Rubus fruticosus* scrub

In the second part of the data analysis, the results of the ordination using canonical correspondence analysis (CCA) are shown in Figure 1.4. The way to interpret this plot is explained fully in Chapter 6. However, the scatter of points on the ordination plot shows that the six sites where *L. urens* occurs are environmentally heterogeneous and there was no obvious limiting response to many of the environmental variables. However, soil texture, microtopography, soil moisture and soil structure were all shown to be extremely important because they are represented by the longest arrows on the plot. Taken together, these were seen as indicators of the importance of microhabitat linked to disturbance, particularly related to the availability of suitable sites for germination of *L. urens* seed.

Thus a new set of hypotheses related to a new research project were established, whereby using both field survey methods and experimental seed beds, the germination and survival rates of *L. urens* seeds and seedlings were measured in great detail and linked to microhabitat conditions (Dinsdale *et al.*, 2000). Depressions in the soil and seedbed created by grazers were shown to encourage the most successful germination which was assisted further by the presence of moss, although also probably impaired

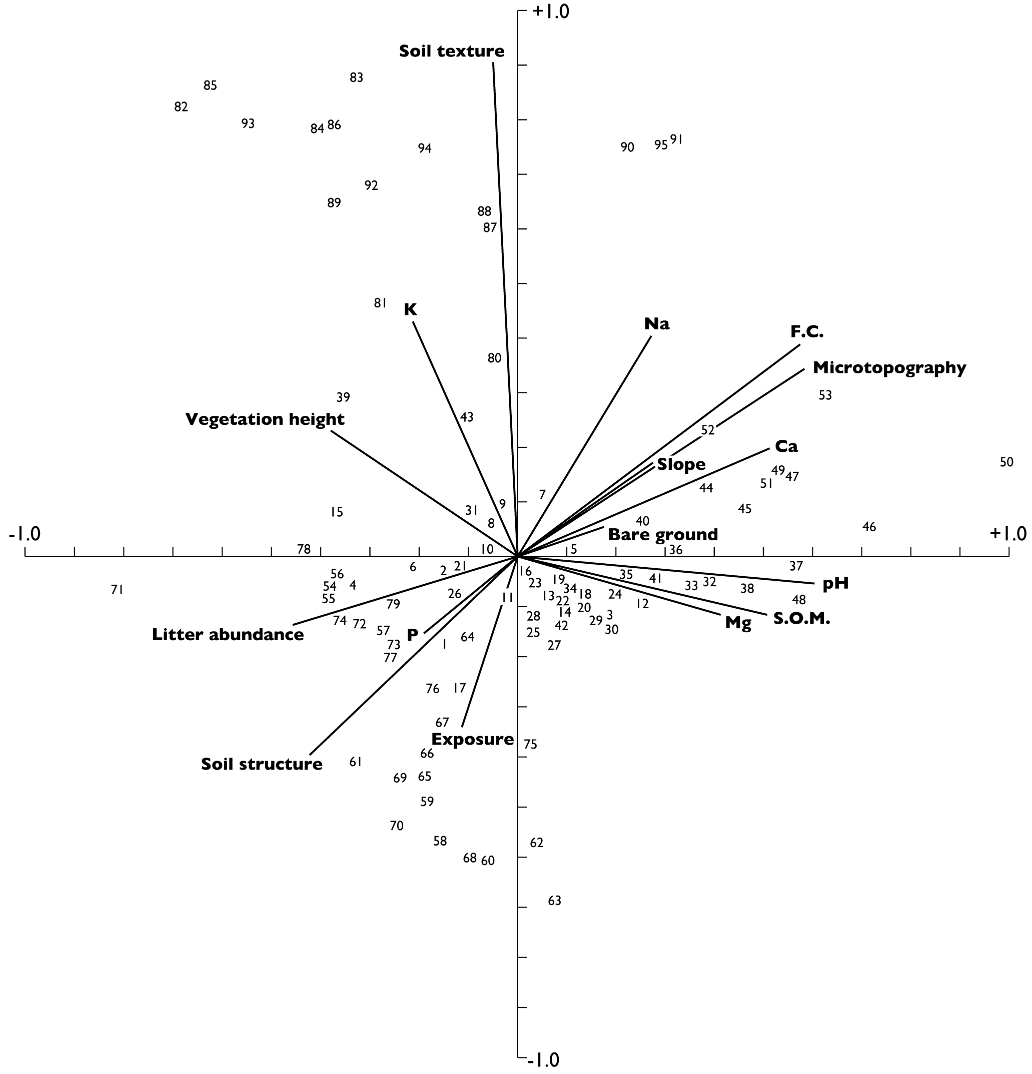

Figure 1.4 A CCA sample–environment biplot of the 95 quadrats collected from six sites in southern England (Dinsdale *et al*., 1997). Redrawn and reproduced with kind permission of Wiley-Blackwell.

by any significant accumulations of litter. These results had considerable significance in that producing the right microhabitat conditions for germination in conservation management is vital for the future survival of the species.

There are numerous interesting aspects to this work. The focus on a single rare species, the sampling design and the matching of community types to a national vegetation classification are important. However, perhaps most important of all is how the use of an initial descriptive survey of vegetation and environmental factors followed by multivariate data analysis led to the generation of new hypotheses and further research on the germination characteristics of the species, linked to microhabitat conditions. The importance of large-scale vegetation description as a precursor to much more focused and detailed research is emphasised later in this chapter.

Case Study 4: The grazing ecology of the Serengeti grasslands (Anderson et al.*, 2007; Augustine and McNaughton, 2004; McNaughton* et al.*, 1998; McNaughton, 1983, 1985)*

This case study is the only one that has been retained from the first chapter of the first edition of this book. The reasons are two-fold. Firstly, it concerns the tropical grasslands or savannas of the world, which comprise one of the most important and extensive world vegetation formation types and a world biome. Such grasslands are predominantly composed of grass and herb species but often have a significant tree component. The factors determining the status of savanna vegetation have long been a matter of debate. Seasonality of climate, fire, grazing, edaphic or soil factors and geomorphology have all been described as of importance in the origin and maintenance of the vegetation (Huntley and Walker, 1982; Boulière, 1983; Boulière and Hadley, 1983; Cole, 1986, 1987; Archibold, 1995; Mistry, 2000).

Secondly, the work of McNaughton on savanna environments represents an excellent example of the manner in which a research agenda in vegetation ecology develops over time. The following main section of this case study is taken from the original summary of McNaughton's 1983 and 1985 papers.

The Serengeti takes its name from the Masai word for a broad open plain and is situated on the border between Kenya and Tanzania, stretching from Lake Victoria in the west to the volcanic Crater Highlands in the east (Figure 1.5). The Serengeti is famous for its fauna, both the large herds of ungulates such as the wildebeest and zebra (Plate 1.4) which roam the open plains, as well as its carnivores, including lions, cheetahs and jackals. According to McNaughton, three distinct subregions are identified: (a) the open Serengeti Plains of the southeast; (b) the Western Corridor which is used by grazers during seasonal changes and whenever rain falls on the Serengeti Plains during the wet season; and (c) the north, which is used by migrants at the height of the dry season. The greater part of the plains area is included within two national parks which have been established largely to protect the fauna: the Serengeti National Park in Tanzania and the Masai Mara Game Reserve in Kenya.

McNaughton made the point that prior to his work in the Serengeti, most studies of tropical grassland had been based on descriptive observation and physiognomic classification – description by growth or life form (see Chapter 3). Such studies had often been made in relation to soils and to the distributions of the large herds of ungulates that are characteristic of the biome (Archibold, 1995; Mistry, 2000). Detailed quantitative studies of plant community structure (species composition and association or groupings of species growing together at the same location) were virtually absent. At the start of his original article, McNaughton posed several questions concerning community structure in the vegetation:

(1) Are there repeating combinations of species and community types that occur more or less frequently?
(2) Are there consistent patterns of species abundance and diversity that provide insight into community organisation?

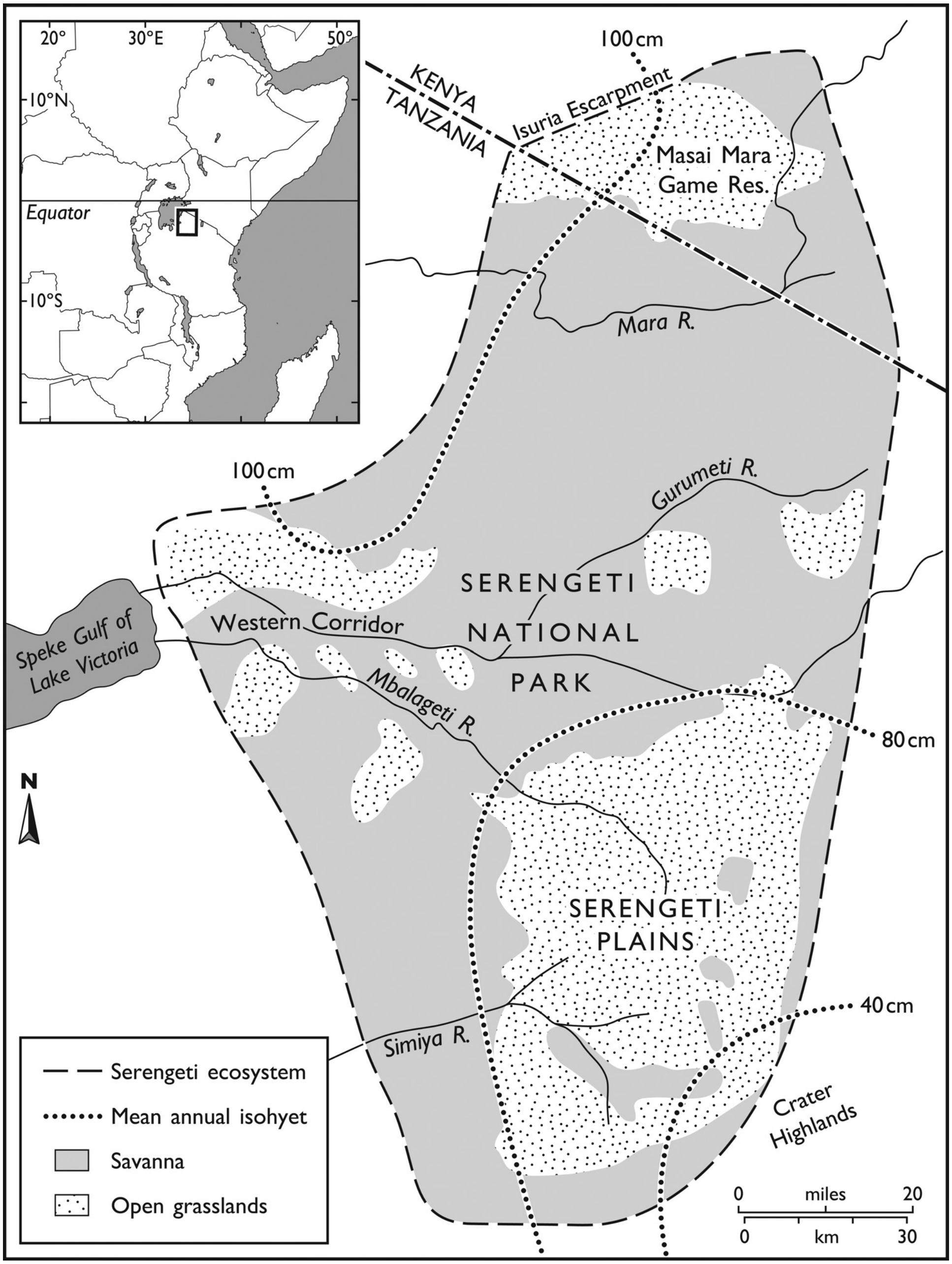

Figure 1.5 The Serengeti Plains of Kenya and Tanzania (McNaughton, 1983). Modified and redrawn with kind permission of the Ecological Society of America.

(3) How important is spatial heterogeneity (local variation of plant communities in space) and what is its role in community organisation?
(4) What environmental factors influence species abundance, spatial distribution and community organisation?
(5) If consistent patterns of community properties and environmental relationships exist, why have they developed and what can be inferred from them about the mechanisms and functional consequences of community organisation?

These questions are typical of those asked at the start of a great deal of work in vegetation science; in many parts of the world, rigorous description of vegetation has only comparatively recently been completed or has yet to be attempted.

Although this research could be seen as primarily academic in emphasis, there were also a number of applied reasons for carrying out the survey. Following control of rinderpest, an acute viral disease of various ungulates and cattle, the population of grazing animals, particularly wildebeest, had increased dramatically from c. 220,000 wildebeest in 1961 to c. 1.4 million in 1977. The scale and extent of burning had declined following the designation of the greater part of the area as a national park. Elephants, which were only reintroduced to the Serengeti in 1951, had undergone a population explosion and were causing much damage to vegetation by uprooting trees and laying waste large areas around vital waterholes in the dry season. All of these factors undoubtedly were exerting serious and often detrimental effects on the grassland ecosystems and community structure.

For all these reasons, McNaughton proceeded to select 105 sites within both national parks to sample the vegetation. Detailed aspects of sampling are described in the papers and the data were analysed once again by methods of ordination and classification as described in Chapters 6 and 8. In the final analysis, 17 different community types could be recognised, largely characterised by perennial grasses. Examination of environmental controls demonstrated that, while rainfall and seasonality were significant in separating different community types, grazing intensity was critical, with a secondary gradient being attributable to soil texture.

At the end of the paper, there is an excellent discussion of where vegetation research should go on to from the results of the survey. McNaughton argued that formulation of hypotheses and design of experiments to quantify the exact effects of grazers within each of the vegetation types is necessary. However, there are many other questions that might be asked:

(a) What is the species composition of the grassland and particularly its local spatial variation?
(b) What are the phenological strategies of the grasses (how does each species time the major events of its life (existence as a seed or vegetative rhizome, germination, growth and leafing, flowering, fruiting, death)?
(c) Is there an overlying tree canopy? How dense is it and what is its impact on the underlying vegetation?
(d) What are the grazing species and what are their densities? Do they preferentially graze certain species at certain times of the year?
(e) Has the vegetation been burned lately? If so, how often and how extensively?
(f) Is the soil wet or dry? What are the detailed chemical and physical properties of the soils and how are they related to the grazing regime?

Since the mid-1980s and the publication of the original papers, McNaughton and his various research teams have published over 100 papers related to research on savanna environments, many of which are directly related to the questions and hypotheses outlined above. A search of the Google Scholar database or the Web of Science or Scopus databases available in many university libraries will reveal the range of papers – good examples are Anderson *et al*. (2007), Augustine and McNaughton (2004) and McNaughton *et al.* (1998). Careful reading of these papers will show that many of these questions have been answered but many more remain and require careful thought, hypothesis generation and experimentation (Figures 1.6 and 1.7) to be answered. A further problem is that many of these questions overlap; for example, are the effects of grazing or burning the same on different soil types?

In summary, McNaughton's work demonstrates how a relatively thorough and complete survey of the vegetation of an area in response to one set of aims and objectives generates even more questions which may require many more years of detailed experimental ecology in order to be answered. Having completed this primary survey of vegetation community types and environmental factors in the 1980s, over the next 20–30 years, McNaughton also went on to examine many aspects of primary productivity of vegetation and soil nutrients in relation to grazing, and this work in turn demonstrated the importance of vegetation as both food supply for higher trophic levels and as a habitat for both herbivores and carnivores.

THE SCIENTIFIC APPROACH

Induction and deduction

As with all aspects of science, vegetation description and analysis must be approached in a logical and systematic fashion. All vegetation description and analysis must have a purpose. Nevertheless, there are many different approaches to vegetation study. The collection and analysis of vegetation data provides the principal form of ecosystem description and classification. However, simply to describe and observe patterns of variation in vegetation data over space is not the sole aim of vegetation science. A further very important concept is the idea of explanation. Explanation is the attempt to answer the question 'Why?'. 'Why is one area of vegetation different to another?' 'Why are certain plant species found in some locations but not in others?' 'Why do certain vegetation types appear to be undergoing change – due either to natural processes of succession or to human-induced effects?' 'Why is the vegetation of a particular area under stress and showing signs of damage or disease?'

To attempt to answer these kinds of questions and find explanations, we have to have some view or theory of the manner in which the world functions. For any part of science, there is always an existing body of knowledge and theory, which is generally accepted at the time. Often this initial body of knowledge has been collected by a process known as induction (Figure 1.6a). With induction, the data are collected without formulation of prior hypotheses (descriptions of existing notions of how the ecological world functions) or any preconceived ideas, and explanations are then derived from the data collected. Ideas of induction date from Frances Bacon back in the early seventeenth century and John Stuart Mill in the nineteenth century. They argued that one can only start to make valid explanations once all the necessary facts and information relevant to the situation have been collected. Such data were thought to be particularly secure, because the

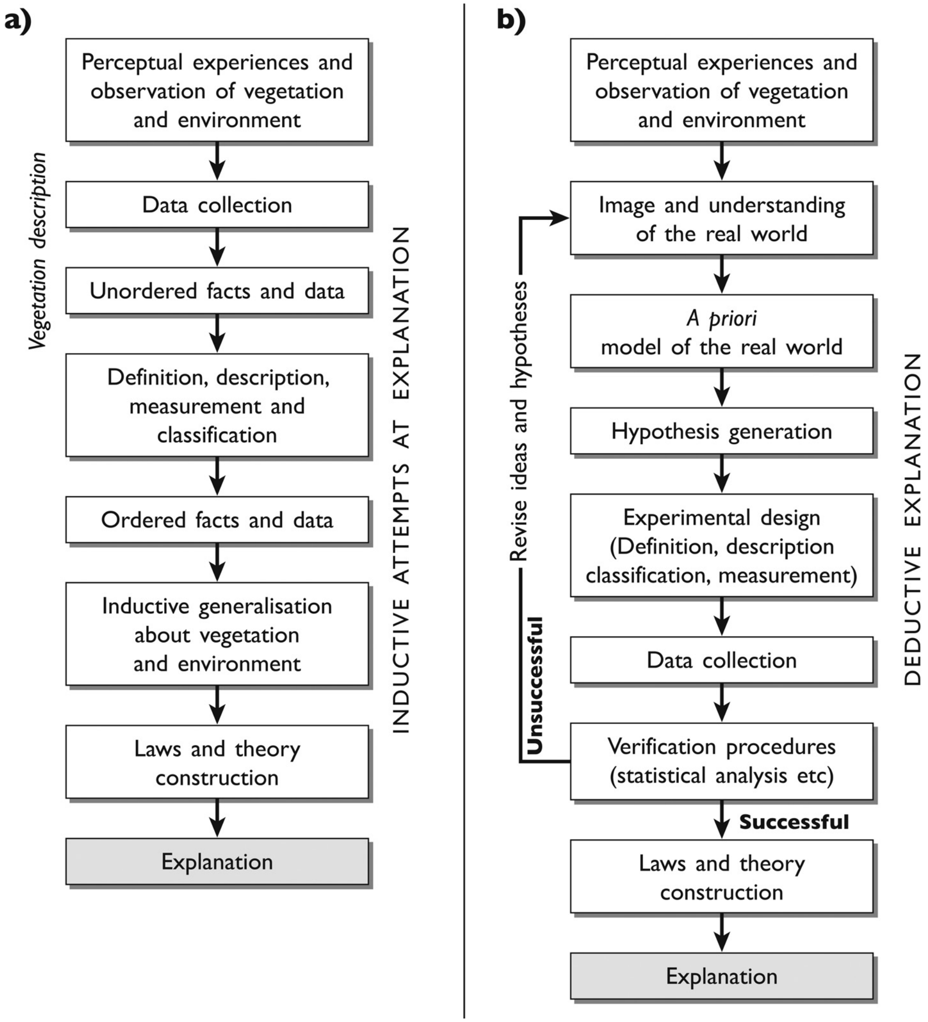

Figure 1.6 (a) Inductive and (b) deductive approaches to scientific enquiry. Reproduced with permission from John Wiley & Sons, Inc.

collection and ordering of facts for their own sake are not based on any biased or selective guesses or hypotheses. The problems of the inductive approach are many and particularly centre on the inefficient process of collecting a large amount of data which may not be immediately (or even eventually) relevant or useful and which cannot ever prove convincingly a theory or hypothesis.

On the basis of this existing knowledge and theory, a scientific approach may often involve the generation and testing of hypotheses concerning observed variations in vegetation cover and their causes. This is usually known as the deductive approach (Figure 1.6b). The sequence of activities as shown in Figure 1.6b is commonly described as ‘scientific method’. The method involves setting up both null and alternative hypotheses (described fully in Chapter 5) and is often also described as the null hypothesis testing (NHT) approach. It follows a rational and logical sequence of thought processes and actions. Most scientists would probably subscribe to that view and are thus known