PLANT ECOLOGY

EDITED BY Michael J Crawley

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This book is dedicated to
the memory of
E.J.SALISBURY FRS &
H.A.GLEASON
two of the founders of
modern plant ecology

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Preface

This book is about the factors affecting the distribution and abundance of plants. It aims to show how pattern and structure at different levels of plant organization (communities, populations and individuals) are influenced by abiotic factors like climate and soils, and by biotic interactions including competition with other plants, attack by herbivorous animals and plant pathogens, and relationships with mutualistic organisms of various kinds. One further aim has been to convey something of the excitement and dynamism of modern plant ecology. For too long the subject has been regarded as the poor relation of animal ecology. It has been transformed over the last two decades into a veritable growth industry, thanks chiefly to the inspiration of John Harper, and to the wide dispersal of the students he trained.

The present work differs from other textbooks on plant ecology in stressing dynamics rather than statics, and by espousing an experimental rather than a descriptive methodology. Throughout the book, the patterns of plant abundance which we see in the field are interpreted as the outcome of dynamic processes involving gains and losses. For example, we view the species richness of communities as the resolution of immigration and extinction, population density as the balance of recruitment and mortality within single species, and the size of individual plants as the result of births and deaths of modular component parts.

This book is based on a plant-centred view of ecology rather than the traditional, quadrat-centred view. Traditional quadrat-based measures like 'percentage cover' consign individual plants to oblivion, and discourage thinking about the evolutionary ecology of individuals. Quadrat based tests of association may detect positive statistical associations between species, even when the individual plants of the two species never grow next to one another, and never influence one another's population dynamics! The plant-centered view of ecology is intended to rectify some of these defects by focusing attention directly on the interactions between a plant and its immediate neighbours, and between plants and their mycorrhizal associates, pollinators and natural enemies. Throughout the book we are at pains to stress that our ultimate objective is to measure the impact of the processes we describe on the *fitness* of individual phenotypes (difficult though we recognize this task to be).

If there is a single philosophical strand running through the following chapters, it is this: 'seek simplicity but distrust it' (Lagrange). Our approach to ecology is to develop theory by the recognition of patterns in the field and the development of simple models to describe them. As Lewontin and Levins have said, only slightly tongue-in-cheek, 'Things are similar—this makes science possible. Things are different—this makes science necessary'! The role of theory in ecology is rather different than in some other sciences. It is not, for example, intended to make accurate predictions, as in astronomy or physics. Rather it attempts to separate the expected from the unexpected, the possible from the impossible and the surprising from the unsurprising (Lewontin). In the past, however, plant ecologists have tended to emphasize the complexity of ecological systems and to decry simple, theoretical models as being naïve and unrealistic. So prevalent, indeed, is this viewpoint amongst practising ecologists, that it has now been elevated to the position of a formal school of thought. During a recent botanizing trip to a species-rich area of serpentine soils, we had recourse to the local botanists' guide book. It promised enlightenment of the most profound kind. It began 'the factors responsible for the richness of the serpentine flora are . . .' we held our breath in anticipation . . . 'many, complex and interacting'. On that day the 'MC&I School' of ecology was born. Many and various have been its subsequent publications!

Of course this is not the only modern school of plant ecologists. Other recognizable disciplines include the 'Nothing's Happening School' (who believe in null models, random processes and non-equilibrium communities), the Biochemical Ecologists (the 'Find 'em and Grind 'em School'), the Mathematical Modellers (quantifying the bleeding obvious), the Agricultural Ecologists (spray and pray), and the Phytosociologists (ignore that plant, it shouldn't be here). There are as many schools of thought represented in this book as there are different contributors to it. Your editor, however, is a confirmed adherent to the Experimentalist School who 'suck it and see'!

The layout of the chapters is upside down in terms of the conventional, atom–to–universe textbook. I have chosen to begin with communities and work progressively downwards through populations and individuals for three reasons. First, it is with communities that we gain our initial impressions of plants and of plant ecology. Second, the theory of community ecology is relatively straightforward, so the theoretical material becomes more, rather than less challenging as the book goes on. Third, it makes a change!

It is worth pointing out explicitly what the book is *not* about. First and foremost, it is not about ecological methods. There is a vast literature on methodology which we have made no attempt to précis.

Students would do well to study carefully the problems of sampling plant populations, and to acquaint themselves with the statistical analysis and presentation of data. Only then, perhaps, should the more rarified quantitative methods like pattern analysis and the plethora of multivariate techniques be addressed. Three particularly good introductory papers for those about to embark on ecological experimentation are Lewontin (1974), Hurlbert (1984) and Bender, Case & Gilpin (1984). Other important aspects of plant ecology not covered by this book are micrometeorology, soil science, plant anatomy, plant physiology, plant evolution, plant geography and ecological biochemistry. Not only do these fields provide vital background information, but they also afford a variety of different perspectives from which plant ecology can be viewed.

Finally I should like to thank the many people who have helped in the preparation and production of this book.

Ascot, 1985 Michael J. Crawley

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Chapter 1 The Structure of Plant Communities

MICHAEL J. CRAWLEY

1.1 Introduction

The stature, colour and texture of plants give landscape its unique character. As Darwin wrote, a 'traveller should be a botanist, for in all views plants form the chief embellishment'! The cast of the vegetation's features (its physiognomy) is determined by the size of the dominant plants (whether they are trees or bushes, herbs or mosses), by their spacing (whether they form continuous cover or are widely spaced-out), and by their seasonal prospect (whether the plants are deciduous or evergreen, and whether they undergo striking seasonal colour changes).

The first generation of plant ecologists (Warming, 1909; Raunkiaer, 1934) dedicated themselves to understanding why certain structures of vegetation are restricted to certain combinations of climate and soil. While these problems are far from resolved, modern plant community ecologists are occupied by questions involving species richness (why do so many (or so few) species of plants grow here?), species abundance (why is a single species dominant in one place, but many species co-dominant in another?), and patterns of spatial and temporal change (what determines the observed gradients in species composition we see as we climb up a mountain side, and what factors influence the succession of species we observe after disturbance?). The purpose of this chapter is to introduce the various structural attributes of plant communities, and Chapters 2 and 3 will consider the dynamics of how these patterns come about.

1.2 The definition of plant community

The plant 'community' is an abstraction of exactly the same kind as the 'population'; a community simply consists of all the plants occupying an area which an ecologist has circumscribed for the purposes of study. This definition draws attention immediately to the two key issues involved in studying plant communities; 1) how large should the area be? and 2) where, precisely, should the sample-area be put? These apparently trivial questions have fuelled the most heated controversy ever since the study of quantitative plant ecology began, towards the end of the nineteenth century (Goodall, 1952). Failure to standardize the size of study areas, and failure to agree on whether the areas should be subjectively positioned in the most 'clearly typical' parts of the vegetation cover, or more objectively stationed by some form of randomization, have led to a great divergence of experimental approaches, and meant that clear comparisons between the findings of different studies are difficult or even impossible. Superimposed on these practical difficulties was a fundamental difference of opinion about the nature of the plant community itself. The two most polarized positions in this debate are represented by the views of the American ecologists Frederic Clements and H.A. Gleason. Clements believed that the plant community was a closely integrated system with numerous emergent properties, analagous to a 'super-organism'. In contrast, Gleason saw plant communities as random assemblages of adapted species exhibiting none of the properties of integrated organisms like homeostasis, repair, and predictable development alleged by Clements.

1.2.1 Clements' view of community structure

Clements (1916, 1928) studied plant communities throughout North America and was struck by the vast extent of the rather uniform vegetation types he found. He called these 'climax communities', and proposed that the nature of the climax was determined principally by climate. Clements felt that the developmental study of vegetation rested on the assumption that the climax formation was an organic entity which arose, grew, matured and died. Each climax was seen as being able to reproduce itself, 'repeating with essential fidelity the stages of its development', so that the life history of a community was a complex, but definite and predictable process, comparable with the life history of an individual plant.

Clements recognized three major classes of climax vegetation in North America; grasslands, scrub and forests and he subdivided each climax into a number of 'formations'. The grassland climax was divided into true grasslands (dominated by *Stipa* and *Bouteloua*) and sedgelands (*Carex* and *Poa*); the scrub climaxes into sagebrush (*Atriplex* and *Artemisia*), desert scrub (*Larrea* and *Franseria*) and chaparral (*Quercus* and *Ceanothus*); the forest climaxes into woodland (*Pinus* and *Juniperus*), montane forest (*Pinus* and *Pseudotsuga*), coast forest (*Thuja* and *Tsuga*), subalpine forest (*Abies* and *Picea*), boreal forest (*Picea* and *Larix*), lake forest (*Pinus* and *Tsuga*), deciduous forest (*Quercus* and *Fagus*), isthmian forest and insular forest. Each formation was then further subdivided into 'associations' (today, these are simply called communities).

Clements has been accused of espousing a static plant community in which the climax was a fixed, and spatially invariable organism, where individual plants were replaced faithfully by recruits of their own species. In fact, Clements was adamant that 'the most stable association is never in complete equilibrium, nor is it free from disturbed areas in which secondary succession is evident. Even when the final community seems most homogeneous and its factors uniform, quantitative study . . . reveals a swing of population and a variation in the controlling factors'.

Clements' view of succession was of a relatively orderly, predictable approach to a dynamic equilibrium. He identified six stages to the process: 1) nudation, 2) migration, 3) establishment, 4) competition, 5) reaction and 6) stabilization. Each of these might be 'successive or interacting', but the early processes tend to be successive and the later ones are more likely to be interacting (i.e. the frequency, strength and complexity of ecological interactions tend to increase through succession). Thus, in the course of development from bare substrate, through lichens and mosses to the final trees, there would be a series of recognizable (though ephemeral) communities before the climax was achieved (he called these 'seres'). He also distinguished clearly between primary successions, which were essentially soil-forming processes (and where there was no seed bank, and no reserve of vegetative propagules in the substrate at the outset), and secondary successions where the soil initially contained the propagules of many species characteristic of different stages of succession. Primary successions are dominated by the immigration of species from other areas, and occur on lava flows, dunes, rocks and in lakes, and tend to be associated with the accumulation of nutrients and organic matter in the soil. Secondary successions occur in fallow fields, drained areas, clear-cut forests, in the aftermath of fires, and so on. They involve only slight changes in soil (often nutrient *depletions*), and are less dependent on immigration of species.

1.2.2 Gleason's view of community structure

Gleason's name is associated with the 'individualistic concept' of plant community structure (Gleason, 1917, 1926, 1927). He freely admitted the *existence* of plant associations; 'we can walk over them, we can measure their extent, we can describe their structure in terms of their component species, we can correlate them with environment, we can frequently discover their past history and make inferences about their future'. In his view, however, recognizable plant communities owed their visible expression simply to the juxtaposition of individual plants, of the same or of different species, which may or may not interact directly with one another. The structure of the plant community was the result of continuously acting causes, chiefly 'migration and environmental selection' which operate independently in each place, and have 'no relation to the process on any other area; nor are they related to the vegetation of any other area, except as the latter may serve as a source of migrants or control the environment of the former'.

Where Gleason differed most from Clements was in his belief that the community 'is not an organism, but merely a coincidence'. He saw every species of plant as a law unto itself, and denied the emergent properties attributed to plant communities by Clements. He stressed the heterogeneity of community structure caused by accidents of seed dispersal, minor variations in environment, differences in the abundance of parent plants which could act as sources of seed, and the brevity of periods between disturbances.

Another fundamental difference from Clements' view was Gleason's denial of the determinism and directedness of succession. Gleason (following Cooper, 1926) emphasized the random elements of seed immigration and seedling establishment, highlighted the different durations of similar successional stages in different places, and pointed out that different initial conditions and different histories of disturbance could lead to different endpoints. (Clements stressed convergence to a single climatic climax.) Gleason also believed that disturbance was so frequent, and so patchily distributed in space, that most ecological communities should not be regarded as equilibrium assemblages.

Gleason's views are best summarized by one of his own examples. Assume a series of artificial ponds has been created in farmland. "Annually the surrounding fields have been ineffectively planted with seeds of *Typha* and other wind-distributed hydrophytes, and in some of the new pools *Typha* seeds germinate at once. Water-loving birds bring various species to the other pools. Various sorts of accidents conspire to the planting of all of them. The result is that certain pools soon have a vegetation of *Typha latifolia,* others of *Typha angustifolia,* others of *Scirpus validus*; plants of *Iris versicolor* appear in one, and *Saggitaria* in another, of *Alisma* in a third, of *Juncus effusus* in a fourth. Only the chances of seed dispersal have determined the allocation of species to different pools, but in the course of three or four years each pool has a different appearance, although the environment, aside from the reaction of the various species, is precisely the same for each. Are we dealing here with several different associations, or with a single association, or with merely the embryonic stages of some future association? Under our view, these become merely academic questions, and any answer which may be suggested is equally academic" (Gleason, 1927).

1.2.3 The modern synthesis

The modern synthesis is very close to Gleason's view of community structure and dynamics (see Chapters 2 and 3, and the studies of recruitment in plant populations in Chapters 4 and 5). The issue is not whether there are identifiable (if vague) kinds of communities (no one seriously disputes this); the question is, to what extent do *biological* interactions (between one plant and another, between plants and their herbivores, or between herbivores and their natural enemies) influence community structure, compared with limitations imposed by the physical environment (abiotic conditions like soil, weather and exposure).

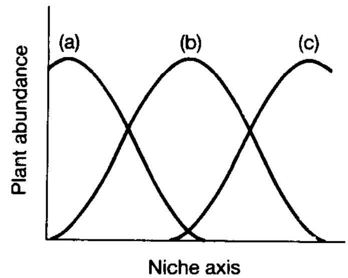
Despite the severe criticisms levelled against most of the underlying assumptions of the climax concept (Cain, 1947; Egler, 1947; Mason, 1947), the term 'climax community' is still quite widely used. There may, indeed, be a place for a word to describe those communities that have been left alone long enough to pass through several generations of the dominant plants. Many ecologists, however, feel that the word 'climax' is so steeped in religious and ethical prejudices (continuous improvement, directed progress towards an ultimate goal, etc.), not to mention Freudian imagery, that its use is probably best avoided!

The legacy of Clements' 'super-organism' is to be found in Tansley's (1935) definition of the ecosystem ('the whole system . . . including not only the organism-complex, but also the whole complex of physical factors. These ecosystems . . . form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom'). It also provides the philosophy behind 'whole-systems ecology', as epitomized by the International Biological Programme of 1964–1974. This 'systems-thinking' has underpinned a good deal of the conservation ethic (Hardin, 1968) and has inspired some terrible poetry (e.g. 'thou canst not stir a flower without troubling of a star'; Thompson, 1918)!

A denial of this holistic approach does not imply that ecological interactions are simple; far from it. As the following chapters will show, most processes really are 'Many, Complex and Interacting' (see page xii)! There is nothing in the reductionist approach which precludes the possibility of plant communities displaying emergent properties. Indeed, there is a marriage to be achieved between the realistic aspects of the climax notion (context-specific interactions between species, multi-species effects, etc.), and the experimental approach of the individualists (Levins & Lewontin, 1980; see Section 1.8).

1.3 The niche concept

The niche is a multidimensional description of a species' resource needs, habitat requirements and environmental tolerances (Hutchinson, 1957). For every vital attribute of a species' ecology it should be possible (at least in principle) to draw an axis to describe the range of possible values for the attribute, and then to plot the performance of the species at different positions along the axis. For example, a plant may not survive at very low or very high levels of soil moisture, but prosper only at intermediate levels (Fig. 1.1).



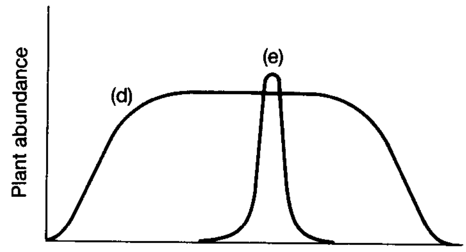


Fig. 1.1. The niche. Idealized relationships between plant abundance (cover, population density or biomass) and distance along a niche axis, of the kind that might be obtained from field transects. (*a*) A species with its peak abundance close to the minimum measured value. (*b*) The 'classic' bell-shaped niche response curve showing sub-optimal, optimal and super-optimal regions of niche space. (*c*) A species with its peak abundance close to the maximum measured value. (*d*) A species with a 'broad niche' growing abundantly over a wide range of niche conditions. (*e*) A species with a 'narrow niche' (a 'specialist') found only under a restricted range of conditions. It is important to distinguish between those broad-niched species which consist of rather uniform, but highly plastic individuals, and those comprising genetically polymorphic individuals, each having a rather narrow niche. Similarly, it is important to distinguish between plants where a narrow niche is caused by narrow tolerances of environmental factors, and those with broader fundamental niches that are restricted to a narrow realized niche as a result of competition with other species.

The niche concept serves as a shorthand summary of a species' complex suite of ecological attributes, including its abiotic tolerances, its maximum relative growth rate, its phenology, its susceptibilities to various enemies, and its relative competitive abilities with other plant species. Plant ecologists, however, have been rather slow to take this originally zoological definition of niche to their hearts. For whilst it is easy to see how resources might be divided up between animal species specializing on diets of different types (e.g. feeding on seeds of different sizes), it is much less obvious how plant resources like light, water or nitrogen could be apportioned between species. Habitat variables like soil moisture, pH or heavy metal concentration make obvious (and easily measurable) niche axes, and species attributes like temperature tolerances, germination requirements, root depth, flowering phenology or disease resistance are amenable to straightforward interpretations. But niche specialization in relation to plant resource partitioning is much less readily incorporated in Hutchinson's original model. In Chapter 2 Tilman presents an elegant solution to this problem by focusing on the performance of plants at different *ratios* of essential resources.