The Nature of Plant Communities

Most people can readily identify a forest, or a grassland or a wetland – these are the simple labels we give different plant communities. The aim of this book is to move beyond such simple descriptions to investigate the 'hidden' structure of vegetation, asking questions such as how do species in a community persist over time? What prevents the strongest species from taking over? And, are there rules that confer stability and produce repeatable patterns? Answers to these questions are fundamental to community ecology and to the successful management of the world's varied ecosystems, many of which are currently under threat. In addition to reviewing and synthesising our current knowledge of species' interactions and community assembly, this book also seeks to offer a different viewpoint – to challenge the reader, and to stimulate ecologists to think differently about plant communities and the processes that shape them.

J. Bastow Wilson was a professor of botany at the University of Otago, New Zealand. He taught ecology from 1971 until his retirement in 2013, when he was awarded the title of Emeritus Professor. He was elected a fellow of the Royal Society of New Zealand in 1997, in recognition of his prominence and global leadership in plant ecology and vegetation science. In 1999 he joined the board of chief editors of the *Journal of Vegetation Science* (including its sister-journal, *Applied Vegetation Science*), and in 2000 he became the chair of the chief editors until his retirement. In honour of his services to plant ecology, Wilson was made an honorary life member of the International Association for Vegetation Science in 2013. Over the course of his career Wilson made sustained, insightful and significant contributions to our understanding of how plant communities function, with his research published in over 230 scientific papers. He passed away in April 2015 after a short illness.

Andrew D. Q. Agnew, now retired, taught students plant ecology and taxonomy in Dundee, Baghdad, Nairobi and Aberystwyth. He has a deep interest in the flora of Kenya, and has published widely on the flora and vegetation of that country. Agnew was a long-term colleague of Wilson, and together they published many scientific papers on vegetation dynamics and plant community ecology.

Stephen H. Roxburgh is an ecologist with the Commonwealth Scientific and Industrial Research Organisation in Canberra, Australia. He has published more than 100 scientific papers and reports on a range of ecological topics including plant community structure and the maintenance of biological diversity, vegetation patterns and dynamics, and greenhouse gas and carbon accounting. He was a former PhD student of Wilson and worked closely with him over the last weeks of his life to help bring to completion *The Nature of Plant Communities.*

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To
Frederick E. Clements

Contents

Preface

The landforms of the earth are mostly clothed with vegetation. We, the authors, have been able to study such vegetation during our full working lives, and it has been enormously rewarding. Like the architectural heritage of the built environment, landscape has the power to be uplifting. This reaction is personal, but nevertheless real. We like being in plant communities. We also like trying to find out how they work: using science to seek the processes that mould vegetation, searching for general patterns and attempting the formulation of community-level theories. Such study is a homage to nature.

Books exist describing the plant communities of parts of the world, or the whole of it. Other books assume that there are rules governing the assembly of communities. We hope to examine plant communities in general terms, but without preconceptions about them. The term 'reductionist' means that we start with the basic attributes of plants, and do not believe the more complex concepts of community ecology without good evidence. We have deliberately concentrated on areas where we feel we have a particular contribution to make to the literature. In a book with such a wide scope, it has been possible to mention only a small fraction of the literature for any particular topic. We have therefore included the work that strikes us as particularly useful or novel, even if occasionally there are some problems with it. We are not generally seeking to summarise the field as a textbook would. Rather, we are often putting forward another view, another emphasis, hoping to stimulate ecologists and their postgraduate students to think of plants, plant communities and the processes that shape them in a different way.

The overall conclusions have been the most difficult. Our argument from first principles has not led us to an overarching theory, but then the closest anyone has come to this is F. E. Clements, to whom we dedicate this book. He saw much and understood much, but his conclusions were mainly descriptive rather than predictive. There is only one recent realistic and comprehensive theory, C-S-R, and the real world turns out to be too complex for it to be more than a guide. At present, community ecologists can only see through a glass darkly.

We have provided a glossary limited to terms that will be less familiar, or have been used in a variety of ways in the literature.

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Glossary

Abundance: Any measure of the amount of a species present, e.g. calorific value (ideal), biomass (the practical optimum), relative cover frequency, cover, local frequency.

Allee effect: Population growth rate is low in sparse populations, probably due to difficulty in contacting a mate but possibly due to problems in attracting a disperser.

Allogenic: Due to causes outside the community.

Alpha (niche/guild): Using particular resources, i.e. different resources than those used by other species in the local community.

Alterative stable states (ASS): Two or more vegetation/environment states in the same underlying habitat, each state locally stable but able to be shifted to another state by a large perturbation.

Altruistic facilitation: A *reaction* by one species that increases the survival/growth/reproduction of another but is disadvantageous to the plant causing the reaction.

Annuation: Variation in species composition from year to year.

Apomixis: The production of a seed by a plant without meiosis or gamete fusion, therefore potentially identical in genotype to the mother plant. Babies without sex.

Arbuscular: Arbuscular mycorrhizae (= AM = VAM = endotrophic mycorrhizae) are a type of fungus-root association in which the fungal hyphae are extensive within the root, and indeed form arbuscules within the root cell.

ASS: *Alternative stable states*.

Assembly rules: Restrictions on the observed patterns of species presence or absence that are based on the presence or abundance of one or other groups of species (not simply the response of individual species to the environment).

Autogenic: Caused by the plant community. In 'autogenic disturbance', the plants disturb each other. 'Autogenic environmental heterogeneity' as opposed to underlying (i.e. abiotic) heterogeneity.

Autosuccession: Succession where climax species regenerate directly, without specialist pioneer species.

Barro Colorado Island: A 1,500-ha island formed when a valley in Panama was dammed to form part of the Panama Canal. It has been used as an example of an area of mainland converted into island status. Numerous ecological studies have been conducted there. The establishment of permanent plots for tree demography by Stephen Hubbell in 1982 is particularly important.

Beta (niche/guild): Tolerant of particular environmental (non-resource) conditions within particular spatial range(s), i.e. differing in tolerances and therefore spatial distribution from other species.

Beta-niche filtering: The exclusion of some species because they cannot tolerate the physical environment.

Bibury: The site of roadside vegetation in southern England that has been monitored yearly since 1958, originally by Arthur J. Willis and E. W. Yemm, and since by other ecologists from Sheffield University. The original aim was to investigate possible use of weed killer to control woody invasion, but the control plots have proved to have the most lasting interest.

BioDepth: A collaborative, multi-site research programme funded by the European Community into the effects of species richness on yield, invasion resistance, etc.

C: Carbon.

C: In C-S-R theory, C habitats are ones where productivity is high and disturbance low, so that competition is intense, and C species are strong competitors able to persist in the vegetation of such sites. These concepts depend on the theory's suggestion that competition is more intense in more productive sites.

Cedar Creek: Cedar Creek Natural History Area, an experimental field area comprising oldfields, belonging to the University of Minnesota, and the site of many experiments by David Tilman and others.

Challenge: A test by an organism of a new habitat.

Chequerboarding: A situation where pairs of species are mutually exclusive across islands/plots.

Circular interference network: Interference abilities of species are A > B, B > C and C > A (or a more complex pattern with circularity).

Climax: A stable endpoint of succession.

Community: The set of one or more species existing within a particular area at a particular time.

Community matrix: A summary of all possible pairwise species interactions in an equilibrium community, expressed as the effect that a small change in the equilibrium abundance of one species has on the equilibrium density of another, whilst holding the abundances of all the other species present at their respective equilibrium values.

Competition: An interaction between individuals, brought about by a shared requirement for a resource in limited supply, leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned.

C-S-R: The theory of J. P. Grime that habitats and species can be arranged in a triangle, comprising a tradeoff between competition (C), stress (S) and disturbance/ruderality (R).

CWD: Coarse woody debris, i.e. litter of branches and whole trees.

Cyclic succession: Two or more vegetation states replace each other in a cycle that is repeated over time.

Disseminule: A sexually or asexually produced dispersal unit capable of developing into a new individual or ramet.

Disturbance: A marked change in the environment for a limited period, often with the removal of plant material.

Ecesis: The process by which a plant or animal becomes established in a new habitat.

Ecotone: A sharp change in community composition, i.e. more rapid than either side of the ecotone.

Embryophyte: Any plant from liverworts 'upwards', i.e. bryophyte, pteridophyte, gymnosperm or angiosperm.

Epigenetics: Changes caused by modification of gene expression, rather than alteration of the genetic code itself.

Equal chance: Each of the species present in the local habitat pool has an equal interference ability, and therefore an equal chance of establishing at any point.

Facilitation: A *reaction* by one species that increases the survival/growth/reproduction of another.

Florula/florule: The flora of a local environment.

Genet: A genetic individual, i.e. the derivative of one zygote. It may be one recognizable 'individual', or it may comprise many plants produced by vegetative reproduction or by apomixis.

Guild: A group of species that are similar in some way that is ecologically relevant, or might be.

Humped-back curve: In this context a relation where species richness is maximal at intermediate levels of productivity (or standing crop plus litter).

Inertia: Tendency not to change.

Interference: This covers *competition*, *allelopathy*, parasitism, pest transmission and other interactions in which the primary effect of one plant on another is negative.

Leaf: 'Although no satisfactory definition of a leaf is possible, I shall assume that we all know what we are talking about': F. G. Gregory, cited by L. Croizat in his 'Principia Botanica'.

Lyapunov (= Liapunov) stability: The ability of a community, after an infinitely small pulse perturbation, to return to its original state in infinite time (assuming external factors and the species pool remain constant).

Macrophyte: Macroscopic plant, e.g. tree.

Mesocosm: A medium-sized experimental community.

Microcosm: A small experimental community.

Mutualism: An interaction between two plants that increases the survival/growth/reproduction of both.

Mycorrhiza (pl. mycorrhizae): A close association between a fungus and a root. The two major types, found in hosts from many families, are ectotrophic and arbuscular. Other types are associated with the Ericales (heaths, etc.) and Orchidaceae (orchids).

N: Nitrogen, generally as nitrate or ammonium salts.

Nesting: A situation where an island/plot contains all the species found in the next most species-poor island/plot, plus additional species.

Niche: A region as 'n-dimensional hyperspace' where the dimensions are all the environmental, resource or behavioural (e.g. phenology, foraging) parameters that permit an organism to live.

Niche complementarity: The tendency for coexisting species that occupy a similar position along one niche dimension to differ along another.

Ombrotrophic (= ombrogenous): Dependent on precipitation for its water and mineral nutrients (a type of mire).

Oskar: A suppressed tree seedling in the understorey, small but old.

Outbreak: A sudden increase in the abundance of a species over a few years followed by a decrease also over a few years.

P: Phosphorus, generally as phosphate.

Paludification: The process of peat bog formation.

Park Grass: The world's longest-running ecological experiment and therefore most important. Established at Rothamsted Agricultural Station in the English Midlands in 1856. There were originally 20 plots with different fertiliser treatments, though most have been subdivided since. They have been monitored, with varying degrees of detail, ever since.

Patch: Small area of vegetation within a larger matrix.

Plant: A photosynthetic organism with chlorophyll a, or a close saprophytic or parasitic relative.

Podzolization: A process of soil formation, particularly in cool, humid regions, in which the upper layers are leached of minerals, which are then concentrated in lower layers.

Polycarpic (of a ramet): Reproducing sexually more than once in a life cycle, generally in more than one year.

Press perturbation: A change in the physical or biotic environment of a community that continues to be applied.

Primary succession: Vegetation change starting in conditions not influenced by any previous vegetation on the site, e.g. bare sand, unvegetated water.

Pseudogamy: Pollen is needed for seed development, and fertilises the endosperm, but the embryo itself is produced by apomixis.

PSU: Photosynthetic unit: the leaflet, simple leaf, cladode, unit of green stem, etc.

Pulse perturbation: A change in the physical or biotic environment of a community that is applied and immediately removed (as immediately as it can be).

Quadrat: A vegetation sample of specified shape and area or volume.

R: In C-S-R theory, R habitats are ones where there is frequent disturbance, i.e. removal of plant material, and R species are the ruderals typical of such habitats. They are similar to 'r' species of r-K theory.

Ramet: A vegetatively produced plant unit, such as a strawberry 'plant'.

Raunkier life form: A classification of species according to the position of their resting buds during the most unfavourable season.

Reaction: The change in local environment caused directly by a plant. 'Ecological engineering' is similar, but perhaps has implications that the change benefits the species/community, comprising a *switch*. 'Niche construction' seems to be a synonym, with 'positive niche construction' causing a *switch* and 'negative niche construction' comprising *facilitation*.

Redox potential: Reduction–oxidation potential, the tendency to donate or accept electrons.

Relay floristics: A caricature of F. E. Clements' concepts of succession, in which vegetation must pass through a relay of seral stages, each stage facilitating the next, ending in the climax.

Reliability: Lack of temporal variation in a community.

Resilience: The degree and speed of recovery of a community after a *pulse perturbation*.

Resistance: Lack of change in a community when a *pulse perturbation* is applied.

RGR: Relative growth rate = growth per unit time per unit biomass. It is equivalent to the *r* of zoological population models. We do not make a distinction between vegetative and sexual reproduction, nor between an increase in numbers and in 'individual' size, so we use RGR to cover all population growth. An RGR of 0.0 means no change, and RGR <0.0 means that the population is shrinking and one >0.0 means that it is expanding.

RGR_{max}: RGR, at the phase of growth when RGR is highest for the species (young) in environmental conditions that produce the highest RGR in that species (which is hard to achieve in practice).

Rheotrophic (= minerotrophic): Receiving water, with mineral nutrients, that has flowed through/over mineral soil (a type of mire).

RYM (Relative Yield of Mixtures): In plant competition experiments, the yield of the mixture compared to the mean of the monocultures.

RYT (Relative Yield Total): In plant competition experiments, the sum of each species' yield in mixture compared to its yield in monoculture.

S: In C-S-R theory, S habitats are ones where productivity is low, and S species are ones typical of such habitats.

Secondary succession: Vegetation change starting after a disturbance where vegetation has previously existed and where the effects of that vegetation remain, typically in soil development.

Seral stage: A vegetation state in succession-to-climax before the climax.

SLW: Specific leaf weight = leaf weight per unit area, e.g. cm^2/g. It is the reciprocal of SLA = specific leaf area, and references to SLA have been converted to SLW for uniformity.

Somatic mutation: The occurrence of a mutation in the somatic (i.e. non-reproductive) cells of an organism, resulting in a genetically mosaic individual.

Spatial mass effect: Some species are present in an area where they cannot reproduce, or cannot reproduce fast enough for a self-sustaining population, but the

population can remain because of an influx of disseminules from a nearby habitat where the species can maintain itself.

Species diversity: *Species richness* and the evenness of abundance among species in an area (e.g. quadrat) of specified size and shape. With the right combination of indices, diversity = richness × evenness.

Species richness: The number of (plant) species present in an area (e.g. quadrat) of specified size and shape.

Stability: see *Liapunov stability*.

Stratum (pl. strata): A vertical layer, usually in an above-ground plant canopy but also below-ground.

Subvention: A positive interaction between plants, including *benefaction*, *facilitation* and *mutualism*.

Succession: Sequential change in vegetation.

Succession to climax: From any starting point there is one pathway of vegetational change to a 'climax', with no reversals.

Switch: A positive feedback between a species or community and its environment, in which the species/community changes the environment by reaction in a way that gives it relative benefit over alternative species/communities.

Synusia (pl. synusiae): A *stratum* or other vertical rôle in a forest such as an epiphyte, aerial partial parasite or liana.

University of Otago Botany Lawn: Established c. 1965 with the sowing of an *Agrostis capillaris*/*Festuca rubra* mix. Thirty-six other species have arrived since then through natural dispersal. Since 1965, the lawn has been mown to a height of c. 2.7 cm, fortnightly in the growing season and monthly in winter.

Vascular plant: Pteridophyte, gymnosperm or angiosperm.