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J. Bastow Wilson, Andrew D. Q. Agnew, Stephen H. Roxburgh
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1 Plants Are Strange and Wondrous Beings

1.1 Introduction

Our aim in this book is to present a fresh perspective on the structure and functioning of plant communities, and especially the forces that limit the coexistence of some species and promote the coexistence of others. We hope this perspective will stimulate ecologists to think afresh about plants and plant communities and, even if they sometimes disagree with us, help them to form their own synthesis.

None of the existing theories of ecological communities has proved truly satisfactory; evidence for MacArthur's deductive theory of limiting similarity is sparse (Wilson and Stubbs 2012; see Section 5.6) and Grime's comprehensive, inductive C-S-R theory is far from being precisely predictive (Wilson and Lee 2000; see Section 6.5). Moreover, theories of the structure of communities are uninformative if no attempt is made to understand the mechanisms involved. Our approach is therefore reductionist, building from basic processes to generalisations about communities, always requiring solid evidence from the real world.

We have concentrated on areas where we feel we have a special insight to offer, and naturally some of these are areas where we have made contributions to the literature. These include species' environmental reaction (the effects of a plant or a community on its habitat, including via litter), interference (negative effects of species on each other by any means: competition, allelopathy, autogenic disturbance, interaction via heterotrophs, etc.), facilitation, switches (*sensu* Howard Odum) and assembly rules (*sensu* Wilson 1999a). There are topics we have not dwelt upon because, whilst interesting in their own right, they do not seem to advance our discussion of the structure and functioning of communities. Examples are species–area curves, the productivity–richness humpback curve, and ordination techniques and their use. Perhaps we could best characterise this book as a monograph on the core principles of plant community structure, approached bottom-up, i.e. from the individual plant to the whole community.

We shall emphasise terrestrial vascular plants because more is known about them, and the processes involved are generally found in them. However, most of the principles must apply also to lower plants, down to macroalgae and plankton (Tilman 1981; Wilson et al. 1995b; Steel et al. 2004), and we shall take examples from any group of organisms when we fancy. We shall not often discuss animals, though; this book is about plants.

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1.1.1 Organisation of This Book

In this chapter we give the background to our topic, the nature of plants. Chapter 2 discusses the manifold ways in which plants can interact with each other. Many of these interactions tend to make species exclude each other, yet vegetation almost always comprises mixtures of species – the ‘Paradox of the Plankton’ – so in Chapter 3 we examine how this happens. Chapter 4 is an account of the collective ecological behaviour of species’ mixes, i.e. of whole-community processes, which is in fact the overall topic of our book. Whilst those four chapters pull together the nuts and bolts of our enquiry, in Chapter 5 we attempt to synthesise by looking for precepts to species’ coexistence in mixtures, i.e. assembly rules – the restrictions imposed on species’ coexistence. In Chapter 6 we examine existing models of plant community structure. Finally, in Chapter 7 we put forward the main processes that structure plant communities as we see them, which we believe is the closest it is possible to come to an overarching theory, at least at this stage, and may always be.

1.1.2 The Plant in the Ecosystem

The five essentials of any ecosystem are: (1) input of energy, mainly from the sun via photosynthesis; (2) the capital of energy in the biomass of living organisms; (3) transfer of energy between trophic levels, e.g. from plants to herbivores; (4) cycling, especially of elements and (5) allogenic rate regulation, i.e. the control of the rates of these and other processes by environmental factors such as temperature (Reichle et al. 1975). The plant cover, i.e. the vegetation, is the major contributor to all of these essentials, in some cases the sole contributor.

Very rarely does a single plant species persist on its own, even when a gardener or farmer tries to make it so. Our subject is therefore multispecies communities. Every language uses terms to divide the plant cover of landscapes into communities; terms such as grassland (tussock, pasture, meadow), forest (conifer, deciduous, evergreen) and scrub (evergreen, summer-deciduous, krummholz). The ability to classify, subjectively or using objective methods (e.g. the British National Vegetation Classification; Rodwell 1991–2000), shows that species’ mixes occur as repeated patterns. This is no surprise, since each habitat within the landscape supports only those species that are physiologically able to tolerate the particular environmental conditions (see Section 1.5.2). Even when a species can tolerate the environment, it might be excluded by the strength of interference from other species (see Section 1.5.3). Further, there might be adaptation to, or even intolerance of, the presence of other particular species or species’ groups; these are the assembly rules (see Section 1.5.4).

Phytosociologists have invoked repeated patterns to rationalise the concepts of *fidelity* and *constancy* in plant associations. The issue is whether these ‘associations’/‘communities’ have definable properties, whether there are distinct associations that can be classified and named. We are not interested in where one community ends and another begins – clearly, there are sometimes discontinuities between species’ mixes, sometimes not – except in so far as the question increases our understanding of the processes that structure communities. Our definition of ‘community’ is therefore empirical:

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

Our journey begins with a discussion of the nature of higher plants and an overview of the core concepts that form the basis of plant community ecology.

1.2 The Nature of Land Plants

Land plants, attached by roots or rhizoids and generally autotrophic, have quite different ecological properties from animals, and ideas developed for other trophic levels can seldom be applied to plants. We find two basic consequences of plant morphology:

1. *Physical movement and stasis*. Once established, land plants are sedentary.[1] However, plant organs have a limited length of life, so the plant must continually produce new modules, and thus inevitably explore new space.
2. *The problem of the individual in plants*: Applying the concept of an ‘individual’ to vegetatively reproducing plants is problematic. Even with seed reproduction, size is plastic and there may be somatic mutation. The great uncertainty as to whether plants can recognise themselves, and recognise kin, raises more questions. The concept of ‘individual’ is not generally useful for plants.

1.2.1 Physical Movement and Stasis

Animals of most species move around but, having grown, maintain approximately the same adult body, replacing organs cell-by-cell or molecule-by-molecule until death, even though in some fish, reptiles and molluscs the body continues to enlarge. Plants are always indeterminate in size, that size depending on the environment.

Plant architecture is modular, and to a considerably greater extent than in animals. Indeed, the plant has been seen as a population of modules (Harper 1977). Sometimes the repeated modules are discrete, such as leaves, flowers and vascular bundles in monocotyledonous trees (e.g. *Cordyline* spp., cabbage trees), though they can be hierarchically arranged, e.g. inflorescences comprising flowers, themselves comprising carpels, stamens, petals and sepals. Sometimes the modules are continuous, such as a year’s growth of *Welwitschia mirabilis* leaves. In other cases the modules are adjoined to neighbours as in syncarpous ovaries, or to earlier modules, such as a year’s addition of new phloem and xylem in a temperate dicotyledonous tree. Again, a hierarchy is possible, for example modules could be distinguished radially between parenchyma rays. Perhaps the exception is in *Wolffia* spp. (watermeal), where the plant comprises only one module, though even this has a stamen as another module. Modular growth is universal in plants.

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[1] ‘Sessile’ in zoological terminology.

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The living cells of these modules have a limited functional lifespan.[2] Because plants are essentially sedentary, defence from herbivores can be only by structure and chemistry, not by running away. This puts a selective premium on cell walls that are low in food value to herbivores but also strong enough to support cell turgor, resulting in cell walls basically of cellulose and lignin. These compounds cannot be recycled within the plant, so aged and dysfunctional modules are generally discarded and replaced by new ones, sometimes several times during the life of a plant.

Over a broad spatial extent plants are sedentary. Yet, replacement modules commonly are formed distally on the stem, or on side branches, so a plant must continually move, explore and expand into adjoining space,[3] and in the process may interfere with its neighbours. Vegetative reproduction, which often serves for resource foraging, is just an extreme form of this general phenomenon of plant expansion. Roots must also grow to explore for immobile phosphorus and, as a result, need to replace the root cap module. In this sense, plants move, whereas animals stay within their adult body. The plant's litter – flower parts, fruit and associated structures, leaves, shed branches and eventually the whole plant – is part of its movement and its effect on neighbours, i.e. part of its extended phenotype. This mandatory movement, often not recognised when plants are described as sedentary, results in autogenic disturbance, and is a major topic in Chapter 3. Some colonial, sedentary animals are similar to plants in that they must occupy new space to stay alive – some Tunicata (tunicates), corals and Porifera (sponges) – though the modules causing mandatory growth in corals are not discarded as leaves are, but sequestered like the xylem in the heartwood of trees. These few animals have similar movements to plants.

1.2.2 The Problem of the Individual Plant

It is difficult to recognise plant individuals (Firn 2004). We see three main problems and one unsolved issue, that of self/kin recognition.

1.2.2.1 The Plant as a Genetic Mosaic

It is well known that due to their basic growth pattern plants can comprise a genetic mosaic, a chimera, one example being sectorisation in trees, another being variegation (Gill et al. 1995). Animals often isolate their gametangial cells early in development, which reduces the risk of genetic transmission errors. In plants, the reproductive cells differentiate late, and the many cell divisions between the original zygote and the production of gametes allow the accumulation of somatic mutations: both base-pair changes and chromosomal rearrangements. Scofield (2006) estimated c. 41,000 cell divisions per metre of height growth in *Quercus rubra* (northern red oak), which allows 1,230,000 cell divisions by the time it has reached 30 m height. Occasionally, the results

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[2] The photosynthetic rate of a leaf declines from quite early in its life, often even before it is fully expanded.
[3] Even cactuses may increase in size during their life (de Kroon and van Groenendael 1997).

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of somatic mutation are clearly visible and adaptive, as when a branch of a *Eucalyptus melliodora* (yellow box) tree has resistance to herbivory that the rest of the tree does not (Padovan et al. 2013).

The rate of somatic mutation is more difficult to estimate. Most mutations will be deleterious, but some will survive, at least if recessive. For technical reasons the rate has been calculated mainly for sublethal, deleterious mutations, which is not directly relevant here. Bobiwash et al. (2013) estimated for *Vaccinium angustifolium* (lowbush blueberry) in Canada approximately three sublethal, partially dominant somatic mutations within each shrub. Klekowski and Godfrey (1989) estimated from a field survey of *Rhizophora mangle* (red mangrove) trees in the Caribbean region a mutation rate for albinism (selectively neutral in a heterozygote) of $6\text{–}7 \times 10^{-3}$ mutations per haploid genome per generation. Gross et al. (2012) provided evidence for considerable somatically generated genetic variation within a clone of the vegetatively reproducing shrub *Grevillea rhizomatosa* (Gibraltar grevillea) in New South Wales, Australia.

Somatic mutations certainly exist, and some survive beyond the cell in which they appear. Epigenetic changes, notably via DNA methylation, could also occur locally within the plant. What our science needs to know, and does not, is the extent to which somatic mutations arise that might be adaptive in some niches, changing the genotype of branches, sectors or the whole plant; mutations that are potentially passed on to future generations. The limited evidence available suggests that evolutionary change and divergence can occur as fast in populations of apomicts as in sexual ones, potentially leading to ecotypic adaptation that might be due to selection acting on somatic mutation (Pellino et al. 2013). Somatic mutation has considerable, unrecognised implications in plant ecology.

1.2.2.2 Production of New Modules

In vegetatively reproducing plants, a genet comprises ramets that are at first dependent, later semi-independent but supporting each other when in need, and eventually independent, perhaps with the group then splitting into patches (Harberd 1962; Marshall 1996). These patches can then become genetically differentiated through somatic mutation, so they do not technically comprise a clone. Similar issues arise with apomictic seeds: the lineage is initially identical in genotype but may later form divergent genetic lines by somatic mutation. Root grafting and occasional branch grafting between different trees is the converse situation: distinct genets that are physiologically interdependent (Dallimore 1917; Fraser et al. 2006).

All plants reproduce asexually in one way or another. There is no basic distinction between the apomictic seeds of *Taraxacum* spp. (dandelion), plantlets from the leaf margin of *Kalanchoe daigremontiana* (mother of thousands), separating rhizome fragments of *Elytrigia repens* (couch grass), root suckers of *Populus tremuloides* (aspen), and a bud that produces new leaf modules. These all replicate an original genotype, but after many mitotic divisions can accumulate mutations. Plant ecologists must cease aping animal ecologists in dealing with individuals, and deal with modules within genets, though even the latter is not fixed in its genes (see Section 1.2.2.1).

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1.2.2.3 Size Plasticity

Another problem with applying the traditional animal 'individual' concept to plants is that whilst most animals are relatively predictable in size at a particular age, individuals of one plant genotype can differ in biomass by several orders of magnitude (Harper 1977). The modules within one plant can differ plastically too, if they are in different microenvironments.

1.2.2.4 Self-Recognition and Defining the Individual

There is some, be it controversial, evidence that the root system of an individual genet or even ramet can distinguish between:

(a) self/others, i.e. its own roots/shoots ('self') versus those of other individuals of the same species ('others') or
(b) kin/stranger, i.e. its siblings or offspring ('kin') versus non-kin of the same species, i.e. no more related to it than the population in general ('strangers').

Some self/others studies have found when plants are grown in contact with roots or whole plants of an identical genotype (i.e. self), they differ, often in root growth or shoot:root ratio, from those grown with other genotypes. Thus, Falik et al. (2003) found in a split-root-system experiment that when a plant was growing with its own genotype it produced significantly less root than when growing (competing?) with roots of another genotype. Similar effects have been seen in kin/stranger comparisons. For example, Murphy and Dudley (2009) found that plants of *Impatiens* cf. *pallida* (jewelweed) growing with the roots of a plant from the same selfed family had lower leaf:root ratios than those grown with strangers.

Some self/other work suggests that self-recognition can wane. Thus, Gruntman and Novoplansky (2004) found a root mass response to self/non-self tillers of *Buchloe dactyloides* (buffalo grass) just after the tillers had been separated, but the effect decreased with time, until after 60 days, self tillers were no different in root mass from stranger tillers. This implies a mechanism somehow based on the physiological state of the plant, not its genotype. However, a physiological basis does not explain the self versus kin results of Murphy and Dudley (2009) and others. One possible explanation for these effects is that if plants are genetically different, there can be niche differentiation, leading to overyield. This is difficult to test because we do not know the factor in which they might differ. Another explanation is that if a plant of one genotype/family grows larger than that of another, it is able to take more than 50 per cent of the pot's resources, giving a greater total biomass. Bhatt et al. (2011) were inclined to discount the latter explanation for their results with *Cakile edentula* (sea rocket) on the grounds that two plants growing together were not significantly more different from each other in biomass when they were from a different selfed family than when they were from the same one. However, non-significance is always poor evidence of no effect, especially since F was here 2.53.

If self/kin/stranger recognition is real, how could it work? One possibility is by the chemical composition of root exudates moving through the soil solution or via common mycorrhizal networks. Biedrzycki and Bais (2010) found that plants of *Arabidopsis*

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thaliana growing in water previously inhabited by the same plant differed in root morphology from those grown in water previously inhabited by self/kin or by strangers, and the latter two differed from each other. The self versus stranger effects were suppressed by the presence of exudation-inhibitor sodium orthovanadate, but self vs kin effects were not. Atmospheric volatiles could conceivably carry a signal that is decodable only by a plant of the same genotype, or by its kin (e.g. Karban et al. 2013). However, a plant could hardly identify itself uniquely via chemicals. A system similar to the ***S*** alleles involved in pollination self-incompatibility would be possible. One locus would not enable identification to an individual genotype, and kin would not necessarily carry the same allele, but trends may still exist. Crepy and Casal (2015) suggested that kin were recognised by light-spectrum signals (R:FR and blue). It seems unlikely that the spectrum could identify genotypes, but they suggested that leaf positioning affected how the signal was received. An explanation in terms of the microflora associated with a plant/genotype is also possible.

Other studies have found no self or kin effects, or found them in some species but not others (e.g. Lepik et al. 2012). This is reasonable: self-recognition might operate in some species but not others.

Such self- or kin-recognition would have huge impact on plant community assembly, as indeed it does for social animals. The effects seem sporadic, and some ecologists explain them away in terms of root exploration of soil volumes, or of nutrient (NPK) competition (Nord et al. 2011). Scientists are always cautious about accepting results when it is difficult to imagine what mechanism has caused them. The ecological significance with respect to communities of these self- and kin-recognition experiments is still unknown.

1.2.2.5 Conclusion

Because of modular structure, plastic variation in size, vegetative reproduction, apomixis and somatic mutation, the concept of the ‘individual’ is not always valid for plants, demographically, ecologically or genetically, and indeed the concept of ‘self’ is contentious. Plants can be viewed as colonies of modules.

1.2.3 Species and the Plant Community

For an ecologist, a meaningful species must have a unique phenotype, with consequently unique environmental tolerances and reactions. The name of a taxonomic species allows us to predict much of a plant’s morphology, physiology and growth. ‘Morphospecies’ can predict only the attributes already known.

1.3 Reaction

1.3.1 The Concept

The plant is affected by its environment, but it also changes its environment. Clements (1904, 1916) coined the term ‘reaction’ for ‘the effect which a plant or a community

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exerts upon its habitat. . . . Direct reactions of importance are confined almost wholly to physical factors', and listed 20 such factors. Gleason (1927) agreed with Clements, as he almost always did (Section 6.2). The acidification caused by *Sphagnum* species in bogs is a well-known example, but for example, shading is a reaction too, on the light environment. Eviner and Chapin (2003) gave a comprehensive list. With more knowledge, biotic reaction would now be included. Reaction is the very basis of community assembly.

Any organism must cause reaction. The effect varies from slight to major, but plants especially cause reaction because of their bulk, their surface area, their absorption of resources, their aerial and below-ground secretion or leakage of materials, and their production of litter. These reactions modify local light availability, micro- and macroclimate, environmental chemistry and geomorphological processes, and thus the whole ecosystem. A species' response to its own reaction can be negative, i.e. altruistic facilitation (Clements 1916; this volume Section 4.3), or positive (a switch: Wilson and Agnew 1992; this volume Section 4.5). The near-synonyms 'ecosystem engineering' (Jones et al. 1994) and 'niche construction' (Odling-Smee 1988) were coined more recently, but we use 'reaction' because:

(a) 'Reaction' has priority.
(b) 'Niche construction' was coined, and is often used, more narrowly to include both ecological change (reaction) and consequent evolutionary change (Post and Palkovacs 2009), even with genotype/environment feedback that makes it a switch in evolutionary time (Scott-Phillips et al. 2014), whereas we are addressing here *environmental* change. Elsewhere, 'niche construction' is used more broadly, e.g. to include breeding system and herbivory response (Shuker 2014). Moreover, niche construction can be negative, a quite different process that leads to succession-towards-climax or to cyclic succession (Sections 4.3 and 4.4). However, 'niche construction' is useful in some contexts, and we shall sometimes refer to it.
(c) Both 'ecosystem engineer' and 'niche construction' imply that only a few species have such effects, whereas we (with Clements 1904 and Gleason 1927) emphasise that all species have them.

Each species, with its unique phenotype, necessarily differs from others in its resource requirements, acquisition efficiencies, by-products, and phenologies of production and litter deposition, and thus in its reactions. These reactions are the basis of the great majority of types of plant interference and facilitation (Chapter 2), and indeed are behind the great majority of ecological processes. Since species are almost always spatially aggregated, the result will be autogenic heterogeneity in environment and resources, adding to the intrinsic heterogeneity (Section 7.3).

1.3.2 Reaction on Physical Factors

Reaction can readily be seen in the light regime beneath and beside different species, though much more is known of species' differences in total light transmittance than of

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changes in spectral composition (Section 2.2.4). Temperature, relative humidity and O_2/CO_2 concentrations can all change along with the light environment, and do.

Soil reactions are caused by foliar leaching, the decay of above- and below-ground litter, nutrient and water uptake, root exudation and occasionally changes in the soil atmosphere. They generally occur slowly, but for example it is clear that a few species, such as *Picea abies*, *Calluna vulgaris* (heather) and *Sphagnum* spp., differ strongly from other species in their community in the magnitude of their reaction on pH. The clearest evidence for autogenic heterogeneity in reactivity comes from forests, where the sheer size of trees (relative to scientists) makes their patches large and easy to sample. For example, Pelletier et al. (1999) found that in a mixed-species forest in Quebec, Canada, soil of the forest floor was different beneath different species. For example, extractable soil Ca was lower below *Fagus grandifolia* (American beech). In most such observational studies there is a chicken-and-egg problem: perhaps the soil differences are determining which species grows at a point, not the reverse. Fujinuma et al. (2005), finding higher ammonium-acetate extractable Ca and Mg beneath *Tilia americana* (basswood) than beneath *Acer saccharum* (sugar maple) in a 1−ha patch within Michigan forest, discussed this issue, but considered that preexisting soil heterogeneity at that scale was unlikely. Pelletier et al. (1999) went two steps further: (a) they used spatial statistics to remove spatial correlations, attempting to examine the effects of individual trees, and (b) they offered evidence that *F. grandifolia* produces litter which, from its Ca, lignin, polyphenol and tannin contents, was likely to reduce soil Ca. The study of Ehrenfeld et al. (2001) produced evidence in another way. They found higher pH below two exotic species in a deciduous forest in New Jersey, USA, than beneath the native *Vaccinium* spp., but they also grew the species in the greenhouse on field soil and found similar pH differences to that observed in the forest.

The ideal evidence is from long-term randomised experiments, and Binkley and Valentine (1991) reported that in a 50-year-long replicated experiment in Connecticut, USA, soils under *Picea abies* (Norway spruce) were lower in pH, with less than half the exchangeable Ca, Mg and K, and higher in Al, than under *Fraxinus pensylvanica* (green ash). Changes in pH can be accompanied by, or effect, changes in nutrient availability, e.g. decreased pH can increase P availability. The experiments in Augusto et al.'s (2002) review show the effect of *P. abies* lowering pH to be quite general; indeed there are hints that it may be more generally true of gymnosperms. Challinor (1968) in a 30-year experiment with four tree species in North America found under *P. abies* the soils had greater pore space, higher total soil N and exchangeable K, and higher exchangeable Ca at the surface. Sartori et al. (2007) found higher extractable K after seven years beneath *Larix decidua* (larch) than beneath five *Populus* (poplar) species/hybrids/cultivars. However, the experiment of Alriksson and Eriksson (1998) with five tree species growing for 23 years showed, apart from a difference in pH in the litter +organic layer, which can be seen as a difference in the litter itself, only a difference in exchangeable Mg in the uppermost of five mineral soil layers.

Most of these changes will come via differences in the species' litter and possibly root exudates, but the process is difficult to observe. Even genotypes within a species can differ in their litter decomposition (Madritch et al. 2006), and thus possibly in their

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reaction on the soil. Experiments with soil litter bags normally last 2–5 years, whilst it might take 50 years to see the effects, and such experiments are usually established to examine the litter, not the underlying soil.

1.3.3 Biotic Reaction

Reaction can also be indirect, via the soil biota, potentially giving heterotroph-generated autogenic heterogeneity. Bezemer et al. (2010) found differences in bacteria, fungi and enchytraeid worms beneath two grassland forbs. Viketoft et al. (2005) demonstrated that the nematode communities differed markedly below field monocultures of 12 grassland herbs, both in total numbers and in species' composition; and in follow-up work Viketoft (2008) reported similar effects for six of these species from a greenhouse experiment, where the soil could be defaunated by alternate freezing and heating, then reinoculated with nematodes and microflora, to give a uniform starting point. Nematode community abundance and species' composition differed between plant species. Whether these differences affect the plant species differentially is not known, but there are fascinating hints in the work of van Ruijven et al. (2003) who demonstrated negative impacts of *Leucanthemum vulgare* (oxeye daisy) on invasion success in experimental mixtures, with results implicating nematode populations associated with the *Leucanthemum* as a potential explanation.

1.3.4 Conclusion

The unique characteristics of species result in unique reactions on their environment, and those reactions are the forces behind almost every process determining community organisation, which is the central topic of this book. Yet many aspects of physical reaction are hardly known, and in spite of recent work even less so for biotic reaction.

1.4 Niche and Guild

Grinnell (1904) and Elton (1927) introduced 'niche', both defining it as a zone within habitat space, outlined by physical and trophic parameters. Hutchinson (1957) formalised this as 'a region in *n*-dimensional hyperspace' where the dimensions are all the environmental, resource or behavioural (e.g. phenology, foraging) parameters that permit an organism to live.[4]

Niche and guild are central concepts in community organisation and assembly. They are closely related: a guild is a group of species with similar niches.

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[4] Hutchinson uses 'environmental variables' to describe the axes of the hyperspace, which implies only beta niche (see below), but his subsequent discussion clearly includes resources, making the hyperspace one in alpha+beta niche.