Assembly and response rules:
two goals for predictive community ecology

Keddy, Paul A.

Department of Biology, University of Ottawa, Ottawa, Ontario, Canada, K1N 6N5;
Tel. +1 613 564 3447; Fax +1 613 564 5014

Abstract. Assembly rules provide one possible unifying framework for community ecology. Given a species pool, and measured traits for each species, the objective is to specify which traits (and therefore which subset of species) will occur in a particular environment. Because the problem primarily involves traits and environments, answers should be generalizable to systems with very different taxonomic composition. In this context, the environment functions like a filter (or sieve) removing all species lacking specified combinations of traits. In this way, assembly rules are a community level analogue of natural selection. Response rules follow a similar process except that they transform a vector of species abundances to a new vector using the same information. Examples already exist from a range of habitats, scales, and kinds of organisms.

Keywords: Community ecology; Fire; Flooding; Island; Natural selection; Prediction; Model; Species pool; Trait.

Introduction

Given the world's growing environmental problems, the need for accurate predictive models for ecological communities has never been greater. However, there appears to be little consensus upon how they will be developed. This lack of agreement has been described by Lewontin (1974) as the agony of community ecology. Indeed, a major criticism of community ecology is that it is still a soft science dealing primarily with description of plant and animal associations rather than a hard science making accurate predictions about specified state variables. The transition to a hard science is not only important for the growth of the discipline, but is essential to guide political decision making about environmental issues. Whether at the global scale (e.g. climate change) or the local scale (e.g. pollution of a single lake) the questions remain the same: can we predict the future states of communities? The ability to answer such questions rather than speculate about them is essential.

In the last decade, it appears, a major transition has occurred. In a range of studies (e.g. van der Valk 1981; Haefner 1978, 1981; Box 1981; Nobel & Slatyer 1980) designed for different purposes, in different communities, in different parts of the world, one can find a consistent set of features which focus upon accurate ecological predictions. It appears that when community ecologists set the goal of prediction rather than description, that decision in and of itself leads to certain recurring research strategies and outcomes. These can be called 'assembly rules' and 'response rules' (Keddy 1989). My objectives here are to draw attention to these developments, illustrate the progress which has already been made, formalize the procedure further, and suggest some future possible developments for the discipline.

Context

Before proceeding, we need to briefly consider the context of the problem, the scale and level of organization at which community ecology operates, and the state variables which it explores. It is easy to confuse the levels of population and community ecology, perhaps because they have similar historical roots (McIntosh 1985) and because there are population ecologists who suggest that the community level of organization can only be studied by examining the component population (e.g. Harper 1977, 1982).

However, in theory and in practice there are differences between these levels. Community ecologists seek to predict the properties of aggregations of populations, just as population ecologists wish to predict the properties of aggregations of individuals (Table 1). There are many possible properties of aggregations of populations; to date community ecologists have concentrated on a few such as species richness, biomass, diversity and life form. But in spite of the many possibilities, much of traditional community ecology is a description of a community in terms of its component populations - a

species list for different habitats. In other cases abundances are also known, so that the description is a vector of species abundances. These do not begin to exhaust the many possible state variables which might be used to describe the community level of organization, but since we have so much information on vectors of species abundances, these serve as the starting point for assembly and response rules.

What follows is an explicitly 'top down' research strategy. That is, it begins with specified properties of the community level of organization, and asks about the minimum level of knowledge necessary from lower levels of organization to predict the community level properties. Prigogene & Stengers (1984) and Allen & Starr (1982; see also Allen & Hoekstra 1990) have explored the difficulties in relating properties at one level of organization to those of another, and there are compelling arguments for why reductionistic research strategies will not work for certain problems in ecology (Wimsatt 1982; Rigler 1982). None-the-less, what follows is a reductionist approach in that it relates the properties of both populations and individuals to the community level. At the same time, however, it emphasizes that the community level perspective can guide the selection of variables at these lower levels of organization, rather than the reverse.

Assembly rules

The objective of assembly rules is to predict which subset of the total species pool for a given region will occur in a specified habitat. It basically is a problem of deleting those species unsuited to a specified set of environmental conditions (Fig. 1). A first objective would be simply to predict the presence or absence of species in a habitat. The second objective would be to predict
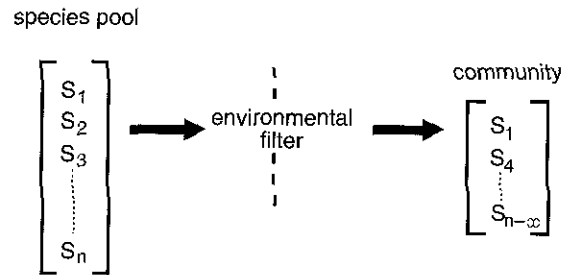

Fig. 1. Assembly rules specify which subset of species in the total pool (left) would tolerate specified conditions and form a community (right).

abundance as well as presence.

The process of constructing communities from species pools is in many ways analogous to the processes of evolution through natural selection. At the heart of our understanding of evolution is the process of natural selection. Habitats serve as filters for genotypes, with the least suited genotypes being filtered out, and the best suited surviving to reproduce. In the case of assembly rules, habitats are again serving as filters. However, in this case, the filters operate on traits and eliminate those sets of traits which are unsuitable to that environment. The species which comprise the community are those which survive the filter.

An early attempt at 'assembly rules' was carried out by Diamond (1975) who used descriptive data (lists of bird species present on islands) to generate rules about species composition on islands of different size. There are two major criticisms of his approach. First, the rules were only descriptions of the data rather than actual predictions. Second, the assumed mechanism was competition. The harsh criticism of this work (Connor & Simberloff 1979) and a long list of exchanges in the

Table 1. Comparison of three levels of organization in ecological research.

	State variables measured	State variable predicted	Organizing concepts
Community ecology	traits environment biomass	species present guilds present diversity	assembly rules response rules
Population ecology	birth rates death rates immigration emigration	population size age classes	life history evolution population regulation
Population genetics	gene flow heterozygosity inbreeding	breeding system mode of reproduction	evolution reproductive allocation

literature thereafter (e.g. Grant & Abbott 1980; Diamond & Gilpin 1982; Gilpin & Diamond 1982; Wright & Biehl 1982; Simberloff 1983, 1984) seem to have detracted from recognition that the goal itself was laudable (Keddy 1989). Is there another approach which focuses on the goal rather than the methodology?

Assembly rules might be developed as follows. We begin with a total species list for an area of landscape - say a bird check list or a plant species list. We also collect systematic data on the traits of these species; these traits could include morphological, physiological or ecological features. We then specify a particular set of environmental conditions. Our objective is then to devise a series of rules that will predict which subset of those species will be found under the specified set of environmental conditions. The best way to visualize this is as a process of deletion where the environment acts as a filter removing species which lack traits for persisting under a particular set of conditions.

Assembly rules therefore require two initial data sets for ecological communities: a species pool, and a matrix giving the traits of species in this pool (Fig. 2). 'Assembly rules' then specify which particular subset of traits (and therefore species possessing them) will be filtered out. More precisely, in the situation where we have knowledge of n traits for each species in the pool, we are looking for a procedure to specify whether or not certain traits (or sets of them) will permit a species to persist under a defined set of environmental conditions. A general (but obviously over-simplified) approach might be as follows: for a specified habitat, we can try to find a series of coefficients using t traits to assign a value of p to each species. That is, for each species in the pool

$$at_1 + bt_2 + ct_3 + dt_4 + \ldots + nt_{14} = p \qquad (1)$$

If $p > P_{crit}$, the species will be present in the habitat. If $p < P_{crit}$, it will not. In this way, a species list for that habitat might be assembled. The exact procedures for doing this most effectively need further work. Two promising examples are the expert systems approach (Noble 1987) and ecosystem assembly grammar (Haefner 1978, 1981). Analogous methods might be used to sort species into expected categories of abundance. Examples of this already exist, and it may be easiest to picture the general approach by considering three of them.

Assembly rules for wetlands

An early attempt to predict species composition in wetlands in this manner is found in van der Valk (1981). Species in prairie wetlands must periodically regenerate from buried seeds. The problem was to predict species composition in these wetlands after a specified change
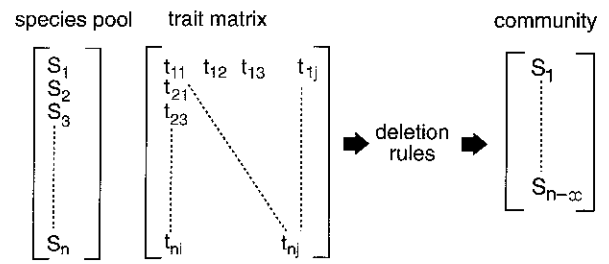

Fig. 2. The general form of assembly rules. Two data sets are needed. The total species pool, and a series of traits for each species. Deletion rules then determine which traits (and therefore which subset of species) form the community.

in water level. A key element of van der Valk's model was the recognition that only one major trait was necessary to predict regeneration: whether or not a species could germinate under water. By measuring only this one trait on all species one can predict which part of the species pool will occur under either set of conditions (Fig. 3). The particular appeal of this model lies in the simplicity of the trait matrix and resulting equations. For a flooded wetland, the equation is simply:

$$at_1 = p$$

where t_1 is % germination under flooded conditions. If $p > 0$, the species will be present in the vegetation.
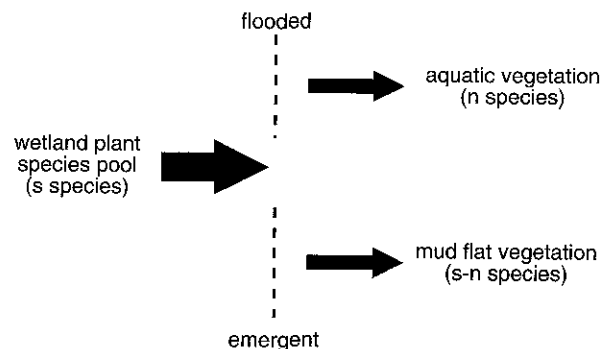

Fig. 3. An example of assembly rules from vegetation cycles in prairie marshes (van der Valk 1981). The species pool (left) can yield either aquatic vegetation or mud flat vegetation depending upon water levels for germination. Ability to germinate under water is the sole trait which must be measured to make this prediction.
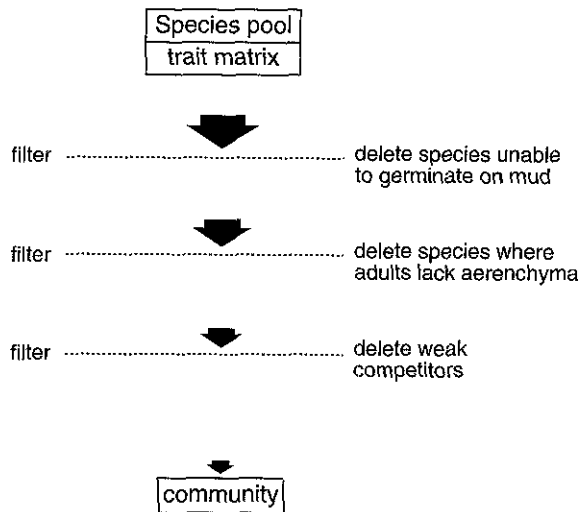
Species pool
trait matrix

filter .... delete species unable
to germinate on mud

filter .... delete species where
adults lack aerenchyma

filter .... delete weak
competitors

community

Fig. 4. Several sequential deletion rules can be likened to filters which progressively reduce the subset of species which will form a community.

Assembly rules for birds on islands

A second example is found in the work of Haefner (1975, 1981) who developed a series of rules for predicting the species composition of foliage-gleaning passerine birds on small coastal islands. His predictor variables were measured characteristics of the islands. His objective was to "construct an algorithm such that, given an arbitrary species pool and an arbitrary collection of environmental factors, the output of the algorithm is a list of species associated with the environment". This was done through an ecosystem assembly grammar (Haefner 1978). In this case the trait matrix consisted of published habitat requirements for the species concerned. Based upon knowledge of an island's habitat features (e.g. tree size), Haefner was able to predict species composition on the islands with surprising accuracy. A potential criticism of this work is that the trait matrix describes habitat characteristics rather than the traits of organisms themselves.

Assembly rules for world vegetation types

A final example can be found in the work of Box (1981) who used methods similar to Haefner to predict world vegetation types. Again, known information about the environmental conditions tolerated by different plant growth forms was used to filter out plant types in the pool until only a subset was left. Box, however, then applied a second set of rules which essentially ranked the remaining subset of species according to their relative competitive abilities. Filtering out all except the dominants left a second, smaller set of plant types, which corresponded well with existing world vegetation types.

In its simplest application, only one rule might need to be applied to assemble a community. However, as Box's work illustrates, a series of sequential deletion rules may be necessary. Fig. 4 shows a hypothetical example: three progressive filters which determine species composition in a wetland which is allowed to dry and then flood permanently. First, the subset of species which initially grows is that which can generate on mud. Once the site is reflooded, species lacking aerenchyma are deleted from the foregoing subset. Finally, the remaining species grow and interact, and only those with strong competitive ability persist. These three filters therefore determine final species composition, and three traits (germination requirements, flood tolerance and competitive ability) must be measured to predict the species which will persist. Note that the third filter is imposed by competition from other species. In other systems or environments, traits conferring resistance to predation may require inclusion. Thus this procedure may include traits conferring resistance to either abiotic or biotic components of the environment.

Response rules

Response rules grow out of assembly rules. They specify how an initial vector of species composition will respond when an environmental factor is changed; [Lewontin (1974) has called this 'transformation rules']. Examples would include: how will prairie vegetation respond to fire or grazing? How will bird communities respond to forest clearance? How will stream invertebrates respond to siltation? There are two ways in which response rules would differ in form from assembly rules. First, one begins with a subset of species already present, and must predict how these will respond to the perturbation (deletion rules). Second, one must re-examine the species pool and trait matrix for species likely to replace those presently occurring (Fig. 5) (addition rules). Again, this could be done by specifying coefficients for measured traits and critical p values as in equation 1. Qualitative examples can again be found.

Fire in vegetation

Noble & Slatyer (1980) have described general approaches to predicting the response of plant communities to perturbation by fire. The two stages of response rules are clearly illustrated in their work.

First, a fire removes certain species from the vegetation. These species can be predicted from knowledge of
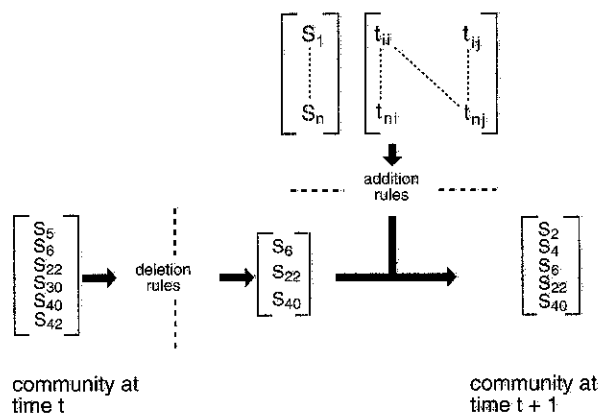
Fig. 5. General procedure for response rules. First the perturbation deletes species from the community, and then based upon the trait matrix, new species are added from the pool. In this case, the vegetation initially consists of six species. Three (S$_5$, S$_{30}$, S$_{42}$,) disappear from the perturbation. They are replaced by two (S$_2$, S$_4$) from the trait matrix, producing a final predicted community of five species.

Fig. 6. Constructing a useful trait matrix requires deciding upon the key life history traits which need to be measured and then developing bioassays for these traits.

traits conferring fire resistance (e.g. bark thickness).

Second, recolonization occurs. Such species can be predicted from traits which allow them to invade newly burned areas (e.g. fire resistance of buried seeds). Although the work is not presented in this context, Noble & Slatyer's work is probably the best example to date of response rules. It is however a qualitative approach. A more quantitative step would be to construct actual equations predicting survival and regeneration under varying fire regimes.

Response rules in wetlands

The above example of van der Valk's (1981) work in wetlands also illustrates both steps of this process. If a marsh is flooded continually, most adults will die from submergence or grazing by muskrats. New vegetation then arises from buried propagules. In terms of the above framework, the deletion rules are constructed from flood tolerances of adults. These might be based upon measured amounts of aerenchyma in each plant species in the pool. The addition rules, based upon regeneration requirements of species, would predict which species can be added to the vegetation. The result is a new vector of species occurrences.
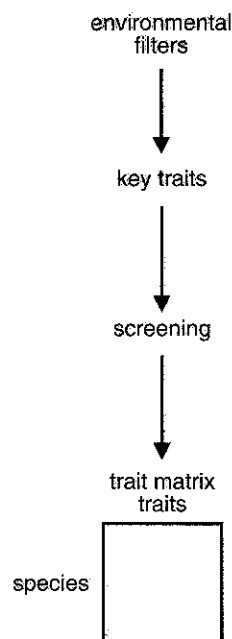
Some methodological considerations

Constructing trait matrices

The two essential data sets for 'assembly rules' are the species pool and the species traits. Species lists for habitats are relatively easy to come by compared with matrices of species traits. Therefore, let us briefly explore trait matrices further. Constructing a trait matrix is a large task (Fig. 6). It requires careful consideration of the key species-environment interactions in any community. That is, it forces explicit consideration of the filters likely to operate and the key traits which organisms possess to protect themselves from these filters. Once this is done, these traits must be measured on all members of the species pool. In the simplest case, this may require simply a morphological measure (e.g. bill length, seed size, gill structure). But in many cases, more complex functional traits will need to be measured such as relative growth rate, competitive ability or tolerance to specified perturbations. This will require developing a bioassay for these attributes so all species can be 'screened' for this property.

This approach was pioneered by Grime (e.g. Grime 1974, 1979) working on the Sheffield flora in England. It has since been applied to an increasing number of traits, e.g. relative growth rate (Grime & Hunt 1975;

Shipley & Peters 1990), competitive ability (Gaudet & Keddy 1988), stress tolerance (Shipley & Keddy 1988), palatability (Sheldon 1987; McCanny et al. 1990). I have discussed this research tactic in more detail elsewhere (Keddy 1990).

We now have increasing numbers of examples of systematically collected life history data including grassland species (Grime, Hodgson & Hunt 1988), wetland species (Shipley et al. 1989; Keddy 1990) and woodland herbaceous species (Givnish 1987). Similarly, Noble & Slatyer (1980) discussed traits which interact with disturbance from fires.

If this were seen as a first step towards predictive ecology, more such matrices would undoubtedly be constructed. It is beyond the scope of this paper to discuss the research activities associated with constructing such matrices, but some key questions would include (1) what traits need to be measured? (2) what are simple and effective methods to screen for them? and (3) what is the minimum number of traits needed for a particular accuracy of prediction?

Species or functional groups?: a question of scale

The preceding examples are based upon a species by species analysis. That is, the components of the species pool are based upon the standard biosystematic approaches found in identification manuals. However, nomenclature designed for taxonomy and phylogenetic reconstructions may not be the best starting point for assembly and response rules (Keddy 1990). Species can be aggregated into groups sharing similar traits. We may be best to begin with assembly and response rules for functional groups, recognizing that predicting which functional groups will be present is easier than predicting which species will represent a particular functional group. This top down research strategy would begin with coarse scale prediction (among functional groups), allowing eventual refinement for fine scale prediction (within functional groups).

This distinction is illustrated by comparing Haefner's work on island birds (1978, 1981) with van der Valk's work on marsh plants (1981). Haefner's rules were much more complex than those of van der Valk, yet they dealt with fewer species. This likely results from Haefner working with a different scale of problem. In the van der Valk example, plants with strongly contrasting ecology were used, so that the model could deal with different functional groups or guilds. In contrast, Haefner selected a group of similar species where a greater degree of precision was needed to separate their habitat requirements. As a limiting case, we might imagine that in some guilds species are complete ecological equivalents (see, for example, Aarssen 1983, 1985; Aarssen & Epp

1990; Ågren & Fagerström 1984; Goldberg 1987; Keddy 1989) in which case no important functional traits would allow us to predict which species will represent a specified functional group.

Studies using functional groups of guilds are becoming increasingly common. Guilds have been described for many bird and mammal communities (e.g. Cody & Diamond 1975; Severinghaus 1981; Pianka 1983; Diamond & Case 1986; Terborgh & Robinson 1986). Functional feeding groups are widely-recognized in invertebrate communities (Cummins 1973; Cummins & Klug 1979). They are also increasingly used in plant community ecology (Grime 1977; Platt & Weiss 1977; Beattie & Culver 1981; Cody 1986; Fitter 1987; Givnish 1987; Day et al. 1988; Keddy 1990).

It may also be the case that predicting which species will represent a particular functional group is qualitatively as well as quantitatively different. We may postulate that the traits which determine the presence or absence of specific guilds deal largely with traits directly related to the environment (e.g. aerenchyma to tolerate flooding, thick bark to tolerate fire). However, within guilds interactions may be among functional equivalents with nearly equal competitive abilities and resource requirements. From the point of view of predicting function of vegetation, it may matter little whether a guild is represented by one or many species.

If our goal is to predict future states of communities for purposes of conservation of biological diversity, how many species and which ones represent a functional group may be critical. To illustrate this, consider the functional group of small evergreen rosette plants in wetlands, termed isoetids (Hutchinson 1975) or stress tolerators (Boston & Adams 1986). These species are characteristic of infertile, wave-washed shorelines, and their presence can be predicted from knowledge of substrate (Pearsall 1920), wave and ice scour (Keddy 1983) or vegetation biomass (Wisheu & Keddy 1989a). However, in some habitats this functional group is represented by the common and widespread species *Lobelia dortmanna* or *Eriocaulon septangulare*. In other cases, this group is represented by the nationally threatened and globally declining species *Sabatia kennedyana* (Keddy 1985; Wisheu & Keddy 1989b). It therefore is critical for conservation that we eventually be able to predict at either the functional group level (presence or absence of evergreen rosette species) or at the species level (presence or absence of *Sabatia kennedyana*). However, given that these species share so many traits, the latter step may require very fine scale resolution. It is also true that the ability to simply predict the conditions for maintaining evergreen rosette species is an essential first step for conserving the threatened *Sabatia kennedyana*.

Conclusion

Assembly rules and response rules provide two clear goals for community ecology which unify several independent lines of research. To devise efficient research strategies we must know in advance what our goals are (Keddy 1989). Assembly and response rules also emphasize prediction rather than understanding. They therefore specify a direction for research and allow us to measure progress towards a goal (see also Peters 1980a, b; Rigler 1982; Keddy 1989). Examples already exist from a variety of community types. If this approach to predictive community ecology is more widely-accepted, several lines of research will need added emphasis. First, more quantitative relationships between traits and environments need to be developed and specified. Second, simple, effective screening techniques for key life history traits are needed. Third, we will need more quantitative approaches to decision rules. There is much to be done, but the existing examples suggest that we have already begun this new phase of predictive community ecology.

References

Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: towards a general evolutionary theory of coexistence in systems of competition. *Am. Nat.* 122: 707-731.

Aarssen, L. W. 1985. Interpretation of the evolutionary consequences of competition in plants: an experimental approach. *Oikos* 45: 99-100.

Aarssen, L. W. & Epp, G. A. 1990. Neighbour manipulations in natural vegetation: a review. *J. Veg. Sci.* 1: 13-30.

Ågren, G. I. & Fagerström, T. 1984. Limiting dissimilarity in plants: randomness prevents exclusion of species with similar competitive abilities. *Oikos* 43: 369-375.

Allen, T. F. H. & Hoekstra, T. W. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. *J. Veg. Sci.* 1: 5-12.

Allen, T. F. H. & Starr, T. B. 1982. *Hierarchy.* University of Chicago Press, Chicago.

Beattie, A. I. & Culver, D. C. 1981. The guild of myrmecochores in the herbaceous flora of west Virginia forests. *Ecology* 62: 107-115.

Boston, H. L. & Adams, M. S. 1986. The contribution of crassulacean acid metabolism to the annual productivity of two aquatic vascular plants. *Oecologia (Berl.)* 65: 615-622.

Box, E. O. 1981. *Macroclimate and plant forms: an introduction to predictive modelling in phytogeography.* Junk, The Hague.

Cody, M. L. 1986. Structural niches in plant communities. In: Diamond, J. M. & Case, T. I. (eds.) *Community ecology,* pp. 351-405. Harper & Row, New York.

Cody, M. L. & Diamond, J. M. 1975. *Ecology and evolution of communities.* Belknap Press, Harvard University Press, Cambridge.

Connor, E. F. & Simberloff, D. 1979. The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140.

Cummins, K. W. 1973. Trophic relationships of aquatic insects. *Annu. Rev. Entomol.* 13: 133-206.

Cummins, K. W. & Klug, M. J. 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* 10: 147-172.

Day, R. T., Keddy, P. A., McNeill, J. & Carleton, T. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology* 69: 1044-1054.

Diamond, J. M. 1975. Assembly of species communities. In: Cody, M. L. & Diamond, J. M. (eds.) *Ecology and evolution of communities,* pp. 342-444. Belknap Press, Harvard University Press, Cambridge.

Diamond, J. M. & Case, T. J. 1986. *Community ecology.* Harper and Row, New York.

Diamond, J. M. & Gilpin, M. 1982. Examination of the 'null' model of Connor and Simberloff for species co-occurrences on islands. *Oecologia (Berl.)* 52: 64-74.

Fitter, A. H. 1987. An architectural approach to the comparative ecology of plant root systems. *New Phytol.* 106: 61-77.

Gaudet, C. L. & Keddy, P. A. 1988. Predicting competitive ability from plant traits: a comparative approach. *Nature* 334: 242-243.

Gilpin, M. E. & Diamond, J. M. 1982. Factors contributing to the non-randomness in species co-occurrences on islands. *Oecologia (Berl.)* 52: 75-84.

Givnish, T. J. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol.* 106: 131-160.

Goldberg, D. E. 1987. Neighbourhood competition in an old-field plant community. *Ecology* 63: 1211-1223.

Grant, P. R. & Abbott, I. 1980. Interspecific competition, island biogeography and null hypotheses. *Evolution* 34: 332-341.

Grime, J. P. 1974. Vegetation classification by reference to strategies. *Nature* 250: 26-31.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 11: 1169-1194.

Grime, J. P. 1979. *Plant strategies and vegetation processes.* Wiley, Chichester.

Grime, J. P. & Hunt, R. 1975. Relative growth rate: its range and adaptive significance in a local flora. *J. Ecol.* 63: 393-422.

Grime, J. P., Hodgson, I. G. & Hunt, R. 1988. *Comparative plant ecology.* Unwin Hyman, London.

Harper, J. L. 1977. *Population biology of plants*. Academic Press, London.

Harper, J. L. 1982. After description. In: Newman, E. I. (ed.) *The plant community as a working mechanism*, pp. 11-25. Blackwell, Oxford.

Haefner, J. W. 1978. Ecosystem assembly grammars: generative capacity and empirical adequacy. *J. Theor. Biol.* 73: 293-315.

Haefner, J. W. 1981. Avian community assembly rules: the foliage-gleaning guild. *Oecologia* 50: 131-142.

Hutchinson, G. E. 1975. *A treatise on limnology. Vol. 3. Limnological botany*. John Wiley and Sons, New York.

Keddy, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology* 64: 331-344.

Keddy, P. A. 1985. Lakeshores in the Tusket River valley, Nova Scotia: distribution and status of some rare species, including *Coreopsis rosea* Nutt. and *Sabatia kennedyana* Fern. *Rhodora* 87: 309-320.

Keddy, P. A. 1989. *Competition*. Chapman and Hall, London.

Keddy, P. A. 1990. The use of functional as opposed to phylogenetic systematics: a first step in predictive community ecology. In: Kawano, S. (ed.) *Biological approaches and evolutionary trends in plants*. Academic Press, Harcourt Brace Jovanovich, London.

Lewontin, R. C. 1974. *The genetic basis of evolutionary change*. Columbia University Press, New York.

McCanny, S. J., Keddy, P. A., Arnason, T. J., Gaudet, C. L., Moore, D. R. J. & Shipley, B. 1990. Fertility and the food quality of wetland plants: a test of the resource availability hypothesis. *Oikos* 59: 373-381.

McIntosh, R. P. 1985. *The background of ecology*. Cambridge University Press, Cambridge.

Noble, I. R. 1987. The role of expert systems in vegetation science. *Vegetatio* 69: 115-121.

Noble, I. R. & Slatyer, R. O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.

Pearsall, W. H. 1920. The aquatic vegetation of the English Lakes. *J. Ecol.* 3: 163-201.

Peters, R. H. 1980a. Useful concepts for predictive ecology. *Synthese* 43: 257-269.

Peters, R. H. 1980b. From natural history to ecology. *Perspect. Biol. Med.* 23: 191-203.

Pianka, E. R. 1983. *Evolutionary ecology, 3rd ed.* Harper and Row, New York.

Platt, W. J. & Weiss, I. M. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. *Am. Nat.* 3: 479-513.

Prigogene, I. & Stengers, I. 1984. *Order out of chaos*. New Science Library, Shambala, Boulder, CO.

Rigler, F. H. 1982. Recognition of the possible: an advantage of empiricism in ecology. *Can. J. Fish. Aquat. Sci.* 39: 1323-1331.

Severinghaus, W. D. 1981. Guild theory development as a mechanism for assessing environmental impact. *Environ. Manage.* 5: 187-190.

Sheldon, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology* 68: 1920-1981.

Shipley, B. & Keddy, P. A. 1988. The relationship between relative growth rate and sensitivity to nutrient stress in twenty-eight species of emergent macrophytes. *J. Ecol.* 76: 1101-1110.

Shipley, B., Keddy, P. A., Moore, D. R. J. & Lemky, K. 1989. Regeneration and establishment strategies of emergent macrophytes. *J. Ecol.* 77: 1093-1110.

Shipley, B. & Peters, R. H. 1990. A test of the Tilman model of plant strategies: relative growth rate and biomass partitioning. *Am. Nat.* 136: 139-153.

Simberloff, D. 1983. Sizes of coexisting species. In: Futuyma, D. J & Slatkin, M. (eds.) *Coevolution*, pp. 404-430. Sinauer, Sunderland.

Simberloff, D. 1984. The great god of competition. *The Sciences* 24: 17-22.

Terborgh, J. & Robinson, S. 1986. Guilds and their utility in ecology. In: Kikkawa, I. & Anderson, D. J. (eds.) *Community ecology: pattern and process*, pp. 65-90. Blackwell, Melbourne.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* 62: 688-696.

Wimsatt, W. C. 1982. Reductionistic research strategies and their biases in the units of selection controversy. In: Saarinen, E. (ed.) *Conceptual issues in ecology*, pp. 155-201. D. Reidel, Dordrecht.

Wisheu, I. C. & Keddy, P. A. 1989a. Species richness - standing crop relationships along four lakeshore gradients: constraints on the general model. *Can. J. Bot.* 67: 1609-1617.

Wisheu, I. C. & Keddy, P. A. 1989b. The conservation and management of a threatened coastal plain plant community in Eastern North America (Nova Scotia, Canada). *Biol. Conserv.* 48: 229-238.

Wright, S. J. & Biehl, C. C. 1982. Island biogeographic distributions: Testing for random, regular, and aggregated patterns of species occurrence. *Am. Nat.* 119: 345-357.