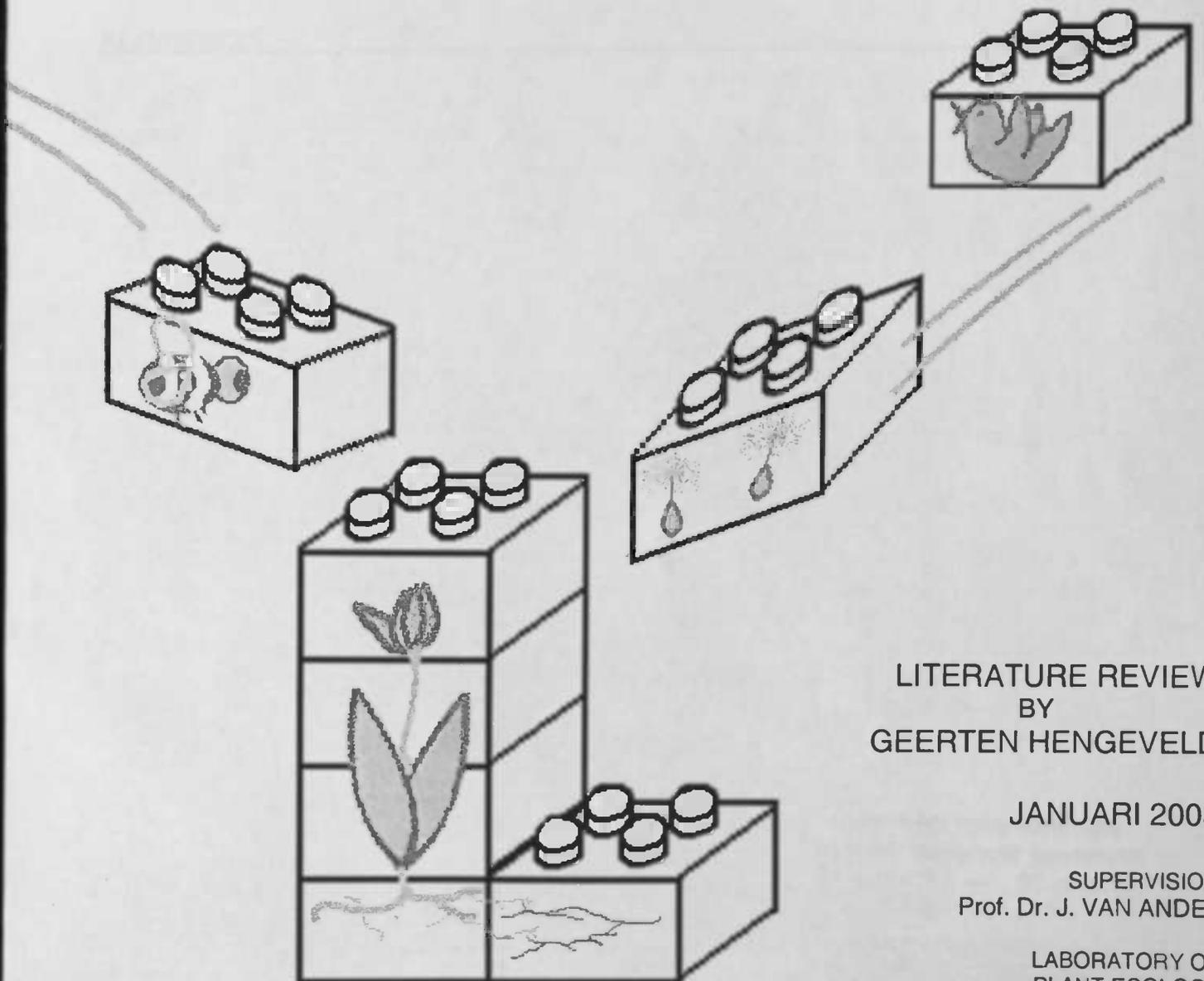


# ASSEMBLY RULES

CONCEPT AND METHODOLOGY



LITERATURE REVIEW  
BY  
GEERTEN HENGEVELD

JANUARI 2003

SUPERVISION  
Prof. Dr. J. VAN ANDEL

LABORATORY OF  
PLANT ECOLOGY  
RIJKSUNIVERSITEIT GRONINGEN

# Contents

<u>INTRODUCTION</u>	<u>1</u>
<u>WHAT ARE ASSEMBLY RULES?</u>	<u>2</u>
<u>ASSESSMENT OF ASSEMBLY RULES</u>	<u>5</u>
<u>NULL MODELS FOR COMMUNITY ASSEMBLY</u>	<u>6</u>
<u>DISCUSSION</u>	<u>8</u>
<u>REFERENCES</u>	<u>9</u>

## Introduction

The term 'assembly rules' was first coined by Diamond in 1975. But the concept of constraints on the (co-)existence of species at a certain spot can be traced back further than that. The problem of 'the constraint on the development of a community' had already been explored by both Clements and Gleason in their pioneer works on succession (Booth & Larson 1999). In the early decades of ecology in the twentieth century most ecologists took, inspired by the work of Clements, for granted that communities exist as natural, repeated, internally organised units with a considerable degree of integration which governed their structure, function, development or succession and even their evolution. Gleason openly attacked them and offered an alternative concept predicated on the individualistic capabilities of species, continuous variation of the environment and diverse probabilities of arrival of propagules (McIntosh 1995). The topic was then not left untouched as argued by May (1984): 'In 1944 [...] Lack, Elton, Varley, and others used various lines of evidence to argue that competition is a major factor in structuring plant and animal communities. Others argued to the contrary'. Still Diamond's book-chapter in 1975 gave a big impulse to the discussion.

The discussion around ecological communities and their assembly is littered with side-tracks and confusion. The old controversy between Clements and Gleason is still standing, although not many people will nowadays go as far as Clements in promoting the community as a super-organism. But the definition of the term community and the debate about the mere existence of them will rouse many ecologists to their writing table to produce more articles on that subject (e.g. Wilson 1991, Keddy 1993, Palmer & White 1994, Mirkin 1994, Dale 1994, Wilson 1994, Looijen & van Andel 1999 and Parker 2001). Drake (1990 cited in McIntosh 1995) even discarded most of what has been studied as communities or assemblages as 'not satisfying a community definition' or possessing 'even a hint of community properties', after which he comes with a new definition about which many other workers will have their doubt.

'Community ecology is often seen as being 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' (Keddy 1992). But Drake *et al.* (1999) argue that 'because all biological systems are assembled in a dynamical sense, any generality in the process would prove valuable to our understanding of nature', apparently they do not agree with Keddy's (1999) call that the time of making predictions has come. To make those predictions, more accurate information about the assembly of a community is needed. The 'mechanics of community assembly' are the phenomena that form 'the primary strut in the framework for a general theory of community organisation' (Drake 1990 cited in McIntosh 1995).

It is these 'mechanics of community assembly', that this paper is about. To find assembly rules, we should (1) 'formulate hypotheses on what generalised assembly rules might exist,' (2) 'find ecological situations to test those hypotheses and' (3) 'see whether there is any evidence for the rules, subject to the usual statistical tests to ensure that the patterns are not due to chance' (Wilson 1994). These three steps will also be the guidelines in this paper. First we will discuss the different opinions on the definition of assembly rules, trying to get one, or several general definitions of the assembly rules that are commonly accepted. Then we will review the methodologies of several workers in the field of assembly rules, addressing problems of the ecological systems they use and their experimental set-up. After that we will discuss the problems that arise when one is to statistically test spatial distributions of species and the various null-models that have been proposed. In the end we will try to integrate these three steps and discuss the problems that still remain. These topics will give a glance on some

of the important factors of the discussion on the concept of assembly rules. There are several peripheral problems that have a large influence on the discussion at hand, like the definition of the community itself, the determination of the species pool and the application of assembly rules in conservation biology. Despite their influence and importance for a good view on the following discussion, they fall beyond the scope of this paper.

## What are assembly rules?

Understanding assembly rules is one of the major tasks of community biology (Wilson 1994). But what is an assembly rule? The first answer one would probably give is that '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' (Keddy 1992). But although there is this intuitive ring to the term, there still is not only a lot of disagreement on the nuances, but also on a quite fundamental level; what processes and forces should or should not be included into these rules, whether or not the rules should be universal, about whether these rules are deterministic or leave opportunities for stochastic processes and about what levels of the environment should be included. If we finally agree on what those assembly rules are, then we could ask the question what should we know about the rules? Do we need to have in-depth information about all the components of a community, or are more superficial data enough to make long-term predictions?

There are two major topics that we will discuss here, the first concerns the questions: 'what effects are included in an assembly rule', the second is about the generality of the assembly rules and the question 'how specific should we make them'. Afterwards we will discuss some dilemmas that stem from these problems.

### At what level do assembly rules act?

We can divide publications on assembly rules in two groups. Within the first group the argument is that assembly rules can include any constraints on the species pool. The second group has a more narrow view on assembly rules. They include only the constraints placed upon species by other species (Booth & Larson 1999):

- The first group – let us call them the 'broad-sense-group' – states that assembly rules are there to predict the assembly of all the species in a community in a given ecosystem from a geographically defined species pool (e.g. Keddy 1992, 1999 and Drake *et al.* 1999). For this group the inter-trophic relations are very important for the assembly of the community.
- For the second group – the 'narrow-sense-group' – these assembly rules only describe the interactions between similar species (i.e. species on the same trophic level) that all

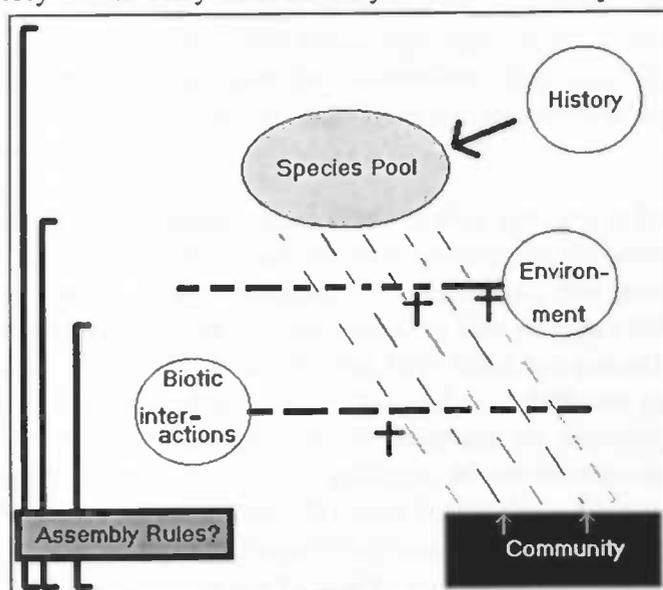


Fig 1.1 The different sieves that filter the species in the species pool to become the community (following Keddy 1999). At what level do assembly rules act?

are suited to live in a given habitat, only not necessarily together. The focus of this group has been on interactions within a trophic level, like competition as an important assembly rule (e.g. Diamond 1975, Fox 1999).

Diamond focused the attention on the coexistence and the absence of animal species that belong to the same guild or to the same taxonomic group. Combinations of species could be forbidden or allowed (Diamond 1975). It is therefore understandable that for him competition is the most important interaction in the assembly of a community. This focus on one taxonomic or trophic group is not uncommon among ecologists who tend to be either 'plant ecologists' or 'animal ecologists' and thus focus on interactions either between plants or between animals. Still there was a lot of critique on the idea that competition is the major factor guiding community assembly (e.g. Keddy 1992).

The broad-sense-group likes to see the assembly rules acting as a filter on the species pool. They tend to divide the rules into environmental and interaction rules; in this way, assembly rules are the community level of natural selection, filtering those species most fit to the environment (Keddy 1992, 1999). Sometimes authors from this group seem to forget the biotic interactions: 'It basically is a problem of deleting those species unsuited to a specified set of environmental conditions' (Keddy 1992), but on other occasions they do explicitly include both levels of interactions (with biotic and abiotic environment) into their sieve model (Drake *et al.* 1999, Booth & Larson 1999). And it is not that the narrow-sense-group ignores the importance of environment and history on the assembly of an ecological community, but they are afraid of losing a term for only the biotic interactions. 'If this happens to 'assembly rule' with the inclusion of the environmental sieve, another term will have to be invented to cover real assembly rules, based only on species interactions. That would be a nuisance' (Wilson 1999). Therefore the disagreement is not on what factors are acting on the community, but more on what level we define the rules. It has been suggested (Brown 1987 cited in McIntosh 1995) that the functional organisation of communities could be characterised by two classes of rules: 1) Capacity rules including all extrinsic processes, both physical and biotic, that affect the capacity of the environment to support the community in question, and 2) allocation rules, the biotic interactions, such as competition, intrinsic to the community. This comes down to the before mentioned broad-sense approach, with a clear distinction for the narrow-sense readers. Brown states that the allocation rules (i.e. the narrow-sense rules) 'ultimately determine the outcome of the interactions within the assemblage' (Brown 1987 cited in McIntosh 1995).

One of the factors that have a major influence on the presence or absence of a species, is the past. Gleason already acknowledged the importance of early arrival of a species for its future success (cited in McIntosh 1995). Drake found, in his laboratory experiments, the great importance of the order of assembly on the outcome of the process, making him to argue that 'assembly rules have a strong historical component, which means that such rules are patently dependent on context' (Drake 1990a cited in McIntosh 1995). Still this makes it difficult for some to allow this past into their definition of the assembly rule: 'If there are no assembly rules, any pattern we discover in vegetation would be due to patterns of environmental patchiness, or to history' (Wilson 1994). What we ought to consider here is that there are very few communities that start on a blank sheet. The process of community assemblage is closely linked to the succession of communities, with constant invasions and extinctions. This makes the different processes hard to untangle: the biotic environment is as much present for a new settler as is the physical environment and the newcomer will probably not be capable of distinguishing between the two. For a large predatory mammal, the interesting biotic interactions will be with rival predators and with their prey, while the difference between

plants or rocks for cover will be quite trivial. So for this particular species, the plants belong to the 'physical' environment and the prey and other predators to the biotic interactions. This also shows the importance of the order of arrival and thus the influence of historic events.

### Functional groups and generalisation

Calls have been heard for definition of the formal structure of assembly rules. It has been suggested to avoid species names and specific locations in formulating assembly rules to allow extrapolation of such rules to other species and places and anticipated 'considerations of meta-rules for the formulation of assembly rules' (Haefner 1988 cited in McIntosh 1995). Attempts of this kind have been made. While Diamond originally came with species-specific assembly rules, naming those species combinations that were, or were not allowed, later authors started to work on the assemblage of species according to their functional position in the community (e.g. Fox 1999). This step towards a higher level of organisation is due to the idea that if assembly rules are to have any general meaning, they should be 'generalisable to systems with very different taxonomic composition' (Keddy 1992). Keddy also states that we should recognise that 'predicting which functional groups will be present is easier than predicting which species will represent a particular functional group' (Keddy 1992).

One of the difficulties of this approach is the recognition of a functional group. The uncertainties of functional group membership (Connor & Simberloff 1984, Simberloff *et al.* 1999) will lower the predictive power of the assembly rules resulting from this membership. And the original assembly rules were constructed to determine the outcome of competition within a functional group, not the stacking of different functional groups (Diamond 1975, Gilpin & Diamond 1984).

### Dilemmas

Summarising, there are three levels of the environment that influence the assembly of species in a community: (1) the historical background, (2) the physical environment, (3) the biotic environment. At which of these levels the assembly rules work, seems to be merely a matter of definition, rather than a fixed law of nature. This makes any generalisation of the assembly rules to real laws of nature a tricky business after all, if we cannot decide at what level the rules kick in, how can we formulate any general rules? If the assembly of a community is approached from a 'functional groups' point of view, comparable problems arise; the main functional groups within a community are partly determined by the physical environment – it is the lack of nitrogen in the soil that invokes the presence of the functional group of nitrogen fixing plants – but one of the most striking questions of community biology is about the choice for a particular member of a functional group instead of for another member of the same group, and that problem still remains in the functional approach. Although some argue that it may 'matter little whether a guild is represented by one or many species' (Keddy 1992). Drake *et al.* (1999) even argue that there are two different types of assembly rules, one type 'defined by the presence of functioning levels of organisation (e.g. individuals, populations, guilds) operating at various levels of scale', the other type 'defined as the dynamical fabric upon which the system operates'. So the first would be concerned with processes of community assembly as imposed by the presence or absence of certain species or combinations of species, while the other type would be concerned with the patterns that might appear due to the present pattern.

But what should the formulation of an assembly rule be? We have seen the discussion about biotic vs. physical environment and functional groups vs. species-specific rules. But this does not tell us how to formulate the rules. There are some authors who say that 'assembly rules

describe patterns that are evidence of [...] processes [by which communities are assembled]'. They claim that the rules we can find are only 'subtle tendencies' (Wilson 1994, 1999). Others state that 'the important task of community-ecology is to find out how these processes work precisely and [that] there is a need to quantify these processes and formulate quantitative rules for the assembly of a community' (Keddy & Weiher 1999). These two opposing views are hard to reconcile, because they are fundamentally different. It originates from a bottom-up or a top-down approach, from the difference between theoretical ideal and the empirical truth that getting information on all the traits of a species is a laborious task (Fox 1999). But 'ecologists should not permit a single philosophical view to be used to dissect the structure of nature' (Booth & Larson 1999). Diamonds' assembly rules (Diamond 1975) were based on an analysis of patterns in empirical data (Fox 1999). Rules derived in this way are by definition probabilistic, they indicate a probability of the emergence of a certain pattern. At present most authors seem to agree on the high influence of stochastic effects on ecological systems and consequently on the uncertainties within predictions stemming from them (e.g. Keddy 1992, Wilson 1999, Drake *et al.* 1999). But it must be said that a more complex system will probably have a higher number of stochastic events and hence will yield a less certain prediction (Booth & Larson 1999).

## Assessment of assembly rules

Apart from conceptual problems with the definition of assembly rules, there are also differences in the design of the actual research. What are the different methodologies that are used to find assembly rules in nature or in the laboratory?

There are many studies on the assembling of communities. Most studies focus on the interactions among species in the same taxonomic groups, research is either done on plant-communities or bird communities. Within the studies of community assembly there is a strong bias towards vertebrates (Keddy & Weiher 1999). A clear distinction again seems to be between the two groups that were also mentioned in the previous chapter. The narrow-sense group, focussing on interactions between species, will mostly look for patterns in species co-occurrence, while the broad-sense group, focussing on environmental constraints, will look for patterns in the relationship between traits of species and their environment (Keddy & Weiher 1999). A third group makes use of microcosms, laboratory experiments with communities of micro-organisms. This group can actually make the step from describing observed patterns to experimenting with the effects of different factors on communities that are equal on all but the factor to be tested (Drake *et al.* 1996).

Since it has been argued that many assembly rules are highly context-dependent (Drake *et al.* 1996), the choice for a particular system and in most cases for a particular taxonomic group, will have a high influence on the assembly rules that might be found. Some researchers claim that their system is 'a natural experiment' (Diamond 1975, Booth & Larson 1999). But the choice of systems is very various. Many researchers use systems with high and similar amounts of productivity. Others prefer systems in harsh environments, that start 'with their backs against the wall', thus reducing both the number of components in the system and the influence of historical and other effects that fall beyond the scope of their research (Booth & Larson 1999). The commonly applied reductionistic approach, reducing the problem to components at a logistically manageable level, is not equally well applicable to the different systems. Drake *et al.* (1999) seriously warn for problems associated with the reductionistic approach: (1) The natural systems will, even in reduced form, be most likely more complex than the observer can handle and (2) when reducing the system to components, not all system-

level features will be apparent. But unfortunately most systems do not allow for a total system analysis.

Apart from the choice of their model system, being either a guild of seed-eating birds on islands in high productive tropical rainforests or all the flora on a bare rocky outcrop, another important factor to be considered is what trait in the species is to be related to what gradient in the environment (Wilson 1994). If there are no apparent patterns in species number, then there could of course be patterns in species relative abundances or the patterns might be at the level of energy flows or functional groups (Caswell 1976). And if one morphological property is not correlated with co-occurrence, another property might. It is from this last possibility that a new discussion is started: how arbitrary are functional groups? (Simberloff 1984, Fox 1999, Wilson 1999). How much *a priori* information is needed before functional groups can be assigned, and on what level should we assign them? But since ecology has the problem of being of such a level of complexity, that it 'contains too many components to be treated analytically and too few for statistical analysis [...] functional groups, guilds and traits all have the potential to simplify medium number systems to small number systems' (Keddy 1999).

A last problem of research on community assembly is the existence of different interfering scales. Interactions between fungi, trees, mammalian herbivores and insects are all on such different scales, that studying the whole complex of the community, might be very difficult and laborious. Drake *et al.* (1996) say they 'are not surprised that few general trends have emerged from *community* studies when in fact such studies fail to agree on the level at hand'. Drake's microcosms might be a solution for such problems. Those laboratory experiments 'first reduce and then increase complexity in a controlled fashion' (Drake *et al.* 1996). We could of course first focus on the key interactions in any community, 'forcing considerations of those filters likely to operate and the key traits which organisms possess to protect themselves from these filters' (Keddy 1992). This still will leave a laborious task to be conducted, since it is by no means clear or generally accepted which interactions or traits are of higher importance than others.

Summarising, the choice of model systems is not an easy task. Not only do researchers tend to cling on to the kingdoms of their training (being either plants, mammals, insects or micro-organisms), these different models all yield different insights and hypotheses on the community and its assembly. In micro-organism studies the emphasis is more often on intertrophic levels, whereas the mammalian studies are often focused on one trophic level only. Apart from that, different ideas on reductionistic and holistic approaches will always yield different ideas about on what scale and on what systems one will get the best insights.

## Null models for community assembly

Diamond's reinvention of the assembly rules was almost immediately followed by an article by Caswell (1976) on the development of neutral models for the structuring of communities. Although not written in reaction to Diamond's assembly rules, it does clearly attack the assumption that community structure is mainly developed and maintained by biological interactions. Caswell argues that the basic activity of scientists is to develop a number of hypotheses that will explain observed patterns in nature. 'Often considerable power can be added to this approach by the use of a "neutral" model. In such a model the entire set of forces competing for a place in the explanation of the pattern are eliminated. The resulting model is neutral with respect to those factors' (Caswell 1976). Such a neutral - or 'null' - model can be used to make predictions about patterns in the absence of the hypothesised factors. Those

predicted patterns can then be tested against the observed patterns in nature. If the patterns predicted by the neutral theory do not resemble the observed patterns significantly, the factors that were omitted are more likely to be important in the formation of the observed patterns. If the neutral model is not rejected, the conclusion that biological interactions do not play the predicted role can be avoided. 'Biotic interactions might operate as specified, but (1) the results might be apparent only in total communities rather than taxonomically defined communities [...]; (2) the results might be apparent only in smaller, more tightly integrated subsets of a taxonomically defined community [...]; and (3) the results might express themselves in terms of biomass or energy flow instead of numbers of individuals' (Caswell 1976). One could also question other theoretical assumptions made in the neutral model.

Where Caswell used many studies as a reference for his neutral model, and weakened his conclusion that biotic interactions may not be the main structuring factor in communities, Connor & Simberloff (1979) were more aggressive in their attack of Diamond's approach. They used the same data set as Diamond did, to make a random distribution of the same species on the same islands with the purpose to test for any pattern in co-occurrence claimed by Diamond. They found no evidence; the observed patterns were not significantly different from the patterns generated by the null model (Connor & Simberloff 1979, 1984). This resulted in a very heated debate between Connor & Simberloff and Gilpin & Diamond in the 1984 volume edited by Strong *et al.* reflecting the debate during the 1981 conference in Wakulla Springs (May 1984). One argument Gilpin & Diamond (1984) use is the same as the main argument Caswell (1976) already used for his own models: the group of species used in the model is not the group of species that have interactions with each other. But according to Gilpin & Diamond there were more flaws in the Connor & Simberloff approach. Their main critique on the approach is that it is an *a posteriori* prediction based on an observed species distribution that already expresses the result of biological interactions. Because 'the proper "null hypothesis" to test effect X consists of "everything-significant-except-X' (Gilpin & Diamond 1984, *sensu* Tokeshi 1986 cited in Wilson 1999), a model that uses observed data, which could be structured in distribution and in number by the factor to be tested, is foolish and even dangerous (May 1984, Gilpin & Diamond 1984). Connor & Simberloff then argue that most of the assumptions, that they were accused of neglecting, were not explicitly made in Diamond's original work (Connor & Simberloff 1984), blaming there faults on Diamond. But that does not mean that the points of critique are not valid. And at the same time, disqualifying a neutral model does not mean that the alternative model is automatically true (May 1984).

The development of neutral models is very difficult. Some authors state that 'to preserve biological realism' (Simberloff *et al.* 1999), species number on a specific site and number of sites inhabited by a species should be the same as in the observed data set (Connor & Simberloff 1979, Simberloff *et al.* 1999). Others believe that this type of *a posteriori* null model, using the same species numbers as observed, is to assume the results (May 1984, Gilpin & Diamond 1984), and thus would not yield any deviation from the null model. Some of those authors think that to construct decent null models is either impossible or at least beyond the possibilities of present day science (Diamond & Gilpin 1984, Weiher & Keddy 1999b). In this light a few examples of the use of the null model approach are interesting; Colwell & Winkler (1984) use modelled communities, with and without biological interactions as observational data, testing in this way for biases inherent to the design of a null model. They conclude that because it is impossible to know the evolutionary and ecological history of a community, and thus the impossibility to correct for the 'ghost of competition past' or for correlations to traits associated with selection pressures from the past, one should be very careful in constructing null models (Colwell & Winkler 1984). Another example I

would like to add is the use of multiple models of increasing complexity as in the work of Haefner (1988 cited in McIntosh 1995); 'Haefner (1988) constructed a series of models ranging from random 'null' models to those incorporating increasing ecological detail and compared their predictions to a community of *Anolis* lizards. Haefner's results indicated that a complex competition model performed better than most random models when applied to data from another island' (McIntosh 1995).

'The null hypothesis tested in any analysis of biogeographical data is not that empirical data do not differ from random ones, but that they do not differ from patterns generated by a particular model of the world' (Colwell & Winkler 1984). Starting their article with those words, the authors conclude with the warning: 'Community-level analyses are of great heuristic value in detecting community patterns. The patterns thus detected, however, must not be overinterpreted as proof of process'. May (1984) adds another important warning; 'given some apparent pattern in the organisation of an ecological community, does it really derive from biological interactions among and within species? [...] or may the pattern simply be a statistical property of the system – a true pattern, but having no biological significance'. At the recent symposium on spatial ecology organised by the NecoV (22 November 2002, Wageningen), this was amplified by De Roos. He argued that although we can very easily find patterns in biological systems, and most probably can replicate these patterns with a plausible model, there are other, equally or less plausible, models that could yield the same patterns, not because the underlying processes are the same, but because patterns are inherent to spatial distributions.

Summarising, there are two problems with the statistical testing of spatially structured systems. The first problem is with the construction of a 'null model', is it possible to untangle the different hypothesised effects on the data to such an extent that predictions can be made of what the data would look like without the influence of these effects. The second problem is with the recognition of patterns and their origin. Are all patterns we see the result of biological processes or are some patterns a result of the spatial structure of the system? The first problem is one that most biologists will recognise, especially in the work of others. To deal with this problem there is the need of being sceptical of all models, how plausible they may seem. Understanding the hypotheses and mathematical derivations that underlie a certain model, and judging the value of each (null-)model individually will be necessary to restrain ourselves of falling victim to this problem. The second problem is probably beyond the scope of the biology and will need a firm mathematical attention.

## Discussion

Ecologists seem to define as a community anything from all the biota in an ecosystem (also called the biocoenosis) to groups of similar and related species in the same habitat (also called guilds). Some authors refer to the community as an integrated system with properties that exceed the sum of the parts and resilient to changes, whereas others look at the community as nothing more than a randomly assembled group of individuals. 'The ornithologist's "community" is the community ecologist's "guild" and the palaeontologist's "noise" ' (Drake *et al.* 1996). This confusion seems to indicate most of the discussion on the definition of the assembly rules. Differences in interpretation of the language used is one of the main problems of this field of research (Booth & Larson 1999). Not only because different researchers use different levels to apply the rules to, but also because most researchers seem 'to have missed that the original chapter that offered the term assembly rule simply took advantage of an often used technique of ecological pedagogy: when faced with a truth that more or less applies at least some of the time, try to present that truth in the form of a 'law' or, when even greater

uncertainty is involved, as a 'rule' (Booth & Larson 1999). As we all know 'rule has a satisfying sound of something to be rigorously followed, like the Golden Rule, but it is not clear that assembly rules for communities currently proposed are more regular than what were called principles in an earlier era in spite of more quantitative apparatus' (McIntosh 1995). Diamond was not proposing anything new when he invented the term assembly rule (Booth & Larson 1999), he merely adapted the concept that there are certain regularities in communities to a new era of 'exact thinking' in ecology.

Still the assembly of a community is a difficult concept because the 'particular species and community types are but transitory occurrences at any location' (Keddy, 1999). Communities are subject to succession, constantly changing from one type to another. The assembly of a community is therefore automatically the destruction of another and the present community will make the rules for the assembly of a new community along the assembly trajectory. So when Booth & Larson (1999) put forward the problem that 'one difficulty with empirical field studies is determining whether the identified mechanisms are important to community development or whether they are simply important in maintaining the community', they miss the fact that most communities are part of an ever changing dynamical natural environment.

The form of the assembly rule is not clear. Are the rules describing possible new patterns that will arise now the present pattern is there, or is community assembly basically Darwin's 'survival of the fittest' but then on a shorter time scale (*sensu* Keddy 1999), forcing the species to survive in an environment created not only by physical factors, but also influenced and moulded by the biotic surroundings? Is the general purpose of the assembly rules to gain insight and be able to predict the outcome of this struggle for existence? Is the community the battlefield, where several species can try their luck, the only price for victory being persistence and more battles to come? 'Further progress will hinge on the development of a general and robust theory of complex systems, self-organisation and the creation of emergent order' (Drake *et al.* 1999), where all the above mentioned levels are probably interacting with each other.

The very nature of assembly rules is probably only a definition problem. In the future we might be able to make the predictions that Keddy is so hard looking for (Keddy 1992, 1993, 1999, Keddy & Weiher 1999), but the current progress in the field of the assembly rules is, despite over 25 years of research, still pioneering the possibilities. For the moment we could possibly only state that 'clearly, assembly pervades every aspect of biological structure and organisation, but the general nature of control within and among systems remains elusive' (Drake *et al.* 1999). The first focus of future research should therefore be to find out what the general nature of control is within ecology. Do we turn to energy flows, or do we stay with the current trait-environment or competition paradigms or do we combine aspects of all of them. Perhaps new possibilities of individual-based simulations, enabling the modelling of ecology from an individualistic point of view will give more insight.

## References

Booth, B. D. & D. W. Larson, 1999, Impact of language, history and choice of system on the study of assembly rules in Weiher, E. & P. Keddy, 1999, *Ecological assembly rules, perspectives, advances, retreats*. Cambridge University Press, Cambridge, pp 206-229

Caswell, H., 1976, Community structure: a neutral model analysis, *Ecological monographs* 46: 327-354

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

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

Connor, E. F. & D. Simberloff, 1984, Neutral models of species co-occurrence patterns, in Strong, D. R., D. Simberloff, L.G. Abele & A. B. Thistle eds., 1984, *Ecological Communities, conceptual issues and the evidence*, Princeton University Press, Princeton, pp 316-331

Dale, M. B., 1994, Do ecological communities exist?, *Journal of Vegetation Science* 5: 285-286.

Diamond, J. M., 1975, Assembly of species communities, in Cody, M. L. & J.M. Diamond eds., 1975, *Ecology and evolution of communities*, Harvard University Press, Cambridge, Massachusetts pp 342-444

Drake, J.A., C.R. Zimmermann, T. Purucker & C. Rojo, 1999, On the nature of the assembly trajectory, in Weiher, E. & P. Keddy eds., 1999, *Ecological assembly rules, perspectives, advances, retreats*, Cambridge University Press, Cambridge, pp 233-250

Drake, J.A., G.R. Huxel & C. L. Hewitt, 1996, Microcosms as models for generating and testing community theory, *Ecology* 77: 670-677

Fox, B.J., 1999, The genesis and development of guild assembly rules in Weiher, E. & P. Keddy eds., 1999, *Ecological assembly rules, perspectives, advances, retreats*. Cambridge University Press, Cambridge, pp 23-57

Gilpin, M.E. & J. M. Diamond, 1984, Are species co-occurrences on islands non-random, and are null-hypotheses useful in community ecology? in Strong, D. R., D. Simberloff, L.G. Abele & A. B. Thistle eds., 1984, *Ecological Communities, conceptual issues and the evidence*, Princeton University Press, Princeton, pp 297-315

Keddy, P. & E. Weiher, 1999, Introduction: The scope and goals of research on assembly rules in Weiher, E. & P. Keddy eds., 1999, *Ecological assembly rules, perspectives, advances, retreats*. Cambridge University Press, Cambridge, pp 1-20

Keddy, P., 1993, Do ecological communities exist? A reply to Bastow Wilson, *Journal of Vegetation Science* 4: 135-136

Keddy, P., 1999, Epilogue: from global exploration to community assembly in Weiher, E. & P. Keddy eds. 1999, *Ecological assembly rules, perspectives, advances, retreats*, Cambridge University Press, Cambridge, pp 393-402

Keddy, P.A., 1992, Assembly and response rules: two goals for predictive community ecology, *Journal of Vegetation Science* 3: 157-164

Looijen, R. C. & J. van Andel, 1999, Ecological communities: conceptual problems and definitions, *Perspectives in Plant Ecology, Evolution and Systematics* 2: 210-222

May R. M., 1984, An overview: real and apparent patterns in community structure, in Strong, D. R., D. Simberloff, L.G. Abele & A. B. Thistle eds., 1984, *Ecological Communities, conceptual issues and the evidence*, Princeton University Press, Princeton, pp 3-16

McIntosh, R. P., 1995, H.A. Gleason's 'individualistic concept' and the theory of animal communities: a continuing controversy, *Biological Review* 70: 317-357

Mirkin, B.M., 1994, Which plant communities do exist?, *Journal of Vegetation Science* 5: 283-284

Palmer, M. W. & P.S. White, 1994, On the existence of ecological communities, *Journal of Vegetation Science* 5: 179-282

Parker, V. T., 2001, Conceptual problems and scale limitations of defining ecological communities: a critique for the CI concept (community of individuals), *Perspectives in Plant Ecology, Evolution and Systematics* 4: 80-96

Strong, D. R., D. Simberloff, L.G. Abele & A. B. Thistle eds., 1984, *Ecological Communities, conceptual issues and the evidence*, Princeton University Press, Princeton

Weiher, E. & P. Keddy eds., 1999a, *Ecological assembly rules, perspectives, advances, retreats*. Cambridge University Press, Cambridge

Weiher, E. & P. Keddy, 1999b, Assembly rules as general constraints on community composition. in Weiher, E. & P. Keddy eds. 1999, *Ecological assembly rules, perspectives, advances, retreats*, Cambridge University Press, Cambridge, pp 251-271

Wilson, J. B., 1991, Does vegetation science exist?, *Journal of Vegetation Science* 2: 289-290

Wilson, J. B., 1994, Who makes the assembly rules?, *Journal of Vegetation Science* 5: 275-278

Wilson, J. B., 1999, Assembly rules in plant communities in Weiher, E. & P. Keddy eds., 1999, *Ecological assembly rules, perspectives, advances, retreats*, Cambridge University Press, Cambridge, pp 130-164