**Introduction**: The scope and goals of research on assembly rules

*Paul Keddy and Evan Weiher*

Why should assembly rules be studied, why should a symposium be organized, why should a volume on the topic be published, and why should anyone bother to read it? These are all perfectly reasonable questions, and it is our task to briefly address them by way of introducing this volume.

For some time, ‘community ecology’ has been the name loosely applied to a collection of studies and methods that apply to more than one organism, but that apply at scales below the landscape. Many books on community ecology appear to offer little more than a disparate hodgepodge of studies that are unified solely by the above vague restrictions. This may seem a harsh criticism, and a peculiar way to open a book written for community ecologists. But, these sort of criticisms form the ground of this volume (some might suggest charnel ground), and it is not an original observation by any means. Indeed, Pianka (1992), a prominent member of our discipline, has felt obliged to apologize on our behalf in a paper titled ‘The state of the art in community ecology’, observing therein that ‘community ecology has for too long been perceived as repugnant and intractably complex’. He apologizes to a world symposium that ‘the discipline has been neglected and now lags far behind the rest of ecology’.

He is not alone in his survey, opinion and prognosis. Nearly two decades earlier Lewontin (1974) wrote of the ‘agony’ of community ecology. More recently, the late Rob Peters (1991) annoyed many when he decried the lack of apparent progress in our discipline. Lawton (1992) then attacked Peters; Keddy (1992) criticized his criticisms. Scheiner (1993) then criticized Keddy for criticizing Lawton, and Keddy replied (Keddy, 1993), and then Scheiner replied to him (Scheiner, 1994). Lacking tangible progress, people turn upon one another. If there is agony in community ecology, as Lewontin suggested, much of it appears to be self-inflicted. Meanwhile, thick compendia under the name of community ecology arise with frustrating regularity and repetitive
content. This situation is what led Keddy (1993) to observe that, without far more emphasis upon measurable properties, critical tests and rational decision-making, community ecologists run the risk of becoming more like the humanities than the sciences, prone to political and emotional conflicts rather than debates using rational criteria. In Camille Paglia’s (1992) essay ‘Junk bonds and corporate raiders: academe in the hour of the wolf’ one can read her view that ‘the self-made inferno of the academic junk bond era is the conferences, where the din of ambition is as deafening as on the floor of the stock exchange. The huge, post-1960s’ proliferation of conferences … produced a diversion of professional energy away from study and toward performance, networking, advertisement, cruising, hustling, glad-handing, back-scratching, chitchat, groupthink’. Mercifully, community ecologists (and this volume) are completely immune to this risk because we are doing science.

Why a symposium on assembly rules, and why a book you may still be asking? Plans for the symposium were rooted in the above circumstances, combined with two common-sense observations. These were:

(a) if there are not some common goals for community ecology, then they are unlikely to be achieved;
(b) a prominent theme in the discipline is the attempt to predict the composition of ecological communities from species pools.

The first observation appears self-evident, but apparently in some circles there is still a suspicion of research ‘agendas’. There appears to be a naïve belief that the way to build a spaceship and land a human on the moon is to trust that, if everyone indulges themselves in an idiosyncratic and self-indulgent pastime at the taxpayer’s expense, the outcome will be positive. Like Voltaire’s Professor Pangloss, there is the insistence that this must be the best of all possible worlds, however inefficient or painful it may appear on the surface. If progress is forgotten about entirely, and our discipline is seen as a mere pastime for the tenured and well to do, there is no particular need to be concerned about goals, progress and social contribution. As long as ecologists have jobs and the chance at a large grant, why worry? Volumes with this kind of philosophy are too frequent as it is, and given that it has been said in print (Keddy, 1991), as editors we were careful to insist upon a common purpose. Within this common purpose, a diversity of views about the details and the strategies and tactics for achieving it was welcomed.

The second observation may be less evident, but if the many topics that have arisen in community ecology over the years are considered, the common thread may not be in level of organization, methodology or number of species, but in the underlying problem that is being addressed. Moreover,
adapting this goal clarifies a common source of confusion among ecologists themselves: community ecology is different from evolutionary ecology. Figure 1 shows a possible framework for community ecology. Community ecologists are concerned with the question mark: how does one get from the pool to the community? Evolutionary ecologists are concerned more with the top box and arrows: how do speciation and extinction produce the pool? From the perspective of community ecology, the pool is just the source of raw materials, and the process that creates the pool, while of interest, generally occurs at longer time scales than are normally considered relevant.

A new name could be invented to describe the study of how communities are built from pools, but if the literature is looked back on, there is a good deal of terminology that can already be borrowed. There is always a risk in using pre-existing terminology, because it all comes with baggage. The baggage includes assumptions about the kinds of organisms worthy of study, past controversies that are actually tangential to the issues at hand, and past confusions that entangled ecologists. It is for this reason that the Roman armies called baggage impedimenta. Ecologists do not need more impediments. But, neither does there seem to be any point in inventing new terms when perfectly good ones are already there. To do so would be to throw out the wisdom of past work because the baggage is feared. Thus the term ‘assembly rules’ has been adopted to describe the problem of assembly communities from pools; this accords rather well with Diamond’s original (1975) usage of the word. There may be doubts about using birds as a model system, about
descriptive as opposed to experimental studies, about inferences about mechanisms that may not be justified, about controversies that have generated more heat than light, and about habitual ways of trying to solve these problems that appear self-defeating. All of these objections (and more,) were raised either by participants in the symposium, or by other practising ecologists. The term assembly rules, however, still captures the essence of the problem in Fig. 1. Moreover, it nicely fits in with Pirsig’s (1974) observation that assembling a rotisserie is not unlike fixing a motorcycle, that the challenge of putting something together properly from the pieces (assembling it) is a challenge with worthy mechanical and philosophical dimensions.

And so, the symposium was called ‘assembly rules’, and researchers were sought out who were studying how communities were assembled out of pools. In spite of ourselves, the perceptive reader will discern certain biases. For example, Fig. 2 gives one perspective upon the composition of ecological communities upon Earth’s surface; more recent calculations would expand the invertebrate and fungal component. This would seem to be a common-sense starting point in designing the discipline of community ecology. In spite of ourselves, we have ended up with a disproportionate representation of vertebrate examples. Our defence is that, while trying to collect a representative set of studies on community assembly, a highly biased and artificial pool from which to make the draw was being dealt with, and so the distortions of our literature have been included. Our only plea is that we consciously tried to avoid the worst distortions. Further, to the extent that

![Diagram of ecological community composition](image)

*Fig. 2. The importance of different life forms in the biosphere, measured according to biomass (left) and number of species (right). (From Keddy, 1989.)*
they have been reproduced, others can only be encouraged to rectify the situation.

Two existing paradigms

Within the literature, and within this volume there are at least two developing paradigms for the assembly of communities (Fig. 3). The first we call the island paradigm because it deals with mainlands, islands, immigration, and coexistence. The second we call the trait–environment paradigm because it begins with pools, habitats as filters, and convergence. This is not to suggest that there are only two ways forward, or that either of these is the best. These simply happen to be two themes which will be evident in this concert. The challenge for a musician is to build upon a theme in an entertaining way without being repetitive.

**Island paradigm**
- Mainland
- Dispersal
- Immigration/extinction
- Nestledness
- Competition
- Overdispersion (divergence)

**Trait–environment paradigm**
- Pools
- Filters
- Traits
- Screening
- Assembly vs. response rules
- Underdispersion (convergence)

Fig. 3. The two most common paradigms for community assembly are the island paradigm (**top**) and the trait–environment paradigm (**bottom**).

**Type 1: Island models**

Many studies are built upon the raw data lists of species on islands. In terms of Fig. 1, the pool is the adjoining mainland, and the list of species from the island is considered to be the community. The basic series of steps is as follows:
(a) make lists of organisms in each habitat;
(b) create one or more null models for possible patterns;
(c) test for patterns in these lists;
(d) offer explanations for these patterns;
(e) state the explicit rules for community assembly.

A good example of this sort of study comes from Diamond’s (1975) work on the avifauna of New Guinea (Fig. 4). There is now a large literature on this topic, and a growing body of literature on null models, but a good deal of controversy about the costs and benefits of null models and the kinds of data appropriate to them (Gotelli & Graves, 1996). Moreover, while there have been many searches for evidence of pattern, few brave souls have reached step (e).

Fig. 4. The island paradigm for assembly is built upon studies of bird distribution on offshore islands. Are there patterns, do they differ from those predicted by null models, and are there rules that predict them? This example shows the distribution of two species of *Ptilinopus* fruit pigeons, where split circles are co-occurrences and dots are co-absences. (From Keddy, 1989 after Diamond, 1975.)
**Type 2: Trait–environment models**

One can also approach community assembly not by using lists of organisms, but by focusing upon their traits. The environmental factors are then viewed as filters acting upon these traits. In this case the procedure is as follows:

(a) determine the key traits the organisms possess;
(b) relate the traits to key environmental factors;
(c) specify how trait composition will change with specific changes in environment;
(d) relate this back to the particular organisms possessing those traits.

We are not interested in general properties of the traits themselves, but in the relative abundances of the organisms that possess them. A good example of this sort of study is the work on prairie potholes by van der Valk (1981). The water level in the pothole acts as a filter determining the kinds of plant species that will occur there; the two key states are drained v. flooded (Fig. 5).

**What is an assembly rule?**

What would an assembly rule look like if one were found? A goal cannot be attainable unless some criteria are set up to tell when it has been achieved.
assembly rule specifies the values and domain of factors that either structure or constrain the properties of ecological assemblages.

Overall, there are four parts in the procedure of finding assembly rules:

(a) defining and measuring a property of assemblages;
(b) describing patterns in this property;
(c) explicitly stating the rules that govern the expression of the property; and
(d) determining the mechanism that causes the patterns.

Contrary to common practice, merely documenting a pattern is not the study of community assembly. Plant ecologists have described plant patterns for more than century, and appear ready to continue doing so for yet another; simply describing patterns is not the study of assembly rules. Nor is an improvement, the added demonstration that pattern exists against a null model, sufficient to qualify. Asking if there is pattern in nature is akin to asking if bears shit in the woods. Null models provide a valuable and more rigorous way of demonstrating pattern, but they still do not specify assembly rules. Within this realm of pattern (step 2), one, of course, needs to ask what kinds of patterns might occur and at what scales (Fig. 6). But actual assembly rules, step 3, require further effort yet. They might include statements such as the following:

‘If an assemblage of plants is flooded, the subset of species that survives will all have aerenchyma.’

‘In the absence of predators, a pond in the temperate zone can be expected...
to have between 5 and 10 amphibian species. If a predatory fish species is introduced to the pond, this will fall to between 0 and 2 species.’

‘The ratio of insectivorous to granivorous birds in deciduous forests is between 0.25 and 0.33, whereas in boreal forests the ratio falls between 0.45 and 0.55.’

‘If a herbaceous plant community with biomass of 500 g m$^{-2}$ is fertilized with NPK fertilizer, the mean number of species per m$^2$ will decline by 10% with each x g m$^{-2}$ of fertilizer.’

‘There is a linear relationship between the number of beetles in deciduous forests and the volume of coarse woody debris. The equation relating the two is as follows …’

These statements all are expressed in terms of measurable properties and their range or variation in relation to another factor. The following statements would not qualify as assembly rules.

‘Similar organisms tend not to coexist.’

‘Competition controls the distribution of birds on islands.’

‘Copepod communities in ponds are not randomly assembled from a species pool.’

‘Tree species diversity increases with decreasing latitude.’

‘The distribution of lizards upon islands deviates significantly from null models.’

Such statements certainly belong within community ecology, and may have within them concepts or models that increase our understanding of certain assemblages. But they are not assembly rules. Rules themselves must be explicit and quantitative if they are to qualify. The other statements are, perhaps, steps on the way to the goal. There seems to be some current confusion on this matter. For example, the existing literature suggest that merely finding a pattern in properties is an assembly rule. Confusing a step on the path with the attainment of a goal only generates confusion.

**Obstacles on the path**

Good generals study the failures of other generals so that they do not repeat their mistakes. One of the consequences of accepting a goal is the recognition and study of obstacles and past errors. This could be considered annoying, something to be avoided at all costs, perhaps because no one wants to admit to having fallen prey to an obstacle. Perhaps our early days in Sunday school are remembered, being told of our committing a sin. But, the delightful side of this is that if obstacles cannot be recognized, they cannot be avoided. That is why road signs warning ‘detour ahead’ are so useful; without
them we could damage our car. Returning to generals, in his chapter Doctrine of Command, General Montgomery (1958) wrote ‘I hold the view that the leader must know what he himself wants. He must see his objective clearly and then strive to attain it; he must let everyone else know what he wants and what are the basic fundamentals of his policy.’ (p. 81)

The frequent reluctance to admit that there are both goals and obstacles to our work is certainly unmilitary, and perhaps unprofessional. It may reflect a desire to remain child-like, innocent and naive, with no responsibility for one’s actions. Once, like General Patton, our intention to be in Berlin next year is announced, everyone will know if it is not achieved. It takes some bravery to announce our goals, and to suggest that society should care whether Berlin or Paris is achieved. Are there some obstacles that have interfered with past campaigns in community ecology. What are some of these errors that might have led to Pianka’s despair? At the symposium the participants were specifically warned against some pitfalls. For those who were not in attendance, they are briefly listed below.

Before the list is presented, one more clarification is necessary. The list offers styles of research which are obstacles to advancement. Elements of such styles are contained in everyone, but in different relative proportions. In an exactly analogous way, all humans have anger, negativity, arrogance, envy, ignorance, greed, suspicion in their psychological make-ups. One of the reasons humans have lists such as the seven deadly sins, or the three poisons, is to be warned to watch out for these states as they arise within own minds. Tradition has taught that these states create confusion for ourselves, and problems for our human communities. In the same way, the following list of styles in intended to illustrate approaches that can be slid into if one remains unaware of one’s own behavior. The intention is not to list obstacles in order to imply that these flaws are found in only a few bad people (see the exchange between Scheiner, 1993 and Keddy, 1993), nor so readers can try to guess who falls into which category, but rather to acknowledge that all humans are subject to such tendencies. Such a list, then, provides gauges for an instrument panel that will warn if one wanders too far into unproductive terrain. Five obstacles are considered.

(a) Bigger is better (‘Mine is bigger than yours’)
Sometimes it is thought that if someone does not know where they are going, then at least the neighbours can be impressed by seeing them drive a bigger car while they try to get there. This is common in the animal and plant kingdoms. Large insects tend to be dominant over smaller ones (Lawton & Hassell, 1981) just as large plants tend to be dominant over smaller ones (Gaudet &