

in: Ecological Assembly
Rules: Perspectives,
advances, retreats.

E. Weiher & P. Keddy, eds.
Cambridge University Press

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 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 naive 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,

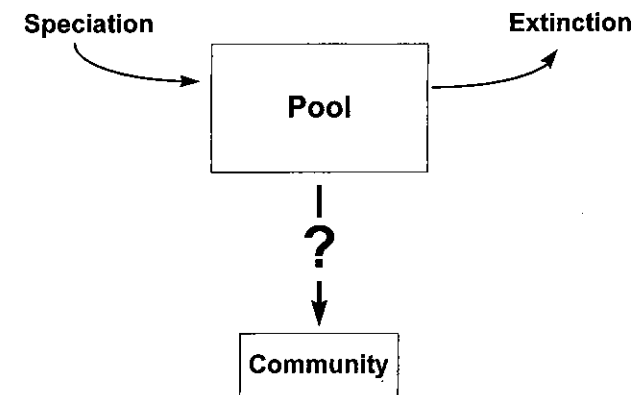


Fig. 1. Assembly rules address a central theme in community ecology: how are communities assembled from species pools. (Evolutionary ecology, by contrast, deals with the formation of the pool.)

adopting 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

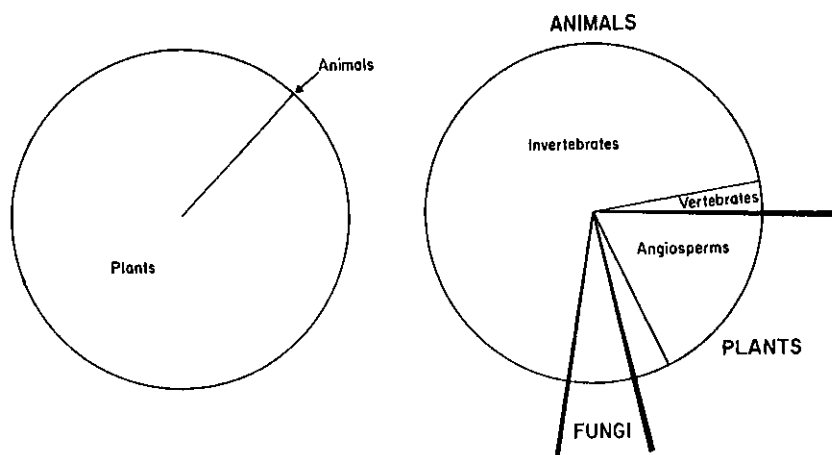


Fig. 2. The importance of different life forms in the biosphere, measured according to biomass (*left*) and number of species (*right*). (From Keddy, 1989.)

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
Nestedness
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:

- make lists of organisms in each habitat;
- create one or more null models for possible patterns;
- test for patterns in these lists;
- offer explanations for these patterns;
- 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).

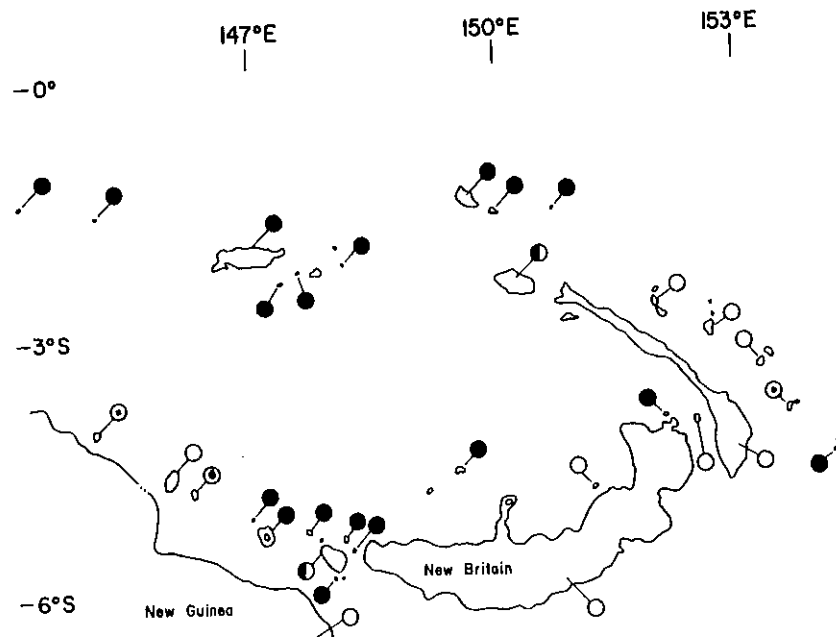


Fig. 4. The island paradigm for assembly is built upon studies of bird distribution on offshore islands. Are there patterns, do they differ from those predicted by null models, and are there rules that predict them? This example shows the distribution of two species of *Ptilinopus* fruit pigeons, where 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:

- determine the key traits the organisms possess;
- relate the traits to key environmental factors;
- specify how trait composition will change with specific changes in environment;
- 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).

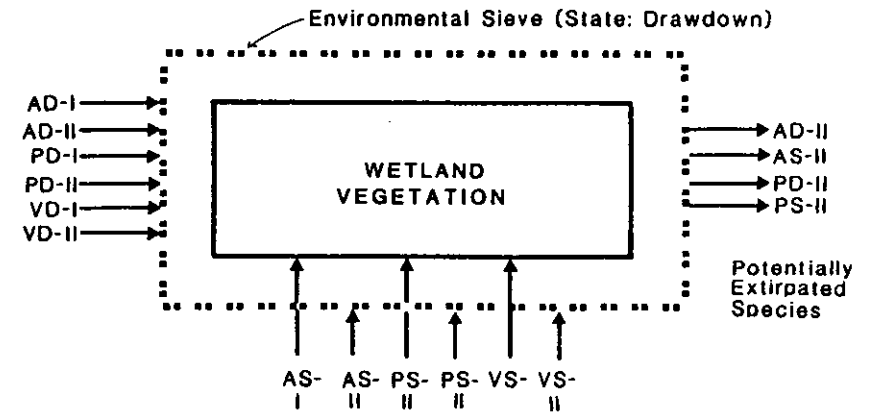


Fig. 5. The trait environment paradigm for community assembly focuses attention upon the pool of species, the traits they possess, and the environmental filters operating in a particular situation. The example shows that the composition of vegetation in a pothole wetland depends upon whether the pool of buried seeds is exposed to flooded or drained conditions. (From van der Valk, 1981.)

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. An

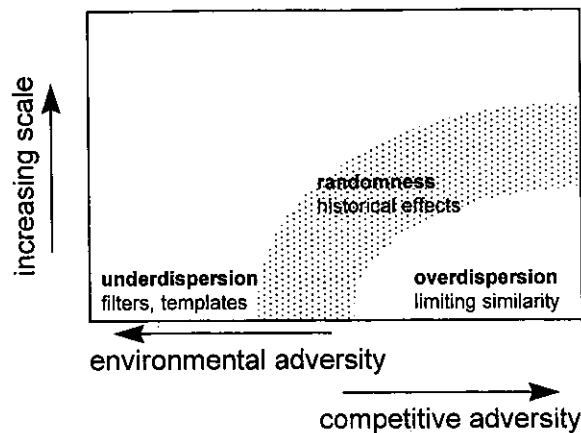


Fig. 6. A first step in the search for assembly rules is the search for pattern. Island modes have tended to search for overdispersion (*right*) whereas trait-environment models have tended to focus upon trait underdispersion (*left*). A larger view suggest that both are possible, depending upon the scale of enquiry. (From Weiher & Keddy, 1995.)

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:

- defining and measuring a property of assemblages;
- describing patterns in this property;
- explicitly stating the rules that govern the expression of the property; and
- 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 m² 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 is 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 &

Keddy, 1988). Display of wealth or economic power is a standard technique humans use to maintain authority over neighbours (Kautsky, 1982), the culmination of which is perhaps seen in the arms races during and after the Second World War (Keegan, 1989). There is no need here to impress the audience with a Cray 2 supercomputer when only a pocket calculator will make the point. Similarly, there is no need to show the helicopter or float plane that it took to reach the study site.

(b) Complexity is impressive ('I know more natural history than you')

Many people know a great deal about nature. Keddy could, for example, lecture for hours (and write for pages) upon the plants that grow in wetlands or in Lanark County where he lives. If he did so in a sonorous and authoritative voice, he might even convince you that your time listening was well spent. But he would mislead if he tried to pass off his delightful knowledge of natural history under the term assembly rules. Merely knowing where organisms are found, and describing it in exquisite detail, is not the study of assembly rules. Otherwise, Tansley and Adamson (1925) would have to be credited with assembly rules for British grassland. In their study of grazing, they reported on factors controlling composition in three patches along a gradient of 'progressive increase in height and density of vegetation, with an increasing number of species'. In one paragraph they observe:

'Of the mosses, *Barbula cylindrica*, *B. unguiculata* and *Bryum capillare* decrease and disappear with complete closure and increasing depth of the turf; *Brachythecium purum*, one of the most ubiquitous of chalk grassland mosses, though not a 'calcicole' species, appears in (b) and increases in (c); while *B. rutabulum*, *Mnium undulatum* and *Thuidium tamariscinum* first appear in the damper conditions of (c)'

These sorts of descriptions are possible for all manner of ecological systems; the real problem is to discover the generalities that underlie the remarkable diversity of life (Mayr, 1982). General Montgomery (1958) says 'It is absolutely vital that a senior commander should keep himself from becoming immersed in details ... If he gets involved in details ... he will lose sight of the essentials which really matter; he will then be led off on side issues which will have little influence on the battle ...' (p. 86).

In general, simple hypotheses are preferable to complex ones (Aune, 1970). We need to remember the late Rob Peters' warning (1980a,b) that there is an important difference between natural history and ecology. It might be recalled that even an omniscient and omnipotent deity felt it necessary to give Moses only ten rules to guide all the complexities of human conduct.

(c) Sycophancy ('My friends are more important than yours')

Humans are primates, and the primate mind appears to have evolved for survival in social/tribal settings (e.g., Leakey & Lewin, 1992). It is therefore entirely natural for authority figures to be created, like the old silver back males in the Gorilla tribe, and then deferred to, whether people live in the world's most powerful democracy (Dye & Zeigler, 1987) or a Stalinist prison camp in Siberia (Shalamov, 1982).

There have been sycophants as long as there have been authority figures. Socrates is often presented as a courageous man of science who died rather than appease the Athenian rulers. But, in a compelling re-evaluation of the historical records, I.F. Stone (1989) reached quite a different conclusion. At the time, he notes, Athens was repeatedly threatened by tyrants; in both 411 and in 404, the conduct of the aristocratic dictators was 'cruel, rapacious and bloody'. Socrates was strangely silent while all this happened. Stone looks in vain for Socrates to show compassion for the poor, or opposition to tyranny, and notes that the famous *Republic*, later written by his student Plato, advocates a tyranny remarkably close to the modern Communist state, complete with internal security police ('guardians'). Socrates, concludes Stone, was a sycophant for the tyrants. He did not plead for freedom of speech because it was a principle he did not believe in, and he could not bring himself to argue before the democrats using their own principles. If Stone's interpretation is correct, using Socrates as an example for scientists may have far darker connotations than has been realized, and comes rather close to Saul's (1992) contemporary view that intellect is too often used to reinforce authority rather than challenge it.

Apparently it is natural for humans to divide themselves into tribes and attack one another (Ignatieff, 1993). It further seems natural to kick and bite (or at least ostracize) members of our tribe who do not seem to want to groom the same dominant that the others do (Browning, 1992). They may even favor their own gender (Gurevitch, 1988). The fact that this was natural behavior for primates on the African plains does not mean that it is defensible or useful behavior for contemporary scientists. Indeed, in other settings, such as religion, people frequently react with annoyance when they see blind obedience and the exercise of authority. Ape instincts such as sycophancy seem obvious when they creep out of the tribe and into our of politics, but perhaps less so when they appear in the sciences (Keddy, 1989). Appeals to authority, the selective citation of friend's work, and division into tribal units do not contribute to the advancement of science. All are all to be avoided here.

(d) Self-indulgence ('Playing with yourself is harmless fun')

It may be true that masturbation does not cause blindness, but neither is it necessarily a healthy substitute for a relationship with another human being. Similarly, self-indulgent work aimed at building up egos may not cause irreparable harm to science, but it certainly is no substitute for thoughtful goals, collegiality, care, respect and social responsibility. The motivation that is brought to our work will necessarily influence the way in which it develops. It is therefore necessary to think about where we are going and how our discoveries might be of use to society. The alternative is unpleasant for everyone. The Roman historian Plutarch describes how one Roman emperor after another 'lavished away the treasures of his people in the wildest extravagance'. One was killed by a tribune amongst his own guards, another was strangled, another killed himself, but the waste of resources caused by this self-indulgence caused immense human suffering and the diminution of the resources of the Roman empire. Are precious scientific resources being squandered in a similar manner today? Is *Ecology* just *National Geographic* without the color plates?

Hofstadter (1962) suggests that the current American environment of anti-intellectualism is responsible for isolation of scientists from their society: 'Being used to rejection, and having over the years forged a strong traditional response to society based upon the expectation that rejection would continue, many of them have come to feel that alienation is the only appropriate and honorable stance for them to take.' (p. 393) Further, he continues, it is easy to take this to the next logical step and slip into the assumption that alienation has some inherent value itself. As an example, a science reporter tried to interview one of our participants by asking 'What is the practical importance of this work on assembly rules?'. The answer 'None, I hope' perhaps illustrates Hofstadter's point.

Guarding against this self-indulgence is necessary not just because it is other humans who pay our salaries. *The attempt to explain ourselves to others and to solve real world problems actually forces us to do better science.* It may be harmful to indulge in simple natural history, but it is equally dangerous to take the other extreme and retreat entirely to a cosy world of abstraction. When an engineer builds a bad bridge, it falls down. This is a simple example of the pragmatic method, which James (1907) described as 'primarily a method of settling metaphysical disputes that might otherwise be interminable' (p. 10) In contrast, when an ecologist builds a pointless model or publishes a bad paper, it is possible for it to persist and cause unnecessary debates for decades.

(e) Lack of historical context ('My ideas are new and unprecedented') Life is impermanent, and one way to try escape our fears is self-aggrandization. The more history is ignored, the more important it can seem to be. It has been argued that since the 1960s, ecologists have tended to inflate our self-importance by ignoring the roots of our discipline (Gorham, 1953; Jackson, 1981). Consider a recent example. In 1970 Walker tested whether wetland vegetation along lakes showed a progressive and predictable series of developmental stages using 159 observed transitions between vegetation types extracted from 20 published pollen diagrams (Fig. 7). One dominant course was observed (darker lines). Reed swamp (5) was an essential stage through which all successions must pass. Some reversals occur (17% of all transitions), 'but are usually short-lived and might frequently be due to small changes in water level, temperature or trophic status of the lake water ...' Do such observations, perhaps slightly reworded, not qualify as assembly rules? The scale in time and space, and the replication is impressive relative to many other published studies on assembly rules. So, why is work such as Walker so consistently overlooked? See if you can find it cited in the assembly rules literature.

A more recent example of historical revisionism is provided by Gotelli and Graves (1996) in their book on null models. The theme of whether plant communities are discrete communities or random assemblages can be traced back through writings by Tansley, Clements, Gleason, Ellenberg and Whittaker throughout the period from 1900 to 1970; indeed, the study of species distributions along gradients has probably been the defining feature of research in plant ecology. In the early 1970s, E.C. Pielou developed a number of null models for plant distributions along gradients, which she summarized in her 1975 book. There have been only five main papers that report the application of her null models in the field (Pielou & Routledge (1976) in salt marshes, Keddy (1983) on lake shores, Dale (1984) on marine rocky shores, Shipley and Keddy (1987) in marshes, and Hoagland and Collins (1997) in wet prairies), and in each case the null model has been rejected. Yet Gotelli and Graves do not have a chapter on gradient models, nor does their one paragraph on Pielou and Routledge (1976) explain the significance of their work – that the rejection of Pielou's null model constitutes the first demonstration that communities occur in discrete clusters rather than random (individualistic) associations. On page 1, Gotelli and Graves (two male American zoologists) even opine that the term null models for communities originated with two male American Zoologists at a Florida symposium in 1981! Chris Pielou was a woman, she was Canadian, and she was a plant ecologist: to which of these should her erasure from the ecological record be attributed?

ANTECEDENT VEGETATION	SUCCEEDING VEGETATION												T
	1	2	3	4	5	6	7	8	9	10	11	12	
1	.	.	3	2	1	.	.	6
2	.	.	.	2	2	4
3	1	.	.	4	7	1	.	.	13
4	1	.	1	.	9	.	3	1	3	5	.	.	23
5	.	.	.	2	.	1	8	6	7	11	4	.	39
6	1	1
7	2	.	.	2	8	2	3	.	17
8	1	.	1	.	1	2	3	.	8
9	.	.	.	1	2	.	1	.	.	1	10	.	15
10	1	.	.	1	1	.	.	2	.	.	10	.	15
11	1	1	.	1	3
12	.	.	.	1	9	.	4	.	1	.	.	.	15
T	3	0	4	13	33	1	17	12	21	24	30	1	159

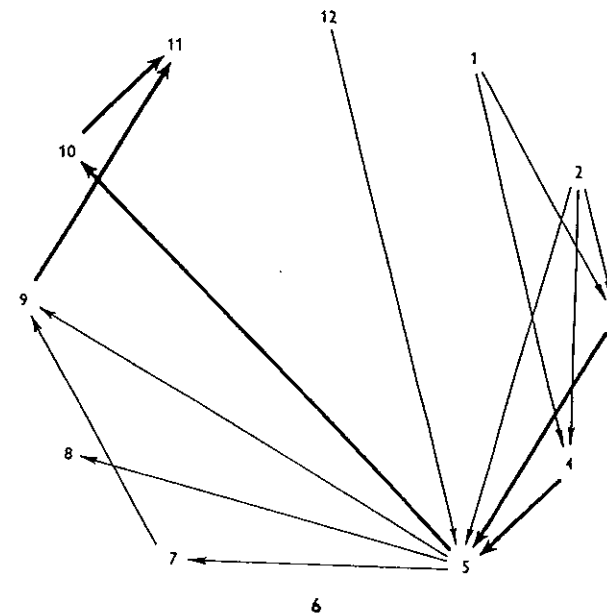


Fig. 7. Frequencies of transition between 12 vegetation stages (ranging from open water (1) through reed swamp (5) to bog (11) to mixed marsh (12)) in 20 pollen cores from a range of wetlands including small lakes, valley bottoms, and coastal lagoons in the British Isles. *Left*, tabulated frequencies, *right*, transition diagram.

In the broader sense, one could argue that our entire culture is becoming focused upon the ephemera of the present where everyone will have their 15 minutes of fame; a consequence is a loss of context or significance for

properly evaluating current events (O'Brien, 1994; Saul, 1995)). Booth and Larson (this volume) suggest that most of the apparent problems with assembly rules arise out of a studied ignorance of ecological principles prevalent in the early part of this century.

Moving forward

Ending with a list of obstacles could be seen as unnecessarily defeatist or negative. The only reason to study obstacles is to avoid them. It can be hoped that, by consciously avoiding these tendencies, everyone will be able to avoid repeating patterns of behavior that limit our personal contribution to the progress of ecology, or spread discord among our colleagues. By defining warning regions, regions which are positive and valuable are equally defined (Fig. 8). It is not, then, that a single narrow goal is being advocated, nor a single path forward.

Rather than insist that there is only one goal for assembly rules, it is asked that each participant explicitly state their goal; then and only then will it be possible to understand their tactics and judge their degree of success in attaining their goal. To return to our travel analogy, some may be aiming for Paris and others for London; so long as they justify their destination, their trip can be judged only against the stated goal. Of course, if someone asserts that they intend to take us to the Louvre, but then drives us towards London instead, it may be gently suggested from the back seat that they review their travel plans, consult the map, or else choose another destination.

Nor would it be desirable to imply that there is room for only a single style of science. Within our community it can be accepted that different practitioners have different strengths and weaknesses; progress in ecology depends upon exploitation of, and respect for, these differences. So while Fig. 8 defines some regions as obstacles, it should be apparent that there is still plenty of room remaining for a diversity of approaches. Some of the relatively sterile arguments in ecology may arise out of simple lack of tolerance for different styles. It is therefore necessary to be clear in our discussions whether disagreement has arisen because of (a) different views on goals, (b) different views on tactics and style, (c) different interpretations of data, or (d) indulgence in one of the above obstacles. On one hand, it is necessary to be open minded to avoid pointless debates that really hinge on differences in personality or style. Equally however, being open minded does not mean that our brains must be allowed to fall out and outright self-indulgence be tolerated.

Having explicitly considered the need for clearly stated goals, some obstacles

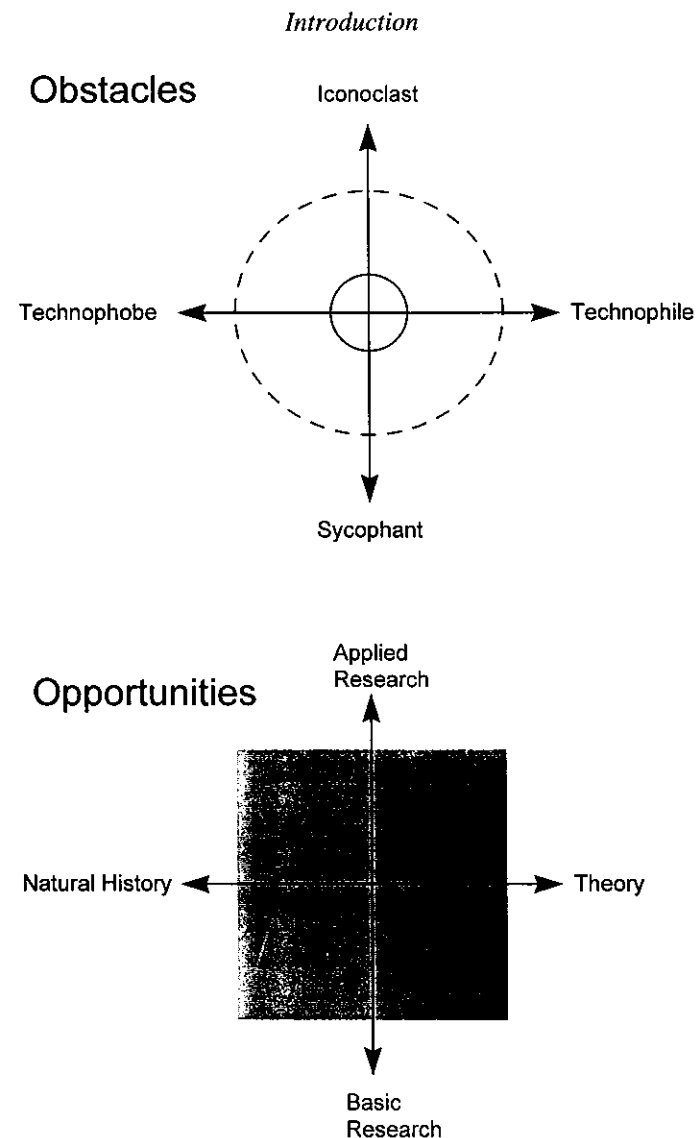


Fig. 8. A variety of psychological obstacles can hamper progress in ecology. By explicitly describing these obstacles, a region is simultaneously defined within which progress is possible; within this region, differences in style enrich collaboration.

to progress, some ways in which researchers may differ in opinion, and the merits of tolerating different approaches, let us return to the study of assembly rules. The problem remains. How do we get from the pool to the community? The introductory talk ended with Fig. 9, so this same figure

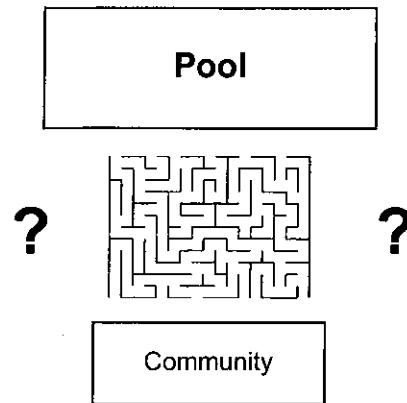


Fig. 9. Participants in the symposium were each asked to chart out their own course though the maze of possibilities that takes us from the pool to the community.

terminates this written introduction. See what the authors have to say in response. In the words of Peter Weiss (1965): 'We ask your kindly indulgence for a cast never on stage before coming to Charenton. But each inmate I can assure you will try to pull his weight.'

References

- Aune, B. (1970). *Rationalism, Empiricism, and Pragmatism*. NY: Random House.
- Browning, C.R. (1992). *Ordinary Men: Reserve Police Battalion 101 and the Final Solution in Poland*. NY: Harper Collins.
- Dale, M.R.T. (1984). The contiguity of upslope and downslope boundaries of species in a zoned community. *Oikos* 47: 303–308.
- Diamond, J.M. (1975). Assembly of species communities. In *Ecology and Evolution of Communities*, ed. M.L. Cody & J.M. Diamond, pp. 342–444. Cambridge, MA: Belknap Press of Harvard University Press.
- Dye, T.R. & Zeigler, H. (1987). *The Irony of Democracy*. 7th edn. Monterey, CA: Brooks/Cole.
- Gaudet, C.L. & Keddy, P.A. (1988). Predicting competitive ability from plant traits: a comparative approach. *Nature* 334: 242–243.
- Gorham, E. (1953). Some early ideas concerning the nature, origin and development of peat lands. *Journal of Ecology* 41: 257–274.
- Gotelli, N.J. & Graves, G.R. (1996). *Null Models in Ecology*. Washington: Smithsonian Institution Press.
- Gurevitch, J. (1988). Differences in the proportion of women to men invited to give seminars: is the old boy still kicking? *Bulletin of the Ecological Society of America* 69: 155–160.
- Hoagland, B.W. & Collins, S.L. (1997). Gradient models, gradient analysis and hierarchical structure in plant communities. *Oikos* 78: 21–30.
- Hofstadter, R. (1962). *Anti-Intellectualism in American Life*. NY: Vintage Books.

- Ignatieff, M. (1993). *Blood and Belonging*. Toronto: Penguin Books Canada Ltd.
- Jackson, J.B.C. (1981). Interspecific competition and species distributions: the ghosts of theories and data past. *American Zoologist* 21: 889–901.
- James, W. (1907). *Pragmatism*. Reprinted In 1990, *Great Books of the Western World*, ed. M.J. Adler, Vol. 55, pp. 1–89. Chicago, IL: Encyclopedia Britannica.
- Kautsky, J.H. (1982). *The Politics of Aristocratic Empires*. Chapel Hill: University of North Carolina Press.
- Keddy, P.A. (1983). Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology* 64: 331–344.
- Keddy, P.A. (1989). *Competition*. London: Chapman and Hall.
- Keddy, P.A. (1991). Thoughts on a festschrift: what are we doing with our scientific lives? *Journal of Vegetation Science* 2: 419–424.
- Keddy, P.A. (1992). Thoughts on a review of a critique for ecology. *Bulletin of the Ecological Society of America* 73: 231–233.
- Keddy, P.A. (1993). On the distinction between ad hominid and ad hominem and its relevance to ecological research. A reply to Scheiner. *Bulletin of the Ecological Society of America* 74: 383–385.
- Keegan, J. (1989). *The Second World War*. NY: Viking Penguin.
- Lawton, J. (1992). Predictable plots. *Nature* 354: 444.
- Lawton, J.H. & Hassell, M.P. (1981). Asymmetrical competition in insects. *Nature* 289: 793–795.
- Leakey, R. & Lewin, R. (1992). *Origins Reconsidered. In Search of What Makes Us Human*. New York: Doubleday.
- Lewontin, R.C. (1974). *The Genetic Basis of Evolutionary Change*. NY: Columbia University Press.
- Mayr, E. (1982). *The Growth of Biological Thought. Diversity, Evolution and Inheritance*. Cambridge, MA: Belknap Press of Harvard University Press.
- Montgomery, B. (1958). *The Memoirs of Field-Marshal the Viscount Montgomery of Alamein*. St James's Place, London: K.G. Collins.
- O'Brien, C.C. (1994). *On the Eve of the Millennium*. Ontario: Anansi, Concord.
- Paglia, C. (1992). *Sex, Art and American Culture*. NY: Random House.
- Peters, R.H. (1980a). Useful concepts for predictive ecology. *Synthese* 43: 257–269.
- Peters, R.H. (1980b). From natural history to ecology. *Perspectives in Biology and Medicine* 23: 191–203.
- Peters, R.H. (1991). *A Critique for Ecology*. Cambridge: Cambridge University Press.
- Pianka, E.R. (1992). The State of the Art in Community Ecology. Proceedings of the First World Congress of Herpetology. In *Herpetology: Current Research on the Biology of Amphibians and Reptiles*, ed. K. Adler, pp. 141–162. Oxford, OH: Society for the Study of Amphibians and Reptiles.
- Pielou, E.C. (1975). *Ecological Diversity*. NY: John Wiley.
- Pielou, E.C. & Routledge, R. (1976). Salt marsh vegetation: latitudinal gradients in the zonation patterns. *Oecologia* 24: 311–321.
- Pirsig, R.M. (1974). *Zen and the Art of Motorcycle Maintenance*. NY: Morrow.
- Saul, J.R. (1992). *Voltaire's Bastards*. Toronto, Ontario: Penguin Books.
- Saul, J.R. (1995). *The Unconscious Civilization*. Ontario: Anansi, Concord.
- Scheiner, S. (1993). Additional thoughts on A Critique for Ecology. *Bulletin of the Ecological Society of America* 74: 179–180.
- Scheiner, S. (1994). Why ecologists should care about philosophy: a reply to Keddy's reply. *Bulletin of the Ecological Society of America* 75: 50–52.

- Shalamov, V. (1982). *Kolyma Tales*. NY: W.W. Norton & Co. (trans. from Russian by J. Glad).
- Shiple, B. & Keddy, P.A. (1987). The individualistic and community-unit concepts as falsifiable hypotheses. *Vegetatio* 69: 47-55.
- Stone, I.F. (1989). *The Trial of Socrates*. NY: Anchor Books.
- Tansley, A.G. & Adamson, R.S. (1925). Studies of the vegetation of the English chalk. III. The chalk grasslands of the Hampshire-Sussex border. *Journal of Ecology* XIII: 177-223.
- van der Valk, A.G. (1981). Succession in wetlands: a Gleasonian approach. *Ecology* 62: 688-696.
- Walker, D. (1970). Direction and rate in some British post-glacial hydroseres. In ed. D. Walker, & R.G. West, *Studies in the Vegetational History of the British Isles*. pp. 117-139. Cambridge: Cambridge University Press.
- Weiher, E. & Keddy, P.A. (1995). Assembly rules, null models and trait dispersion: new questions from old patterns. *Oikos* 74: 159-164.
- Weiss, P. (1965). *The Persecution and Assassination of Marat as Performed by the Inmates of the Asylum of Charenton under the Direction of the Marquis de Sade*. (translated by G. Skelton; verse adaptation by A. Mitchell) London: Calder & Boyards.

Part I:

The search for meaningful patterns in species assemblages