

WETLAND RESTORATION: THE POTENTIAL FOR ASSEMBLY RULES IN THE SERVICE OF CONSERVATION

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Abstract: One of the pressing problems for applied ecologists is the efficient restoration of structure and function to degraded ecosystems. Where some other conservation activities, such as protection of existing wilderness, continue to require making the best of increasingly bad situations, the goal of restoration raises the pleasing prospect of measurable improvement in landscapes. Restoration simultaneously provides the ultimate test for the discipline of community ecology: ecologists should be able to build an ecosystem in the same way an engineer builds a bridge, with a list of parts connected in specified ways leading to certain reliable outcomes. Failures would reveal that scientists do not adequately understand the system. Practical considerations suggest the application of tools that already exist rather than the invention of new ones. The objective of this paper is to suggest that two valuable tools may already exist, tools that provide an intellectual foundation for restoration ecology. Such a foundation is necessary because there has been a tendency for restoration ecology to represent a haphazard collection of individual cases rather than a well-defined discipline with repeatable methods. One possible scheme for unifying studies of restoration is that provided by assembly rules, where predictions are based upon key environmental factors and the responses of species to those factors. The potential of such assembly rules is introduced using three examples: fish in wetlands, plants in salt marshes, and plants in prairie potholes. I then describe an experiment where a standard species pool of wetland plants was sown into twenty-four different sets of environmental conditions, illustrating how landscapes can select communities out of larger pools. A second possible tool is indicators of ecosystem integrity. These can measure whether a project actually works. Clear discrimination between success and failure can improve restoration procedures by accelerating the evolution of management principles and techniques; Holling has called this process 'adaptive environmental assessment.' I conclude with the optimistic view that restoration already has the tools for continued progress; what is needed is primarily their intelligent application. That is, rather than ending with a typically academic plea for more research, I suggest (for a change) that what is needed is only the discriminating application of procedures and principles that already exist.

Key Words: Amazon River, assembly rules, environmental filters, eutrophication, fertility, fish, hydrology, indicators, *Lythrum salicaria*, prairie potholes, management, restoration, seed banks, salt marshes, species pools, tactics, traits, wetlands

INTRODUCTION

The real test of community ecology lies not in how much knowledge practitioners feel that they have, nor in the number of papers accumulated in learned journals, but rather in the practical ability of humans to protect and restore ecological communities. Ecologists

must therefore be able to reliably forecast the response of communities to changes in environmental factors. Changes, used in this sense, could include (1) deliberate human manipulations (e.g., alteration of wetland hydrology, restoration of fire, fertilization), (2) change incidental to human activities (e.g., shifts in climate, eutrophication from agriculture), or (3) ongoing pro-

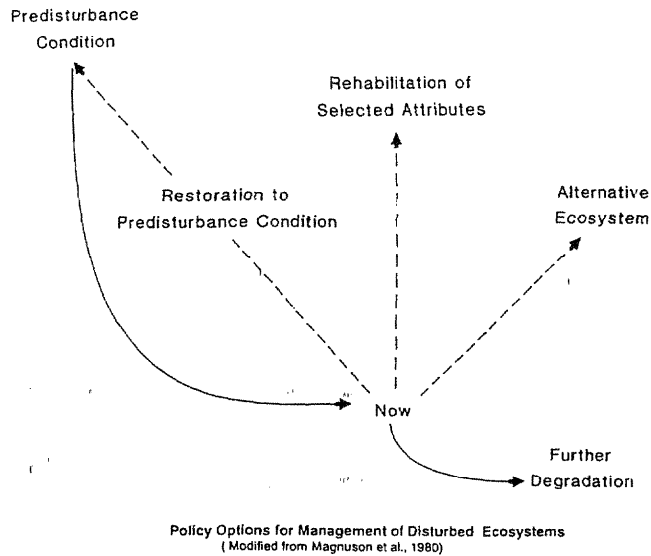


Figure 1. Restoration to predisturbance conditions is one of several management alternatives for degraded communities and ecosystems (from Cairns 1989).

cesses that would occur even without the presence of humans (e.g., climate change, sedimentation in deltas). This paper is primarily concerned with the first category of events, for ecological knowledge (or the lack thereof) is tested when humans set out to re-create an ecological community. The process of re-creating an ecological community is usually termed 'ecosystem restoration' (e.g., Cairns 1980, Jordan et al. 1987, Bonnicksen 1988, Kusler and Kentula 1990).

Ecosystem restoration is growing rapidly as a practice (e.g., Jordan et al. 1987, Kusler and Kentula 1990, Galatowitsch and van der Valk 1994, Pfadenhauer and Klotzli 1996, Lockwood and Pimm 1999); Bonnicksen (1988) refers to it as "an emerging profession within the science of ecology." Several goals are possible: to repair biotic communities, to re-establish them on the same sites if they are destroyed, or to construct synthetic communities if the originals are no longer possible (Figure 1). The choice of goal is critical; it is only when the goal is clearly articulated that an outcome can be evaluated to determine whether or not the management has been successful (Holling 1978, Cairns 1989, Noss 1995).

Noss (1995) traces the roots of restoration ecology back to Aldo Leopold, who observed: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." Hints of restoration can be found even earlier. Clements (1935) wrote an essay appropriately titled "Experimental ecology in the public service" in which he described the applications of ecology to a wide range of applied problems including land rehabilitation. Foresters may have been the first

to address the recreation of ecosystems; in 1883, Phipps wrote a book on the replanting of forests, and Larson (1996) has described what appears to be one of the earliest practical restoration projects in North America, the replanting of a forest in a gravel pit near the University of Guelph by Professor William Brown, an arboriculturalist from Scotland. Similarly, in Beard's classic book on the vegetation of the Caribbean islands (Beard 1949), there are also passing remarks on forest protection activities in the early 1900s. In wetlands, the use of *Spartina anglica* C. E. Hubbard for 'reclamation' of coastal mud flats was practiced in China early in this century (Chung 1982). In the 1930s, the British blocked drainage ditches and used portable pumps to raise water levels in the Woodwalton Fen (Sheail and Wells 1983). Now, there is even a separate scientific society (The Society for Ecological Restoration) and a journal (*Restoration Ecology*) devoted to the topic.

Restoration ecology has the potential to bring together a wide range of ecological activities. It challenges conservationists, applied ecologists, and theoreticians in different ways. Conservationists are challenged to shift some energy from fighting to protect fragments of remaining habitat towards the longer term goal of restoring and re-connecting entire landscapes. The Wild Earth proposal for North America (Wild Earth 1992) is one example. Applied ecologists are challenged to de-emphasize manipulation of single components of ecosystems, such as waterfowl or fish, and instead re-establish entire ecosystems that are self-regulating. Theoretical ecologists are challenged to develop practical tools to guide restoration and monitor its success.

However, the difficulties inherent in restoration are profound, in the literal meaning of the word. The number of components in a system influences the kinds of analyses that can be applied, and general systems theory describes how those systems with medium, as to opposed to few or many parts, are the most intractable (Weinberg 1975). "Small number systems" have few components and few interactions, and these systems are amenable to precise mathematical description. The population ecology of single species might be an example of a small number system, although population models can only be created by artificially removing individuals from the many connections they have with other populations. At the other extreme are "large number systems" where there are so many components that their average behavior becomes a useful description of the system. The ideal gas laws are one example; the position and velocity of a particular gas molecule is not of particular interest, but collective properties such as volume, temperature, and pressure are useful in many ways. Wetland ecosystems, how-

ever, are neither large nor small number systems (e.g., Lane 1985). As "medium number systems," they contain too many components to be treated analytically and too few for statistical analysis. Further, a hippopotamus and a cattail plant cannot be averaged like an ideal gas molecule, nor are their behaviours and population dynamics equivalent to random events. Therefore, as the number of components in a wetland increases arithmetically, the number of interactions increases geometrically. Some method of simplification is therefore necessary in order to solve problems involving medium number systems. This requires carefully preserving critical interactions and components while excising or ignoring others. The inherent difficulty in doing so wisely probably explains why, at present, medium number systems require approaches that are as much an art as a science.

A further problem is that it is possible to collect many published examples without finding principles that can be extrapolated to other sites. The problem of extracting general principles from large numbers of studies is well-illustrated by an example from a different area of ecology, the voluminous studies, extensive reviews, and ongoing divisive debates in the study of competition (e.g., Schoener 1983, 1985, Underwood 1986, Keddy 1989, Grace and Tilman 1990), debates that continue in spite of the increasing numbers of studies and the emerging potential of meta-analysis (Gurevitch et al. 1992). Apparently volume does not guarantee clean answers to questions nor the discovery of generally accepted principles.

In spite of such obstacles, large sums of money are being invested in restoration. These ongoing projects provide an ideal way to test the adequacy of ecological understanding and predictive ability. They promise to put both the methods and predictions of community ecologists and restoration ecologists directly on the spot. Not all studies, however, yet state clear and measurable goals, nor do they test general principles that can be applied to other sites. Moreover, a recent review of 87 published studies with clearly stated goals found that only 17 (20%) were completely successful and an equal number were unsuccessful, the rest being intermediate (Lockwood and Pimm 1999). If restoration predictions are wrong, the failure to re-create the desired community will not only waste the money invested in the program but may even cause further environmental harm. If clear questions are not posed, there is a risk that models and techniques will not be refined nor clearly linked to pre-existing ecological frameworks. In contrast to the great potential of restoration, it sometimes seems from published studies that practical restoration activity is being conducted without a full appreciation of historical roots, scientific foundations, or existing knowledge. Therefore, there is

the risk that restoration ecology will evolve as yet another fragmented state within the increasingly Balkanized realm of ecology and that the art and technique of restoration will be emphasized to the exclusion of the science.

My motivation in raising such problems is not to be negative. Rather, like the (in)famous American commander, General Patton (e.g., Essame 1974), I am simply reluctant to fight for the same ground twice. I have already commented explicitly, perhaps too much so, upon the limitations confronting community ecologists (Keddy and Weiher 1999), including their failure to make full use of developments in restoration ecology. I concluded that "much of the rhetoric around assembly rules cannot yet be translated into practical success on the ground" (Keddy 1999, p. 400). Such arguments, however, cut both ways. I will therefore suggest here that restoration ecology can benefit from the application of (1) assembly rules (the ability to manipulate ecosystems to recreate desired communities) and (2) ecological indicators (the ability to evaluate whether manipulation has produced the desired change). Both tools are briefly summarized below.

STEP 1: MANIPULATION OF ECOSYSTEMS

Any restoration project begins with a set of circumstances, the ground of the problem: (1) initial environmental conditions, (2) a pool of available species, and (3) a list of key factors that can be manipulated. The practical problem is to identify which key factors applied to which pool of species will produce which communities. The term 'assembly rule' is often used to describe the general problem of how restricted communities of organisms are assembled from larger species pools (Diamond 1975, Weiher and Keddy 1999). Let us consider pools, filters, and traits in turn.

Pools

The pool of species available to colonize the site is the raw material for a restoration project; at the largest scale, this pool is the product of long term processes of evolution and extinction (Figure 2). The study of these lies within the realm of evolutionary ecology, and the time scales are generally sufficiently long that the pool can be regarded as a constant for any particular project. At smaller scales, dispersal may also be limiting the pool of propagules for a single site; the importance of dispersal is likely to increase with the degree of isolation of a site (MacArthur and Wilson 1967, Diamond 1975), and the different approaches to assembly rules are partly determined by the emphasis placed upon dispersal as opposed to the local environment (Drake 1990, Weiher and Keddy 1999). There is

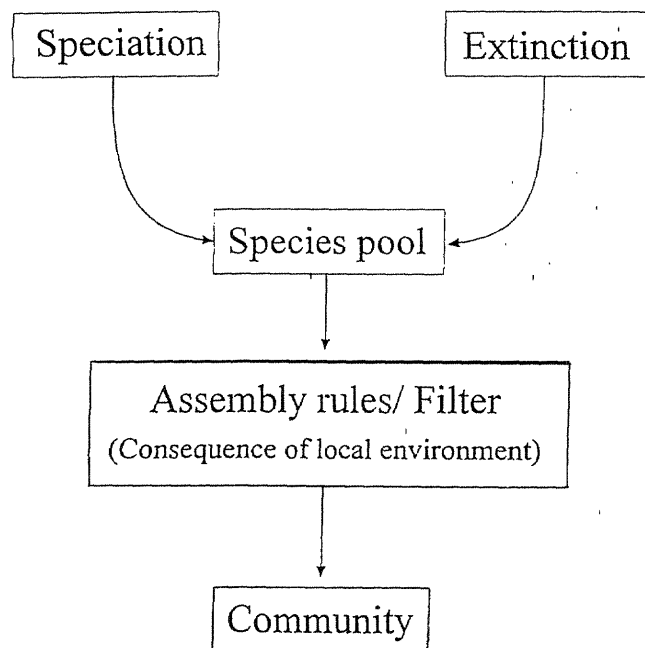


Figure 2. Speciation and extinction determine the size and composition of the potential species pool. The local environment then filters out species from this pool, creating a community (from Weins 1983).

still a good deal of ambiguity in defining pools, with different authors tending to use different procedures for establishing the pool for a site (Eriksson 1993, Zobel 1997). The objective of assembly rules is to predict which subset of the species pool for a given region will occur in a specified habitat. A first objective would be simply to predict the presence or absence of species in a habitat. The second objective would be to predict abundance as well as presence.

The process of constructing communities from species pools is therefore in many ways analogous to the process of evolution through natural selection. In natural selection, habitats serve as filters for genotypes, with the least suited genotypes being filtered out and the best suited surviving to reproduce. In the case of assembly rules, habitats again serve as filters and eliminate those sets of traits that are unsuitable to that environment. The species that comprise the community are those with the traits that survive the filters.

Filters

Some of the most important major filters that control wetland composition are water levels (50%), fertility (15%), disturbance (15%), salinity (15%), competition (<5%), herbivory (<5%), and burial (<5%). Their relative importance in controlling the community structure and composition of wetlands is intended to represent wetlands in general, and individual wetlands are

likely to deviate significantly. Deltaic wetlands may be influenced predominantly by burial, whereas estuarine wetlands may be influenced more strongly by salinity. Nonetheless, there is some sort of natural order and logic that can be used to select appropriate filters for investigation.

These filters provide a shopping list for the factors that can be used or rejected as possible filters for restoring wetlands. Again, the relative importance of the factors may be different from the list, but in any case, hydrology requires first consideration, and if it is neglected, then other factors alone will probably be insufficient to create the desired wetland.

The examples that I will provide below all involve primarily the direct effects of abiotic factors upon living organisms. These examples could be misleading because biotic interactions do, of course, also deserve recognition. Predation can be a strong filter (Wilbur 1984, Carpenter et al. 1987), as can herbivory (Smith and Kadlec 1985, Jefferies 1988, Lodge 1991, Shaffer et al. 1992) or competition (Snow and Vince 1984, Twolan-Strutt and Keddy 1996, Levine et al. 1998). The presence of neighbors can also facilitate establishment or survival by reducing the constraining effects of physical factors (Bertness and Hacker 1994, Castellanos et al. 1994, Bertness and Leonard 1997). The many examples of 'ecological engineering' (Jones et al. 1994), including alligator and beaver ponds, extend further the possible list of biological factors that can determine wetland composition. In isolated fragments of habitat, where dispersal and colonization rates may limit community composition, dispersal capability is itself a measurable trait (Diamond 1975, Keddy 1976, Hughes et al. 1994, Whittaker and Jones 1994). Some ecologists have argued that the term "assembly rules" should be restricted to only local biological interactions, but the chapters in Weiher and Keddy (1999) show that consensus does not yet exist.

Traits

Organisms possess life-history traits that allow them to tolerate different filters. Such traits are often known in a general way, but rarely is there systematic data suitable for predicting how an entire set of species might respond to a particular filter. The best data are collected by exposing large numbers of species to standardized conditions. This procedure, generally called screening, was popularized by Grime and his co-workers (e.g., Grime and Hunt 1975, Grime et al. 1981) working with the vascular flora of the Sheffield area of England, although broad comparisons were previously used, for example, to compare the tolerances of frogs to desiccation (Thorson and Svihla 1943) and the tolerances of reptiles to anoxia (Belkin 1963). Screen-

ing has also been extended to salt marsh plants (Partridge and Wilson 1987), freshwater wetland plants (Shipley et al. 1989), and fish (Junk et al. 1997). Classification of species into functional types or guilds provides another means for identifying sets of species sharing similar traits (Cummins 1973, Cummins and Klug 1979, Severinghaus 1981, Simberloff and Dayan 1991, Boutin and Keddy 1993, Steneck and Dethier 1994).

Given a pool, a list of environmental filters, and a list of traits, assembly rules would specify which particular subset of these traits (and therefore species possessing them) will survive. More precisely, in the situation where traits are known for each species in the pool, the objective is to specify whether or not certain traits (or sets of them) will permit a species to persist under a defined set of environmental conditions. The exact procedures for doing this most effectively need further work, but the potential can be seen in three examples, fish in floodplains, plants in saline coastal environments, and plants in prairie wetlands. These examples are for illustration only, and other groups of organisms and other filters could equally have been used. I will then introduce an experiment that shows how different wetland types can be created by manipulating the filters acting upon the same pool of propagules.

THREE EXAMPLES

Fish in Lakes and Floodplains

In flooded areas, access to oxygen is a critical problem for many living organisms. The Amazon basin has both the largest areas of flooded forest in the world and the largest number of freshwater fish species in the world (Lowe-McConnell 1975, Goulding 1980). Some 70,000 km² of forest are flooded, sometimes to depths of 15 meters, and for up to ten months of the year. Up to 3,000 species of fish may inhabit this region; of the more than 1,300 described to date, about 80 percent are either catfishes or characins. The latter group has radiated extensively in the Amazon lowlands and includes carnivores, frugivores, detritivores, and planktivores.

The annual cycle of tropical fish is closely tied to periods of inundation. "In both Africa and South America where much of the land is very flat penplain, the rivers inundate immense areas, on a scale unknown in temperate regions. Submerged seasonally and drying out for part of the year, these floodplains are interspersed with creeks, pools and swamps, some of which retain water throughout the year" (Lowe-McConnell 1975, p. 90). High water levels then create a vast sheet of water enriched in nutrients from de-

caying organic matter, including the droppings of grazing animals. As the water falls, the enriched water supports an explosive growth of bacteria, algae, and zooplankton; these in turn support a rich fauna of aquatic insects and other invertebrates. Many fish then migrate upstream and move laterally onto the floodplain to spawn. The eggs hatch within a few days, so the young appear when food is plentiful, but as nutrients are depleted and water levels fall, the fish move back into the main river. Some fish are killed by being stranded in drying pools, and predators often hunt the mouths of channels leading back to the main stream. The same general sequence of events occurs in rivers throughout the tropics, including Africa, South America, and Asia, although the timing of floods and the species involved may differ (Figure 3).

Hypoxic conditions pose one of the major constraints upon these fish, particularly after flooding, when shallow pools in floodplains are left filled with debris and exposed to the warming effects of sunlight (Kramer et al. 1978, Junk 1984, Junk et al. 1997). Using closed respiration chambers, Junk et al. (1997) found that lethal oxygen concentrations were normally less than 0.5 mg l⁻¹ O₂ (Figure 4), although some species from well-oxygenated bays were sensitive to levels twice this high. The lowest concentration of oxygen in the water can then be considered to be a filter that selectively removes different portions of the fish fauna. The ability to tolerate this filter can be determined for each fish species, whether by screening (sensu Grime and Hunt 1975) as in Junk et al. (1997) or by reference to other traits. Some nine or ten families of Amazonian fish, for example, can remove oxygen from the atmosphere; the swim bladder of *Arapaima gigas* Cuvier can act like a lung, and catfish may use the stomach to remove oxygen from swallowed air. Other fish can, within a few hours of hypoxic conditions, enlarge the lower lip to better extract oxygen from water. In one small floodplain lake, Junk (1984) reports that 40 out of 120 species were regularly found under pronounced hypoxic conditions. Of these, ten could take oxygen from the air, and ten could use the lower lip like a gill. The adaptations of the others were unknown.

Moving north to central North America, Magnuson and his co-workers (e.g., Tonn and Magnuson 1982, Magnuson et al. 1989) have similarly examined fish in lakes in central North America. Many of these lakes are small, isolated, shallow, and acidic. Fish are the dominant vertebrates in these lakes. Multivariate analysis showed that there were five basic types of lakes: (1) pike lakes, (2) bass lakes, (3) mudminnow-minnow lakes, (4) mudminnow-perch lakes, and (5) fishless lakes. The nature of the lakes suggested two environmental factors that could be acting as filters and elim-

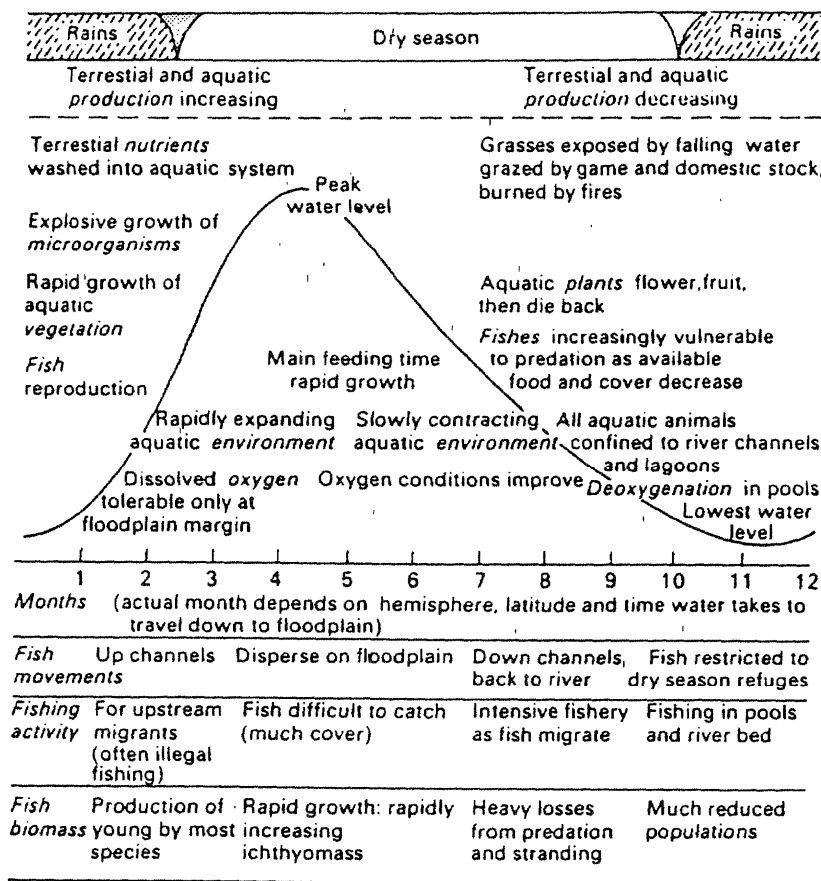


Figure 3. The effects of flooding upon fish in tropical rivers (from Lowe-McConnell 1975).

inating certain kinds of fish from certain kinds of lakes: pH and winter oxygen. When fish were screened for tolerance to low pH, this trait was a useful predictor of their field distribution (Figure 5). The pH and winter oxygen levels were also able to discriminate among lakes with different kinds of fish communities (Figure 6). If low pH and low oxygen act as filters, this can explain why fish with high oxygen and high pH requirements do not inhabit shallow lakes with low pH. However, these filters do not explain the reverse. Why do minnows and mudminnows not inhabit the lakes with higher oxygen and pH? Magnuson et al. (1989) conclude that the reason is predation. The smaller fish are restricted to lakes where predators are absent.

Salt Marshes

Although terrestrial plants may have evolved from oceanic ancestors, saline environments are now hostile to their growth, as illustrated by the restricted pool of herbaceous and woody plants able to occupy saline environments (e.g., Sculthorpe 1967, Tomlinson 1986). Saline wetlands are therefore a marvelous system for the application of assembly rules because they

are so structured by a single factor, salinity (e.g., Frey and Basan 1978, Niering and Warren 1980, Zedler and Onuf, 1984, Adam 1990, Bertness 1991, Bertness et al. 1992). A first task is to screen all common species for relative salinity tolerance. A number of authors have studied salinity tolerances for a few species at a time, but Partridge and Wilson (1987) demonstrated that thirty-one species can be ranked in order of tolerance to salinity, and in general, these species exhibit inclusive niche structure (Figure 7). Similar data have been provided for twenty-nine sand dune species (Sykes and Wilson 1989).

The vertical line in Figure 7 is sea water salinity. Only a small group in the pool can grow with sea water salinity. Consider this line a filter and observe that if a habitat has twice sea water salinity, the pool of 31 species is reduced to only one—*Suaeda novae-zelandiae* Allan. At sea water concentrations, the subset of potential colonists is approximately ten. To predict the effects of increasing salinity (say from increased tidal inundation associated with rising sea levels), it would be possible to forecast which species might disappear first; conversely, if the site is to be impounded and flooded with fresh water, it would be possible to forecast which species might invade. In fact, Zedler

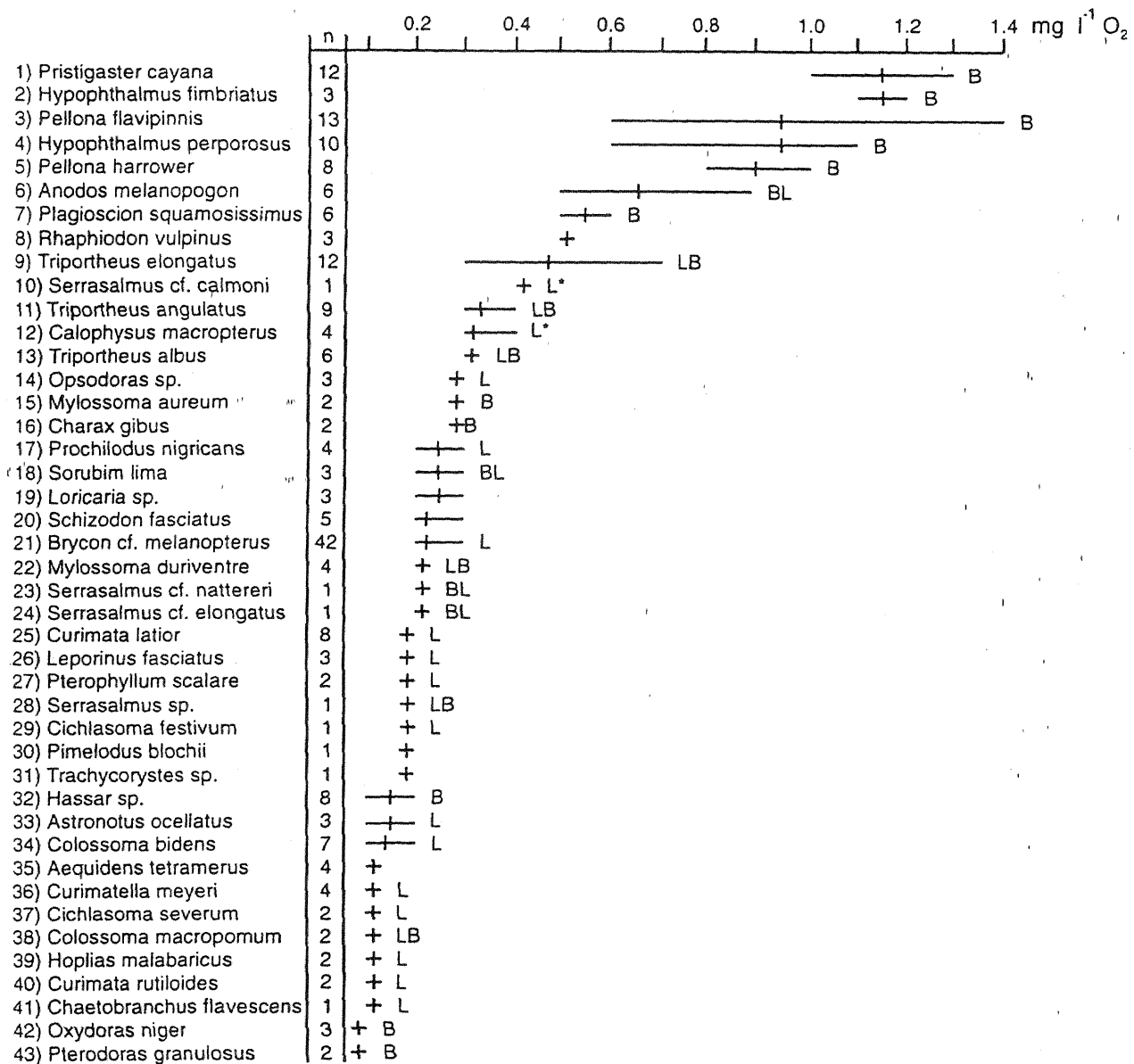


Figure 4. The tolerance of selected Amazonian fish species to low dissolved oxygen levels (from Junk et al. 1997).

and Beare (1986) have argued that periodic flooding with fresh water is essential for the regeneration of salt marsh plants in arid climates. In this case, the filter in Figure 7 is briefly pushed to the left; the greater the input of fresh water, the larger the number of marsh species that can establish.

More generally, saline environments appear to pose a nearly insurmountable obstacle to vascular plants. For example, there are some 200 genera and 2600 species in the palm family, but only four occupy saline conditions (Tomlinson 1986). Similarly, the family Myrsinaceae has over 1000 species in about 30 genera distributed throughout the tropics and subtropics, but only four occur in saline conditions (Tomlinson 1986). As a consequence, mangrove vegetation (mangal) has

very few species, 54 species of mangroves and perhaps 60 more associates in the entire world. In contrast, 90 woody plant species were found in a single 500-m transect of riparian flood plain in Central America (Meave et al. 1991); that is, one small area of riparian forest can have almost as many species as the world mangal flora! The effects of multiple constraints appear to be additive, so that additional constraints such as cold can reduce the number of woody plants in saline environments to near zero (Keogh et al. 1999). In arid zone wetlands where salinity builds up during droughts, brief periods of rainfall or flooding by fresh-water may be essential for most vascular plants to establish (Zedler and Onuf 1984, Zedler and Beare 1986).

Elevation then turns out to be an important predictor

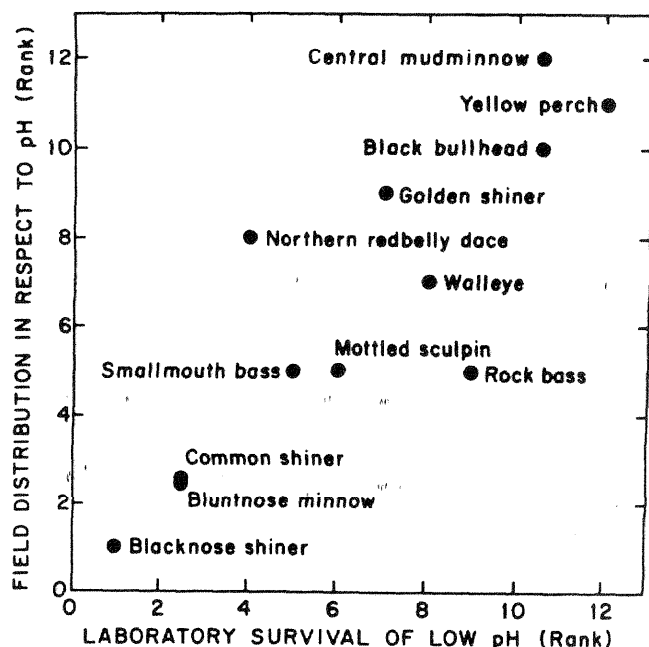


Figure 5. Laboratory measures of pH tolerance can predict the field distributions of fish (from Magnuson et al. 1989).

of the number of species in salt marsh vegetation (Garcia et al. 1993, Gough et al. 1994). As sea levels rise, or coastal wetlands subside (e.g., Shaffer et al. 1992, Boesch et al. 1994, Michener et al. 1997), or as land rises above the sea (e.g., Glooschenko 1980, Bégin et al. 1989), salinity can be expected to change in a known way, and in turn, the wetland vegetation can be expected to shift in predictable directions.

Prairie Potholes

Shallow wetlands that periodically become dry can be found around the world. Perhaps the best studied examples are prairie potholes formed by the glaciers that covered and then retreated from the continent of North America, leaving behind millions of depressions across more than a half million km² of prairie stretching from Alberta south-eastward to Iowa. These depressions are filled by melting snow, and depending on depth, water table, and summer rainfall, the depressions range from ephemeral to permanent wetlands (Kantrud et al. 1989). More than 20 million ducks representing 12 common species breed in this region, and it is considered the most important production habitat in North America for most species (Batt et al. 1989). The rich wetland flora ranges from wet prairie to submersed aquatics and is controlled by three main environmental gradients: water regime, salinity, and disturbance (Walker and Wehrhahn 1971, Shay and Shay 1986, Adams 1988). Buried seeds allow plant species to survive prolonged flooding or drought (van der Valk

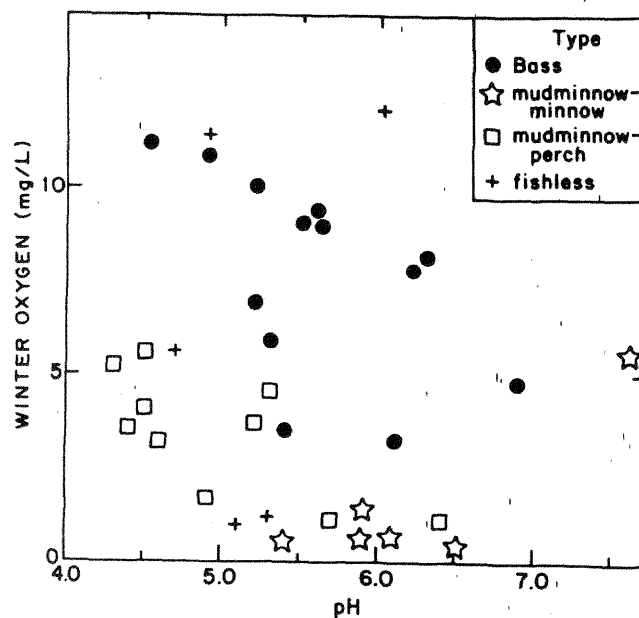


Figure 6. Winter oxygen levels and pH act as filters to create different fish communities (from Magnuson et al. 1989).

and Davis 1978, van der Valk 1981). Further to the south in North America, in the arid high plains, large circular depressions that retain moisture from the spring rainy season are called playas (Bolen et al. 1989, Hoagland and Collins 1997). Some 22,000 playas occur in Texas and New Mexico. Vernal pools extend from southern Oregon to northern Mexico (Bauder 1989). In Eurasia, much less is known about such wetlands, owing in part to an emphasis upon peatlands and mires, but similar shallow pools occur in semi-desert areas as well as in the large loess deposits north-east of the Black Sea. Wetland types can include plavni (reed thickets in continuously flooded areas), as well as firths and padinas (undrained basins filled by melting snow); the latter have genera familiar from North America such as *Phragmites*, *Scirpus*, *Eleocharis*, *Carex*, and *Calamagrostis* (Zhulidov et al. 1997).

An early attempt to predict species composition in wetlands used a few dominant ecological types of wetland plants (van der Valk 1981). A key element of van der Valk's model was the recognition that only one major trait was necessary to predict regeneration: whether or not a species could germinate under water. By measuring only this one trait on all species one can predict which part of the species pool will occur under either set of conditions.

As species become more similar in traits, it is likely to be more difficult to discriminate among their responses to environmental factors. In later work, van der Valk (1988) asked whether the densities of buried seeds of four emergent plants could predict the den-

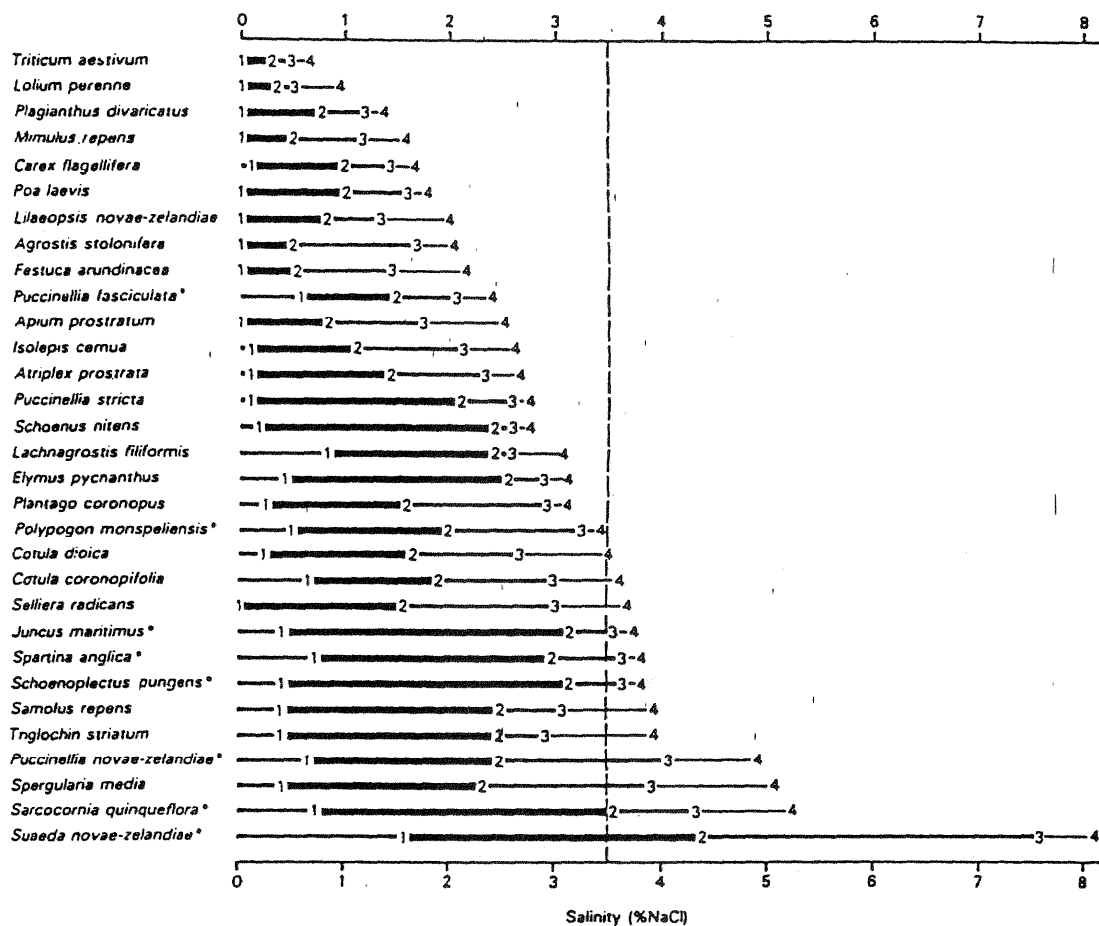


Figure 7. Salt marsh plants can be ranked according to their tolerances for salinity (from Partridge and Wilson 1987).

sities of adult shoots after a reduction in water level. Seedling densities were lower than expected, and rank order correlations between the abundance of buried seeds and seedling densities were variable (*Scolochloa festuacea* (Willd.) Link, 0.93; *Scirpus lacustris* L., 0.76; *Typha glauca* Godron, 0.44; and *Phragmites australis* (Cav.) Trin. Ex Steud., 0.03). In the case of *P. australis*, however, Dore and McNeill's (1980) monograph on grasses for adjoining Ontario expresses doubt as to whether viable seeds are formed and suggests that reproduction may be almost entirely by vegetative means. The seed-seedling correlations are rather better for the other three species, although as van der Valk observes, "there remain discrepancies between predicted and actual densities of seedlings during the drawdown." This illustrates limitations on assembly rules. As species become increasingly similar in their traits, it is increasingly unlikely that simple relationships between traits and environment will predict abundance. When it comes to predicting individual species distributions, van der Valk suggests that "[R]eductionist models based on comparative life-history data will provide the best possible foundation for

vegetation management." The point seems to be that the particular traits that must be selected will also depend up the scale of the investigation and the kind of species involved.

In a more extreme situation, Galatowitsch and van der Valk (1996) have examined prairie pothole vegetation in areas that have been drained and sown to row crops for at least twenty-five years. From a total of 62 such restoration projects, ten were selected on hydric soils that had been tile-drained and completely cultivated for corn and soybeans. That is, in each of these sites, restoration involved re-creation of a wetland where it had been absent for decades and where there was little reason to expect any residual seed bank. Given the importance of hydrology as a controlling factor or filter in the establishment of wetland communities, it might seem reasonable, at least as a first approximation, to assume that appropriate hydrology alone will re-establish wetlands. Perhaps steps as simple as plugging drainage ditches or removing tiles will suffice. In a comparison of ten restored wetlands to ten adjacent natural wetlands, the natural wetlands had a mean of 46 species compared to a mean of only 27

for the restored wetlands. Further, there were differences among functional groups; the restored sites had more species of submersed aquatics but fewer species of sedge meadows plants. The seed banks of the communities also differed; natural sites had nearly twice as many species (15 vs. 8) and nearly twice as high a density of buried seeds (7300 vs. 3000 m⁻²). Submersed aquatics, wet prairie, and wet meadow species were all absent from the seed banks of the restored wetlands. Galatowitsch and van der Valk propose the term 'efficient-community hypothesis' for the situation where vegetation will re-establish itself rapidly after hydrology has been restored, and they reject this hypothesis as a reasonable basis for restoration in prairie potholes. That is, they conclude that, in many cases, the species pool is inadequate for restoration and that dispersal is a limiting factor, rather like birds on oceanic islands (MacArthur and Wilson 1967, Diamond 1975).

The above study on restoration likely represents one end of the continuum of possibilities, as these sites represented an extreme situation of community eradication. In other watersheds, nuclei of remnant wetlands may remain as a source of propagules, and flowing water may disperse those propagules. This is not to deny the importance of their results, only to caution that the general importance of shortages of propagules as a cause of delay in vegetation recovery remains to be established. Three years is a relatively short period, and their data showed that species richness was increasing with time. Further, extensive fields of soybeans and corn may be particularly effective barriers between wetlands, thereby minimizing natural dispersal from native sites. A strength of this study was the proper sampling design and the reporting on two comparable sets of wetlands, rather than the description of a single case. There is also evidence that aquatic invertebrates are under-represented in restored wetlands (Galatowitsch and van der Valk 1994). Given the poor dispersal abilities of some species, Galatowitsch and van der Valk conclude that, at least in prairie potholes amidst farmland, species in guilds with poor dispersal capabilities will have to be reintroduced during restoration in order to re-establish the original ecological communities. This serves to emphasize that in certain situations, dispersal traits may be important predictors of likelihood of re-colonization.

The Experimental Assembly of Wetlands

If this approach to community assembly has validity, different filters should create different communities from a species pool. We have recently explored this process with a microcosm experiment (Weiher and Keddy 1995, Weiher et al. 1996). A pool of 20 wetland

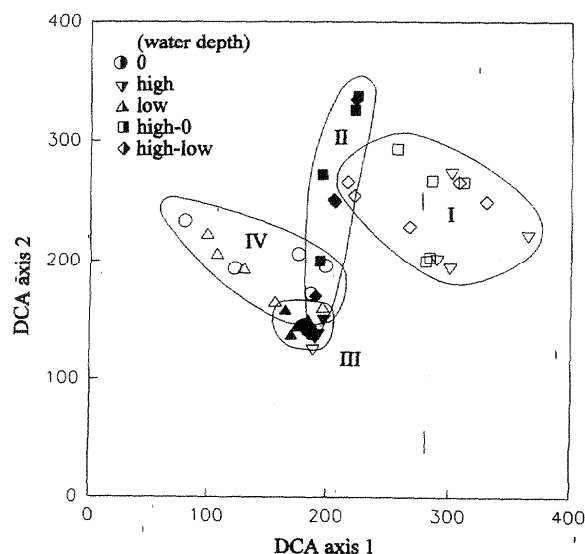


Figure 8. Ten sets of environmental conditions (five different water-level regimes combined with each of two fertility levels; solid symbols are high fertility) produced different wetland vegetation types from a standard pool of 20 wetland species (from Weiher and Keddy 1995).

plant species was sown into 120 containers representing 24 wetland environments. The twenty species in the pool were selected from a group of 91 candidate species based upon criteria including life history type, morphology, and germinability. The environmental conditions manipulated included most of the major variables thought to influence wetlands: (1) water level, (2) timing and duration of flooding, (3) leaf litter, (4) soil surface texture, (5) timing of germination, and (6) presence or absence of *Typha*. Moreover, each of these factors was repeated at high and low fertility. Species composition was then measured for five growing seasons.

Each environmental factor had a significant effect upon species composition; even if identical pools occur, different communities can be selected from this pool by different sets of environmental filters. Although 24 different treatment regimes were provided, water-levels and fertility were the most important filters. Restricting analysis to a subset of five water-level regimes and two fertility levels (ten sets of conditions), Figure 8 shows that four major vegetation types resulted (although not all are clearly separated on the two axes used in the illustration). That is, different sets of environmental factors sometimes produced similar vegetation composition. For example, in fertile treatments with high water or spring flooding (Type I, Figure 8) the vegetation was made up primarily of *Bidens cernua* L. and *Eleocharis smallii* (L.) R.&S. (Nomenclature follows Gleason and Cronquist (1963) for all species). In contrast, fertile treatments with fluctuations in water depth were primarily composed of *Eleo-*

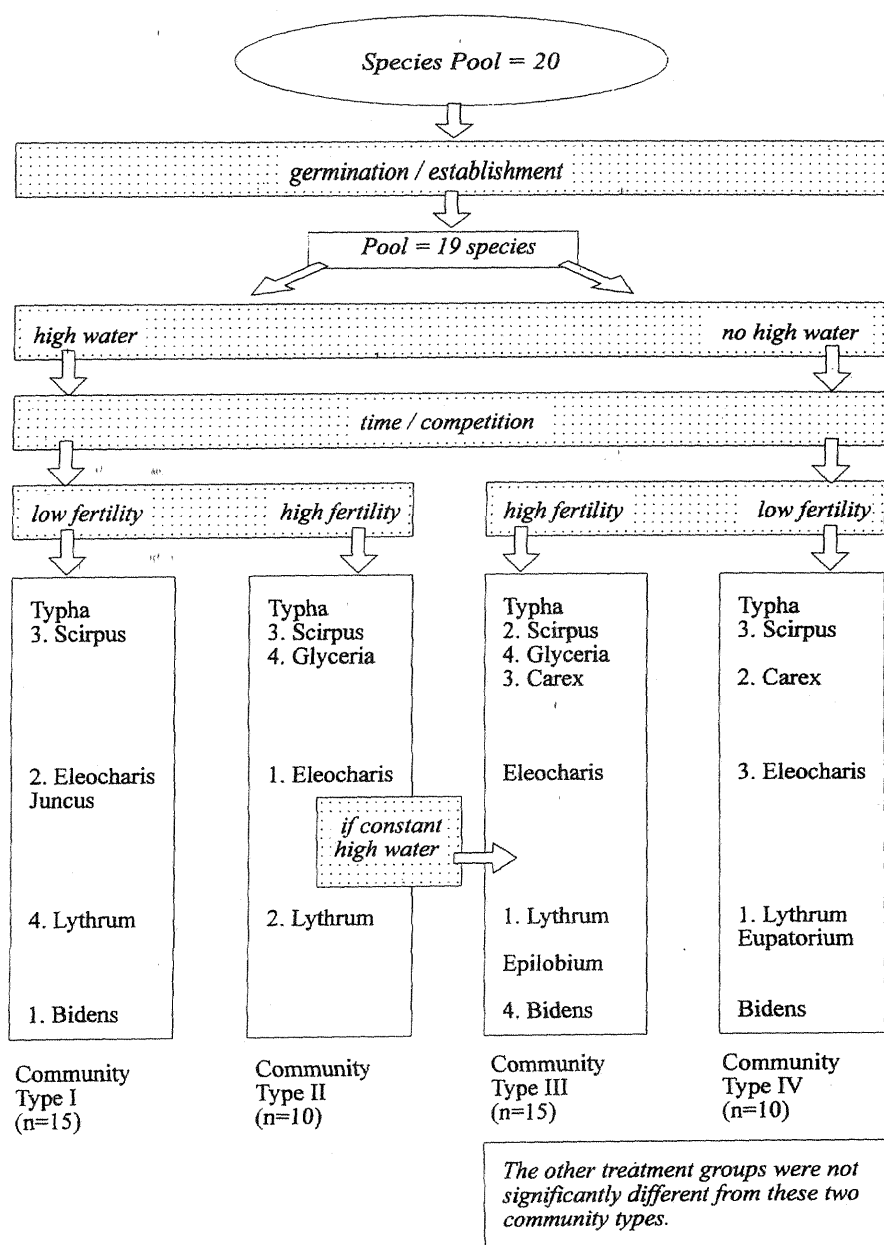


Figure 9. Twenty-four different environmental conditions, each replicated five times, produced four basic wetland vegetation types from a common pool of seeds. Five filters (stippled boxes) appear to account for the observed patterns (from Weiher and Keddy 1995).

charis smallii or *Lythrum salicaria* L. (Type II, Figure 8). Community type III included fertile treatments with constant water level, and were dominated by *Lythrum salicaria* with some *Scirpus acutus* Muhl. Finally, drier treatments were largely composed of *Lythrum salicaria* and *Carex crinita* Lam.

Based upon these results, a few simple filters can be arranged to show how different environments filtered out sets of different communities from a species pool. Taking a community perspective and considering relative abundance and position in DCA space, Figure 9 shows an overview of the results. First, one unknown

filter prevents establishment of one species, *Panicum longifolium* Torr. The second filter represents differences in establishment that were associated with water level. The third filter represents loss of species that did establish but were unable to persist through time (e.g., *Xyris difformis* Chapm.); presumably, such species could not survive the effects of neighbors. Experiments with planted canopies have since shown that established plants are a strong filter upon the establishment of a wide range of native species (Keddy et al. 1998). The remaining species were then sorted by response to high versus low fertility. In one case, an

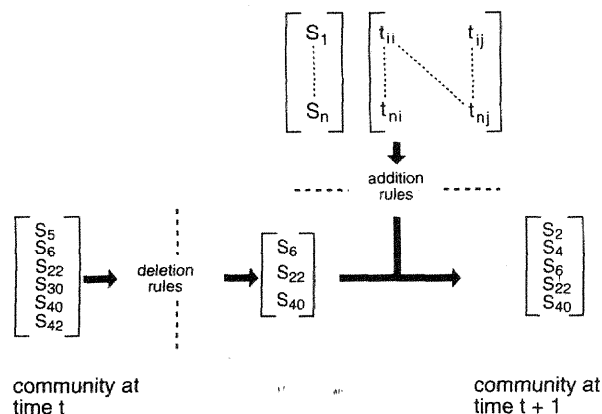


Figure 10. In order to predict change in an existing community ("response rules") it is necessary to consider both deletions from and additions to the community (from Keddy 1992).

added filter of constant high water transferred a community type from the high water to the low water group; that is, different treatments sometimes yielded similar communities.

Response Rules

Assembly rules often involve the creation of new communities in previously unoccupied environments. While this may mimic some restoration problems, (e.g., turning a gravel pit into a wetland), a majority of management problems begin with an established community that managers want to change in certain ways, perhaps to eliminate exotic species or to increase rare species. In such cases, one needs response rules, which specify how an initial vector of species composition will respond when an environmental factor is changed. Lewontin (1974) has called this "transformation rules." Other examples might include how prairie vegetation will respond to fire or grazing, how bird communities will respond to forest clearance, and how stream invertebrates will respond to siltation. In such a situation, a subset of species is already present at the site, and it is necessary to first determine how these will respond to the perturbation (deletion rules). Once the appropriate sets have been deleted, the species pool and trait matrix is screened for those species likely to invade (addition rules). The combination of deletion and addition rules is shown in Figure 10.

STEP 2: MONITORING SUCCESS AND FAILURE

Restoration projects must include monitoring (Holling 1978). From the point of view of basic science, the only way to develop workable assembly rules is to specify the factors, traits, and pool to be combined, make a prediction, and then test whether the commu-

nity responds in the manner predicted. If not, refinements are necessary for progress to occur. From the applied perspective, monitoring is necessary to determine whether the restoration is working. If management funds are being spent, and no useful ecological responses are occurring, the program is worthless. Monitoring requires us to select indicators for wetlands and then specify the target values for these indicators. Habits being what they are, it is always tempting to start counting selected species. In practice, there is a large body of science that deals with the selection of indicators and target values (e.g., Odum 1985, Rapport et al. 1985, Goldsmith 1991, McKenzie et al. 1992, Woodley et al. 1993).

Indicators provide an instrument panel for wetland management (Adamus 1992, Keddy et al. 1993). There is difficulty in choosing indicators precisely because ecology is not well enough developed as a science to specify what the essential properties of wetlands are. There is a great deal of activity in this area, always with the attendant risk that these problems will be tackled in an isolated manner, ignoring the many similarities across systems. Let me therefore outline a process that begins with some fairly pragmatic decisions. The process has three key steps: selecting the state variables, setting critical limits, and testing the indicators with a monitoring program.

Selecting State Variables

What properties of communities should we measure to guide our decision making? In the past, indicators have been developed haphazardly, often reflecting the interests of specific user groups and value systems, rather than according to more broad scale ecological criteria. This history is reflected in the idiosyncratic kinds of databases currently available (e.g., C.J. Keddy and McCrae 1989). As Tansley observed in 1914 (long before the advent of computer-controlled recording devices, satellite imagery, and very large science budgets), "The mere taking of an instrument in the field and recording of observations ... is no guarantee of scientific results." This observation is too often overlooked. A few simple criteria might guide the selection of indicators.

Ecologically meaningful: closely related to maintenance of essential environmental processes (e.g., water-level fluctuations) and ecosystem functions (e.g., primary production).

Macro scale: measuring the state of entire systems or key processes rather than small pieces or selected species.

Pragmatic: guided by measurable or empirical attributes of systems rather than conceptual or theoretical concepts and notions.

Sensitive: quick response to stresses and perturbations, to minimize lag and give maximum response times for decision-makers.

Simple: easy to measure, therefore inexpensive.

With these criteria in mind, there are at least three procedures that might be used to select indicators.

First, those abiotic environmental factors that maintain and control communities could be directly measured. Some of these key factors were listed above, and the examples addressed the response of selected biota to filters such as dissolved oxygen, salinity, and flooding. At one time, physical factors alone were monitored. Cairns et al. (1992) recalls that in 1948, "most pollution assessment was carried out by what were then called sanitary engineers (waste treatment specialists) and chemists. The accepted procedure was, that if certain limited chemical/physical conditions were met ... there was little or no need to examine the biota (p. ix)."

More recently, the biota have received increasing attention. This second approach could be considered indirect, in that the factors are assessed by the impacts upon the biota. However, if it is the biota themselves that are really of interest, then they are being directly measured rather than inferred from abiotic factors. Further, organisms have the ability to integrate the effects of complex environmental factors that vary in space and time. Biomass, diversity, and life forms are candidate ecosystem properties for monitoring.

A third approach emphasizes the evaluation of systems that have already been damaged or stressed to find indicators that appear sensitive to that damage or stress (Woodwell and Whittaker 1968, Odum 1985, Rapport et al. 1985, Rapport 1989, Freedman 1995). Ecosystems that are under stress display certain similar responses, including increased community respiration and increased nutrient loss.

Setting Critical Limits

Once indicators are selected, the next step is to set acceptable and desirable levels for them. Each indicator should have a range of values specified, one limit being the tolerable level and the other being the desirable. If the system moves outside this specified range, remedial action is needed. For example, depending upon the situation, a goal of zero exotics might be desirable for a rare wetland vegetation type, and two exotics might be tolerable. If more exotics

than this invaded the site, investigation and appropriate remedial action would be required. In many cases, of course, a single exotic can have a dramatic effect upon community structure, and it may be necessary to specify that remedial action is required if the exotic exceeds a measurable proportion of the community biomass.

In the long run, it would be useful to have a handbook that would (1) classify major wetland types and (2) specify, for each wetland type, the appropriate indicators with their desirable and acceptable levels. Guides for forest ecosystems such as Jones et al. (1983) or wetland ecosystems such as Racey et al. (1996) illustrate the feasibility of this approach. It is possible that some indicators might have similar levels for all wetland types, but most (e.g., amphibian biomass, population density of exotic herbivores, diversity of carnivorous plants) will have different critical limits for each wetland or habitat type.

Monitoring

Selecting indicators and setting critical limits is an iterative or adaptive process. As scientific knowledge of community ecology and experience with ecosystem management accumulates, it may become necessary to change either indicators or critical limits. Indicators would therefore evolve to reflect our constantly improving knowledge. It is therefore essential to monitor as projects occur and then to use the information from monitoring to revise criteria for future projects (e.g., Holling 1978, Beanlands and Duinker 1983, Keddy 1991, Adamus 1992).

At present, indicators are often selected on a system-by-system basis. While there will always be a need for indicators of factors relevant to local communities, such as particular species of commercial fish, it would be desirable to rapidly try to achieve consensus on a standard and more general series of indicators for wide usage. Not only would a standard list be more efficient, but it would allow comparison and contrast among wetlands and among management strategies.

In a frequently-overlooked book chapter, Bloom (1980) has described a general procedure for setting critical limits and quantifying the recovery of communities after disturbance. He assumes the availability of a pre-perturbation set of samples is available as a reference point. Based upon the species composition of these samples, one can define a 95% confidence interval envelope around the centroid of the original community (Figure 11). While Bloom used principal coordinate analysis to define the space occupied by these samples, any number of other possibilities exists; indeed, one might not even use species composition, but other properties such as functional composition,

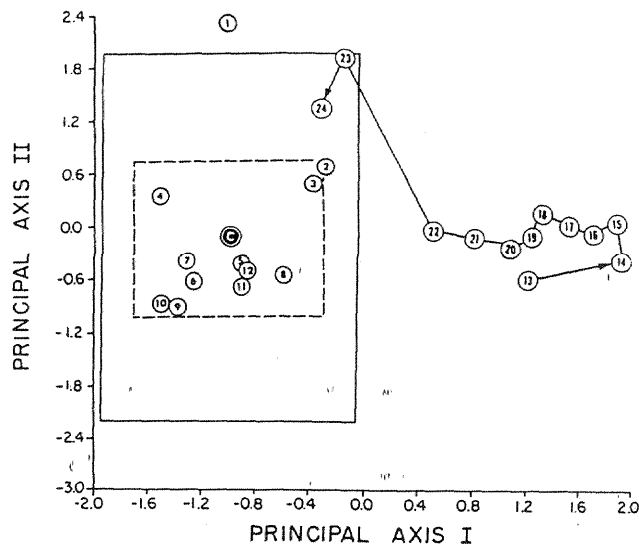


Figure 11. Defining and charting the recovery of a community after perturbation. The data are from a benthic community, with sample units 1–12 before perturbation and sample units 13–24 after perturbation. The solid and dotted boxes represent two procedures for calculating a 95% rejection polygon using parametric and non-parametric methods respectively (from Bloom 1980).

diversity, or biomass. In any such case, the same principles would apply. A perturbation occurs when the community is pushed outside these 95% confidence limits. If the trajectory of the community is then monitored along the same axes, one can track both its degree of departure from the original composition and its recovery; departures are defined as movement away from the centroid and recovery as movement towards it. Recovery is considered to have finished when the perturbed community returns to within the envelope defined by the original samples. The strengths of this approach are that one is provided with an objective space that defines the original state, as well as objective measures of perturbation and recovery.

In many cases, of course, the restoration ecologist inherits a perturbed site that may already be in the region of sample points 13 or 14 in Figure 11. In such a case, it is up to the recovery team to decide upon the desired composition. This could be based on historical data from the site, published data from other sites that provide the desired end point, or new data from other less-perturbed sites. One might even select a different region of the phase space if this region represents a community type that is disappearing from the landscape. Once this decision is made and the appropriate recovery region is defined, the task of the restoration ecologist is to move the community from the right part of the figure into the desired region on the left. The factors covered earlier in this paper should provide the necessary shopping list.

CONCLUSION

Assembly rules may provide a helpful framework to unify ongoing work in community ecology and wetland restoration. I have tried to show that this framework can be applied to existing studies and, perhaps more importantly, that different environmental filters can be used to create different wetland communities from a standard pool of species. Assembly rules can therefore specify a direction for research and allow us to measure progress toward a goal (see also Rigler 1982, Rigler and Peters 1995). While ecologists all know that wetlands are the product of a set of environmental factors, both natural and human-induced, what still remains is the task of predicting how the composition of wetland communities will respond to changes in such factors. This requires systematic attention to species traits and environmental filters, as well to those indicators that monitor success or failure. Once our scientific community can effectively restore wetlands, we may indeed call community ecology a science.

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