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A book, particularly a “textbook” can easily create the impression that it has all the facts and nothing more needs to be learned. Science, however, is a process, and knowledge continues to grow. In principle, scientists should have a short and clear set of questions that need to be answered, and familiarity with the tools that will help answer those questions. Going out and studying the first thing that catches our eye, or measuring everything we can think of, is not advisable. It happens too often. Wetland ecology, more than most, would benefit from a stronger grounding in the methods and tools of science. Here I would like you to think about how wetland ecology fits into the last 100 years of scientific progress, and how we can take it forward for everyone’s benefit. Everyone from new graduate students to seasoned and graying professors can benefit from taking a little time to reflect on the big picture. So let us start with the age of exploration and the search for . . . the source of the Nile . . . and penguin eggs.

12.1 Some context: the great age of explorers

There was a time when exploring the world's geography was a part of science in general, and a part of wetland ecology. Wallace, co-discoverer of evolution, began his scientific career with an expedition to the Amazon. Darwin made his epic voyage to the Galápagos. Von Humboldt set a world elevation record climbing a peak in the Andes. Each discovery generated new questions. One that remained was the source of the Nile River. Another was the nature of the South Pole. Let us use these as examples and leap back a century to this challenge of physical exploration.

It was only a little over 100 years ago, September 16, 1864, to be precise, when the British Association for the Advancement of Science met in Bath, England, and among the celebrities were the two most controversial figures of African exploration, Richard Burton and John Hanning Speke. *The Times* called their impending formal confrontation a gladiatorial exhibition. The topic of debate? A wetland. More specifically, the source of the Nile (Morris 1973).

Consider the challenges they faced. A joint expedition to Africa in 1858, arrival at Lake Tanganyika with Speke nearly blind from trachoma and Burton half-paralyzed by malaria, and then Speke's solitary reconnaissance trip, which 25 days later brought him to the shore of Lake Victoria. On Livingstone's last and greatest adventure, still on the hunt for the Nile headwaters, he was "delayed by tribal wars, constantly sick, losing his teeth one by one" when he reached the Arab slaver's village of Ujiji and languished near death. On November 10, 1871 he was discovered by Henry Stanley of the *New York Herald*, and greeted with the now famous "Dr Livingstone, I presume?"

The era of global exploration ended, in one way, not with the Nile but with the final voyage to the South Pole (Jones 2003). Even then, there were questions as to whether the trip was more of a voyage for national honor than for scientific discovery,

although the British Expedition led by Captain Scott made an effort to include exploration, even to man-hauling many pounds of rock samples back on the already heavy sledges.

It is worth reading more about those times, if only to refine your own thoughts on what the modern role of science should be. Consider. When Captain Scott and his companions reached the South Pole (January 17, 1912) they found a flag already there – left by the Norwegian Roald Amundsen a month earlier. They now faced a 1400-km (850-mile) journey across Antarctic ice to reach their base camp. On the trek back, Petty Officer Edgar Evans collapsed in the snow and died. Captain Lawrence Oates, crippled by frostbite, and fearing that his slow pace would cause the death of his companions, walked into the snow on March 17 and did not return. On March 19, the three survivors pitched their tents in the snow, their food and fuel exhausted, but knowing it was only 18 km from a depot with fresh supplies. This was where their bodies were found a year later by a rescue expedition. Reading the accounts of the suffering, one wonders whether the effort was worth it.

Skeptical questions about the motives and the risks do need to be asked, but when we become cynical, it is worth reminding ourselves that on this same trip, three of the team (Wilson, Bowers, and Cherry-Garrard) (Figure 12.1) made an epic journey to collect eggs of the Emperor penguin, then thought to be the most primitive species of bird on Earth. They wanted embryos to answer questions about the origin of birds and their relationship to other vertebrates. Hence, they sledged for 2 weeks in the continual darkness of an Antarctic winter, dragging their supplies through a succession of blizzards, through temperatures as low as -60°C (-77°F), to reach Cape Crozier and its penguin rookery. Collecting five unhatched eggs, they then had to retrace their steps for another 2 weeks of the same, just to regain contact with the rest of the expedition. Three eggs survived (and are now in the Natural History Museum in



FIGURE 12.1 Exploration! The Cape Crozier party leaves for a 4-week night journey in the Antarctic winter to collect Emperor penguin eggs in 1911. Left to right: Bowers, Henry Robertson, 1883–1912; Wilson, Edward A., 1872–1912; Cherry-Garrard, Apsley, 1886–1959. (Courtesy National Library of Australia.)

London). The account of this trip, titled *The Worst Journey in the World* (Cherry-Garrard 1922), “remains one of the classic narratives of exploration” according to Jones (2003, p. 264). Still, the age of heroic exploration did, in many ways, die with Scott and his team, since their failures received more attention than the scientific successes. Moreover, the following years of the First World War began to make people think more skeptically about science. The outbreak of the First World War saw technology and science used in unprecedented ways, from machine guns to airplanes to tanks to poison gas. It raised, and still raises, troubling questions about just what it is that scientists are trying to achieve, and whether it will benefit or harm humankind.

Setting aside the bigger question of the potential harm caused by science, let us return to the small one. Is there still a role for exploration? The good news is that some exploration will continue to be

necessary. We still need accurate species lists for many wetlands. New wetland species undoubtedly remain to be named. Some wetlands like the Congo River basin, in spite of their global significance, are still imperfectly explored (Campbell 2005; Keddy *et al.* 2009b). There does seem to be something in our human nature that enjoys search and discovery. Every student has the capacity to find something new, whether it is a new species of wetland plant for your county flora, or a new species of dragonfly in a national park. To me, the thrill of finding a new location for a rare plant or animal is part of the pleasure of working as a scientist.

Yet, overall, we are now entering a new era, an era where the essential challenges to the scientist require not the discovery of the headwaters of the Nile, or the enumeration of the palm trees along the Amazon, or the collection of Emperor penguin eggs, but something more difficult. Our new task is the

discovery of things that are essentially unseen and unseeable. They are (1) the essential **processes** that occur in wetlands, and (2) the **relationships** among environmental factors and life forms. You cannot preserve a process in a bottle of formaldehyde, nor can you photograph a relationship with a high-tech camera. Processes and relationships are the hidden laws or rules that are under, or behind, or inside (none of these words is quite right) the biological reality around us. Our current task is to find these, to describe them, to quantify them, and to subject them to rigorous experiment without ever seeing them. The closest we will come to actually seeing them is when we write a report and prepare a graph or figure that exemplifies our ideas.

The closest analogies might be early years in chemistry, going back to the era when scholars first became interested in the composition of the

atmosphere, nitrogen fixation by legumes, or carbon storage in wood, when even the periodic table had yet to be drawn.

While there remain new geographical discoveries to be made, particularly in poorly known groups such as the arthropods and microorganisms, and perhaps in regions under the oceans, the great period of explorers in sailing ships and steamers has passed. We are now in an era of new challenges. Our challenge is to pursue these with the same devotion as Speke and Scott, as Wallace and Darwin. Perhaps, chastened by a century of warfare, of poison gas and nuclear weapons and engineered diseases, we could also add a new requirement. Our efforts should focus on knowledge that will be of benefit to other living beings, not on knowledge that will be used to harm them.

12.2 Four basic types of information

We can identify four basic steps in gaining knowledge about wetlands. We will first consider these types before we move on to cover more sophisticated analyses.

12.2.1 Species accounts

One way of looking at the world is to study individual species. This has the advantage of simplifying the process. Find a species. Find a biologist. Let one study the other. Thus, the book cover has both a snapping turtle and a great egret, rather conspicuous wetland species that have been studied a good deal. People who work with insects and plants in particular find this highly unsatisfactory, because there are far more species than there are biologists interested in them. Perhaps countries like China and India, each with more than a billion people, can afford to have one biologist assigned to each plant and animal species, but even if this were the case, we can argue that it is not a very efficient way to do science. This is not to say that we should not learn the names of wild

species – indeed, I have included many species names in the figures.

There are certain costs to the species-oriented approach. First, species that are not popular get overlooked. When I teach, I tend to meet students who want to study whales and lions and moose. Another group wants to study ducks and deer and trout. I rarely meet ones who want to study mud snails, algae, or methanogens. As a result, our understanding of the natural world is warped. We know a great deal about life forms with backbones and fur. Or feathers. Or gills and scales. We know relatively little about others. Imagine yourself newly arrived on Earth, and interested in wetlands: what species would you choose to study based on the criterion of importance? And how would you decide to measure importance?

Although our knowledge of the natural world is growing, my students are always surprised to find the limitations of information on line. Here are three tests. (1) Try to find a list of the frogs found in one of the world's biodiversity hotspots, the mountains of

southwest China. If you succeed, select one and try to find its range map and diet. And the type of wetland in which it occurs. (2) Birds are particularly well studied. Find a list of the birds nesting in the Congo River delta. Which species of migratory birds use that delta? Which ones nest there, and when? (3) The Hudson Bay Lowland is one of the world's largest wetlands. Try to find an estimate of carbon storage and methane production in that specific wetland. Diamond mines are being dug in that wetland – which plant species occur in the vicinity of those mines, and what is happening to the local water table? The point I am trying to emphasize is that enormous gaps in our knowledge exist. We should plan future work to fill those gaps. Our knowledge of wetlands must extend beyond large charismatic species.

12.2.2 Delineation

We need maps of wetlands. Mapping is one of the most basic parts of geology and biology. If you read the travels of early biologists, you know that much of it was driven by simple questions like “Where does this river go? How big is this forest? How high is this mountain?” These are legitimate questions, and our knowledge of the world now, with an atlas in every library, and satellite images available on line, is truly remarkable. In spite of this, there are important gaps. We still lack good maps for some of the world's largest wetlands. And satellite imagery, while it might be able to differentiate between flooded and non-flooded forest, is a poor substitute for having biologists on the ground.

To produce a map of a wetland, you need criteria for recognizing when wetland stops and upland begins. In the United States, there is a formal process of wetland delineation, and an official technical manual done by the U.S. Army Corps of Engineers (1987). Using criteria like soil type and the presence of wetland plants, biologists are employed to map wetlands at regional scales (U.S. Army Corps of Engineers 1987, Tiner 1999). These wetlands are

then protected by certain legislation and regulations, and government agencies must issue permits for any activities that could alter the wetland.

Plants are a useful guide to the presence of wetlands. The U.S. Fish and Wildlife Service has therefore sorted native plants into several categories of official wetland indicator status, including **obligate wetland plants** and **facultative wetland plants** (www.plants.usda.gov/wetland.html). Obligate wetland plants are entirely dependent upon water, while facultative wetland plants usually occur in wetlands but are occasionally found elsewhere. Some obligate wetland species you have encountered in this book include *Platanthera leucophaea* (Figure 3.4), *Sabatia kennedyana* (Figure 2.5f), *Sagittaria lancifolia* (source of data in Figure 8.6), as well as *Nuphar lutea* and *Pontederia cordata* on the cover itself. The obligate list also includes many trees including cypress (*Taxodium* spp.), tupelo (*Nyssa* spp.), and mangrove (*Laguncularia racemosa*, *Rhizophora* spp.). Such lists provide an important tool for locating and delineating wetlands.

Each country tends to have its own procedures, and these are often modified by state or provincial regulations, so we will leave it as an exercise for you to find out the laws and policies that protect wetlands where you live. To use a Canadian example, all the major wetlands around my home have now been mapped (Figure 12.2). Can you find something similar for your county?

12.2.3 Inventory

Once a wetland is mapped or legally “delineated,” it is natural to ask “What lives there?” Indeed, one of the most basic questions in biology is: what is here? Although young scientists today will find it hard to match Wallace canoeing up the Amazon to ask “What is here?” or Darwin sailing to the Galápagos to ask “What is here?” or Scott sledging to the South Pole to ask “What is there?”, this none the less remains an important question at more local scales.

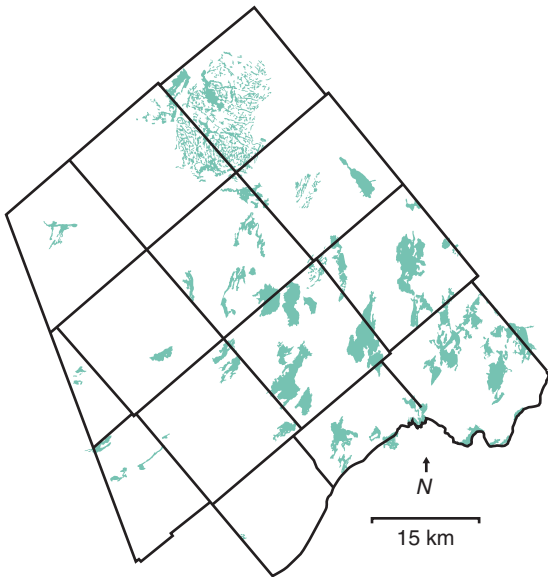


FIGURE 12.2 The vast majority of wetlands in southern Ontario have been mapped, investigated, and evaluated for protection. Here are the wetlands of provincial significance in Lanark County (Ontario, Canada) where the author resides. (Courtesy Ontario Ministry of Natural Resources.)

Many local wetlands still do not have complete inventories. It can be a very pleasant pastime to select a poorly known wetland, and then try to complete a list of all the creatures that live there. It is also an excellent way to hone your skills as a biologist, and contribute to scientific knowledge at the same time. Pick a wetland and go to work. While you are at it, you may discover a new species for your county, or state, or even nation.

Inventories are also done professionally. When an area is designated a protected area in some way (say a park, an ecological reserve, a special management area) it is normal to have a team of biologists explore the area and publish a report. Some of you may find work as a consulting biologist doing exactly this. Of course, once the report is done, the real work begins. The early reports try to describe the area as well as possible. But often it is local biologists and naturalists who take the time to do further exploration and find species that the first report missed.

12.2.4 Evaluation

Once a wetland is mapped and delineated, it is still necessary to measure its ecological significance. So long as cities are growing, and land is being cleared for agriculture, there has to be some way to decide how valuable each wetland is. We saw some approaches to measuring the services provided by wetlands in Chapter 11, but there has to be a simpler system that can be applied systematically to each and every wetland in a region.

In Ontario, Canada, a wetland evaluation system has been used to assess more than 2300 wetlands. The evaluation system has four components: biological, social, hydrological, and special features (Table 12.1). Once each wetland is evaluated, it is then assigned a score. Each category can have up to 250 points, for a total out of 1000. Any wetland that receives more than 600 points in total, or in which the biological or special features component reaches 250, is designated a Provincially Significant Wetland (PSW). Groups of wetlands can be evaluated together as a wetland complex if they meet certain criteria of interconnectedness.

Provincially Significant Wetlands have many kinds of protection. I, for example, am writing this book on the edge of a wetland complex (the Scotch Corners Wetland Complex) that has been evaluated as a PSW. It has rare plants (*Peltandra virginica*, *Galearis spectabilis*) and significant birds (nesting osprey, nesting herons), many mammals (fishers, otters) and at least six kinds of frogs.

Although some people are still unhappy that their farm has designated wetlands, most people now accept maps like Figure 12.2 as a part of our rural heritage. Some people, like me, even buy land because they like knowing that the land will be protected from further development. Developers tend to avoid wetlands because they know that they will encounter expensive delays by trying to build in areas with demonstrated levels of natural value. Increasingly, landowners like having wetlands, because if your wetland is mapped and evaluated as significant, you pay low taxes on the wetland acreage.

Table 12.1 Evaluation criteria for assessing wetland significance in the province of Ontario, Canada. Wetlands scoring a total of at least 600 or scoring 250 for the Biological or Special Feature components are determined to be provincially significant wetlands (see Figure 12.2)

Component	Primary criterion (<i>secondary criterion examples</i>)	Maximum possible score	
		Primary criterion	Component ^a
Biological	Productivity (<i>growing degree days, wetland/site type</i>)	50	250
	Biodiversity (<i>wetland types, vegetation communities, surrounding habitat diversity, interspersed, open water type</i>)	150	
	Size (<i>biodiversity–area index</i>)	50	
	Economically valuable products (<i>wood, rice, fish, furbearers</i>)	50	
	Recreational activities (<i>number and intensity</i>)	80	
	Landscape esthetics (<i>distinctness, human disturbance</i>)	10	
Social	Education and public awareness (<i>education, research</i>)	40	250
	Proximity to areas of human settlement	40	
	Ownership	10	
	Size	20	
	Aboriginal/social values	30	
	Flood attenuation	100	
	Water quality improvement (<i>short and long term, groundwater discharge</i>)	100	
Hydrological	Shoreline erosion control	15	250
	Groundwater recharge	60	
	Carbon sink	5 ^b	
	Rarity (<i>wetland types, number of species and relative significance</i>)		
Special Features	Significant features or habitat (<i>colonial birds, winter cover, waterfowl breeding/staging/molting, fish habitat</i>)	625	250
	Ecosystem age	25	
	Great Lakes coastal wetlands	75	
Total			1000

^a 250 per component assigned for criteria total ≥ 250 .

^b No limit to criterion score.

Source: From Ontario Ministry of Natural Resources (1993).

12.3 Limitations to species-based research

The above four steps will provide a great deal of information for conservation. But they are unlikely to provide good grounds for making predictions

about how wetlands as a whole will change in response to perturbations. Although species-based work is appealing, it may not be a particularly useful

approach to understanding the behavior of communities and ecosystems. This is because wetlands have so many species. Here is the problem, in the words of Rigler (1982), who wrote about the failure of species-based models in limnology

A temperate lake may support 1000 species. If each species interacted with every other species we would have $(1000 \times 999)/2$ or 0.5×10^6 potential interactions to investigate. Each potential interaction must be demonstrated to be insignificant or quantified. If we estimate one man-year per potential interaction it would take half a million years to gather the data required for one systems analysis model.

Indeed, you can divide scientific problems into three categories, small-, medium-, and large-number systems (Weinberg 1975). My own education did not address the importance of general systems theory in research, and so I suspect that most readers will have the same limitations.

Small-number systems These have very few components and few interactions, and are amenable to precise mathematical description. Population ecology is an example. We can predict exponential growth from a few measurements of species biology. Of course, these sorts of models have their own problems. Small-number systems are an artificial construct. They are created by artificially removing populations from the many connections they have with other populations. Hence, the small-number approach may seem appealing, in part because it fits with species-based views of nature, but it succeeds only by ignoring most of the system.

Large-number systems These have so many similar components that the average behavior becomes a useful description of the system. The ideal gas law in physics provides one example. The position and velocity of a particular gas molecule are not of interest, but the properties of volume, temperature, and pressure are. Hence, some people think that we can borrow the approaches of physicists to studying nature. However, as one of my students once told me, a frog is not a billiard ball. What he meant was that many models of large number systems treat each particle as a billiard ball. Ecological systems, however, have components that are very different from one another. My student could also have said a diatom is not a wood stork, or a beaver is not a sedge. It is therefore doubtful that we can treat communities and ecosystems as if they were large number systems.

Medium-number systems The problem in ecology according to Lane (1985) is that ecosystems are neither large- nor small-number systems. They are **medium-number systems**. They are the worst situation. They contain too many components to be treated analytically with species-based models, and too few components (with major difference among them) for statistical analysis.

So what are we to do? There is no easy answer. But to pretend that the problem does not exist is probably the worst option of all. Working with medium-number systems may be as much an art as a science.

I will suggest three approaches that may have value: empirical ecology, assembly rules, and simplification. We will explore these alternative approaches in detail over the next three sections.

12.4 Empirical ecology

The first alternative for dealing with medium-number systems does not have a widely used name. We could call it empirical ecology, or predictive ecology, following Rigler (1982) and Rigler and Peters (1995). This approach to simplification focuses

on predictive relationships among a few key state variables. The challenge here is to measure the most important properties of a system, and seek measurable predictive relationships among them. The main challenge is to find what those important

properties are. In physics they could include temperature and pressure. It is less clear what the equivalents are in ecology.

12.4.1 Measurement of state variables – choose carefully

There are many properties of wetlands that you can measure. Area. Water level. Seasonal variation in water level. Nitrogen and phosphorus levels in the water. Seasonal variation in the foregoing. Rate of primary production. Seasonal and spatial variation in rates of primary production. Rate of secondary production. Seasonal and spatial variation in rate of secondary production. Number of bird species. Number of nesting bird species. Number of frog species. Number of tadpoles. Rates of survival of tadpoles and adults. Number of turtle species. Rates of egg production. Distance from water to nests. Rates of predation on eggs by skunks and raccoons. Number of species of orchids. Number of species of ferns. Number of species of sedges. Number of species of invasive plants. Biomass of plants. Ratio of above-ground biomass and below-ground biomass. Nitrogen and phosphorus content of shoots. Number of seeds buried in mud. Spatial variation in seed density. Number of species of algae. Biomass of algae. Primary production of algae. Seasonal and spatial variation in the foregoing. Number of species of macroinvertebrates. Seasonal and spatial variation in the foregoing. Emergence time for each species of odonate. Amount of coarse woody debris in the wetland. Rectal temperature of turtles. Nutrient inputs from surface flow. Inputs from groundwater. Inputs from rainfall. Inputs from bird defecation. Rates of methane production. Role of ruminants in methane production. Seasonal and spatial variation in methane production. To name but a few possibilities.

The point is that there are an enormous number of state variables that can be measured. There are a few field workers who still seem to take pride in how many different things they can measure. Only recently I was at a high-level meeting about an

important wetland and the assembled scientists could only seem to agree that they should measure everything possible just to be on the safe side. Of course, if you put all your budget into measuring everything possible, it is entirely likely that you will have only one site. In the end, having only one site with lots of measurements is like having only one species with lots of measurements. Neither allows any sort of generalization.

The real questions you have to ask are:

- What is the question you are trying to answer by your study?
- Which state variables do you need to measure to answer the question?

12.4.2 Relationships are essential to the advance of science

What question should you ask?

What state variable should you measure?

Wetland ecology is currently at the point where neither answer is obvious. I personally have a particular soft spot for species including American alligators, Blanding's turtles, and pitcher plants. But this is no justification whatsoever for claiming that the study of them is important to wetland ecology. It might be. Or they might be trivial. How do we tell? If you were in physics, you would know that there is agreement that certain state variables like temperature and mass have importance for a wide range of phenomena. It is less clear in ecology in general, and wetland ecology in particular. Too often people end up measuring certain state variables simply because that is what they learned to do in graduate school. Or simply because they like the species. (As for me, in the end, I chose to study wetland habitats because I thought that the best way to protect species was to protect the habitat. Besides, there were no alligators in Canada, and Blanding's turtles were hard to find.)

One way to think about the problem rationally is to look for examples where we have already found relationships. The vegetation types of peatlands are

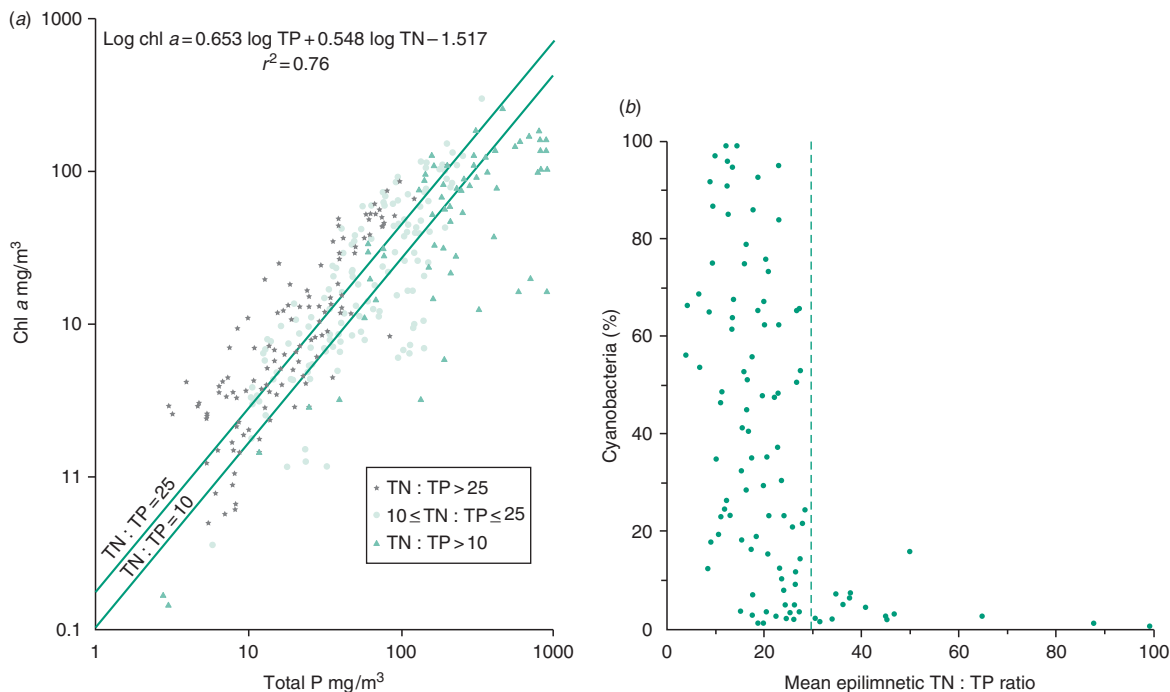


FIGURE 12.3 Two examples of the empirical approach. (a) There is a close predictive relationship between the concentration of phosphorus in water and the abundance of algae (as measure by chlorophyll *a* concentrations). As the ratio of N : P increases, the intercept of the line increases. (From Smith 1982.) (b) The proportion of the algae that are cyanobacteria has a strong threshold at just below a total N : total P ratio of 30. (From Smith 1983.)

arranged along gradients of calcium concentration and pH (Figure 3.15). Nitrate levels in rivers are related to human population in the river basin (Figure 3.8). Competition intensity increases with plant biomass (Figure 5.9). The biomass of mammals decreases with distance from wetlands (Figure 6.6). The biomass of herbivores increases with total net productivity (Figure 6.14). The number of species decreases with increasing road density (Figure 8.12). The number of plant species decreases with salinity (Figure 8.7). The number of species is positively related to wetland area (Figure 9.3).

Lakes provide an example – the biomass of algae is related to phosphorus levels (Figure 12.3a). The ratio of N to P determines the type of algae that occur (Figure 12.3b). Science is built up from the study of such basic relationships among state variables. As we

find more examples of such simple relationships, we can make wetland science increasingly rigorous. Sometimes it is useful to think about an example well outside one's own field – consider here the Hertzsprung–Russell star chart as a fine example of one figure that includes an enormous amount of information about stars (Figure 12.4). What are the equivalents in wetland ecology?

There is even a measure of our success at finding such relationships among state variables. It is the percent of variance that the independent variable predicts. There are standard statistical tools in multiple regression analysis that allow us to determine how tightly the pair of state variables are related. Increasingly, tools like multiple regression analysis allow us to explore how a set of variables can account for one state variable, providing useful

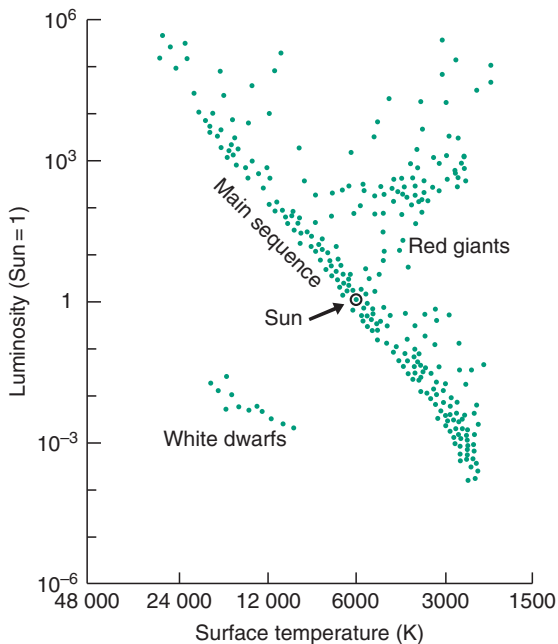


FIGURE 12.4 The Hertzsprung–Russell diagram summarizes fundamental relationships among stars, providing an example of how large amounts of information can be summarized along only two axes. (From Keddy 1994.)

information on correlations and causation (Shipley 2000). In Figure 8.13, for example, you saw how an entire set of independent variables each contributed to the number of plant species found in a wetland.

Once you have found a relationship between a pair of state variables you can use it to make useful predictions. One could argue that the ability to make predictions is the only legitimate way to measure scientific progress. As Peters (1980a, b) observed so many times, to justify a study as “increasing understanding” merely says that the study will affect the psychological state of the scientist.

In general, then, the predictive approach encourages us to measure a few important variables in a large number of systems. This means that when you go out to a wetland, you could measure a few simple properties and see how the wetland fits into the natural variation. This is a standard approach in limnology, as you can see from Figure 12.3. From this perspective, the worst research strategy is to pick one species or one wetland and measure as many things as possible.

12.5 Assembly rules driven by key factors

The second alternative approach to working with medium-number systems is the framework provided by assembly rules (Weiher and Keddy 1995). Assembly rules draw attention to a relatively small number of environmental factors that organize communities. In this book, we began with hydrology and fertility as key organizing factors. From this perspective, nature can perhaps be cleaved with a few sharp cuts into meaningful patterns. Hydrology, fertility, salinity, and a few other factors provide the sword to cut apart the complexity of wetlands. Experiments can then manipulate these factors to sort out causal relationships, and managers can manipulate these same factors to produce the desired characteristics of wetlands.

12.5.1 A few key factors select from the species pool

The raw material for a wetland is the pool of species available to colonize the site; the pool of species is the product of long-term processes such as evolution and extinction (Figure 12.5). The objective of assembly rules, then, is to predict which subset of this species pool for a given region will occur in a specified habitat (Keddy 1992a; Weiher and Keddy 1999). It basically is a problem of deleting those species unsuited to a specified set of environmental conditions. 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.

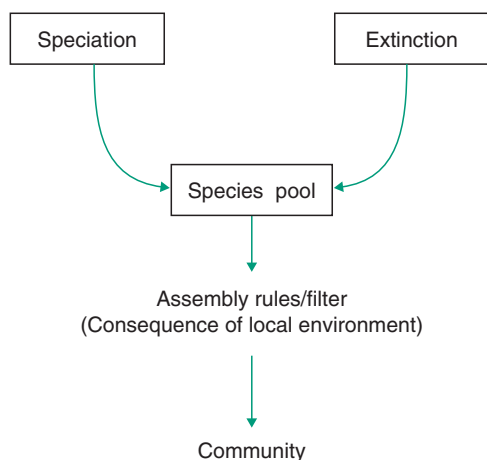


FIGURE 12.5 The local environment filters out species from the pool of available species, thereby creating a community. This is one possible theoretical foundation for wetland restoration. (After Wiens 1983.)

The process of constructing communities from species pools is therefore in many ways analogous to the processes 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 filter. We have systematically explored the important wetland filters in this book (Table 12.2)

Given the list of environmental factors that act as filters in wetlands, two biological data sets for ecological communities are needed: species pool and matrix of the traits of species in this pool. “Assembly rules” then specify which particular subset of traits (and therefore species possessing them) will be filtered out. More precisely, in the situation where we have knowledge of traits for each species in the pool, we are looking for a procedure to specify whether or not a trait (or sets of them) will permit species to persist under a defined set of environmental conditions. The exact procedures for doing this most effectively need further work. The following examples illustrate some of the potential.

Table 12.2 The estimated relative importance of environmental factors that determine the properties of wetlands. These can be considered the key filters for assembling wetlands from species pools

Environmental factor	Relative importance (%)
Hydrology (Chapter 2)	50
Fertility (Chapter 3)	15
Salinity (Chapter 8)	15
Disturbance (Chapter 4)	15
Competition (Chapter 5)	<5
Grazing (Chapter 6)	<5
Burial (Chapter 7)	<5

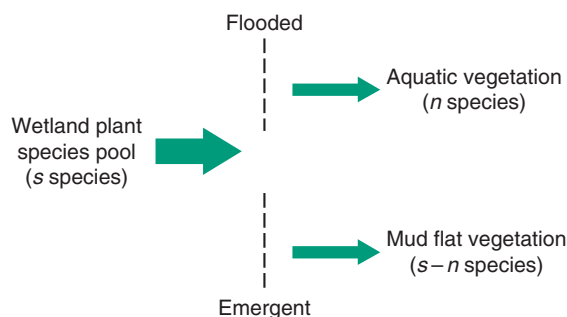


FIGURE 12.6 Flooding acts as a filter by controlling buried seed germination, thereby determining the composition of plant communities in wetlands. (From Keddy 1992b.)

12.5.2 Prairie wetlands: hydrology as a filter

Species in prairie wetlands must periodically regenerate from buried seeds (recall Table 2.2 and Figure 8.3). The problem is to predict species composition in these wetlands after a specified change in water level. Only one trait is necessary to predict regeneration: whether or not a species could germinate under water (van der Valk 1981). By measuring only this one trait for all species, one can predict which part of the species pool will occur (Figure 12.6).

In later work, van der Valk (1988) asked whether the densities of buried seeds of four emergent plants predict the densities of adult shoots after a reduction in water level. The results were slightly less satisfying – but of course, the study was asking a species-level question. All four species were large graminoids, which might be expected to have rather similar traits (*Scolochloa festuacea*, *Scirpus lacustris*, *Typha* × *glauca*, *Phragmites australis*). While assembly rules might be useful for predicting whether one has mud flat annuals or large monocots, it may be asking any model to predict which mud flat annual or which graminoid will appear. The use of such similar species to test assembly rules based upon traits perhaps illustrates the tendency of ecologists to think in terms of species rather than functional groups.

12.5.3 Fish in lakes: oxygen and pH as filters

We have already seen the importance of hypoxia in controlling fish distributions and life history in floodplains. The lowest concentration of oxygen in the water can then be considered to be a filter, which 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 (1984), or by reference to other traits.

Let us look at an example with fewer species. In central North America, Magnuson and his co-workers (e.g. Tonn and Magnuson 1982; Magnuson *et al.* 1989) have studied the distributions of fish in lakes in the lake district of Wisconsin and Michigan. One county alone, Vilas County, has over 1300 lakes. Typical fish range from mudminnows and redbelly dace to large predators such as northern pike and largemouth bass.

Overall, the lakes can be divided into those without and with large predators: *Umbra*–cyprinid and centrarchid–*Esox* lakes. Low oxygen levels in winter are the key filter. The lakes with large predators can be divided into two types depending on whether bass or pike is the dominant predator (Tonn *et al.* 1983).

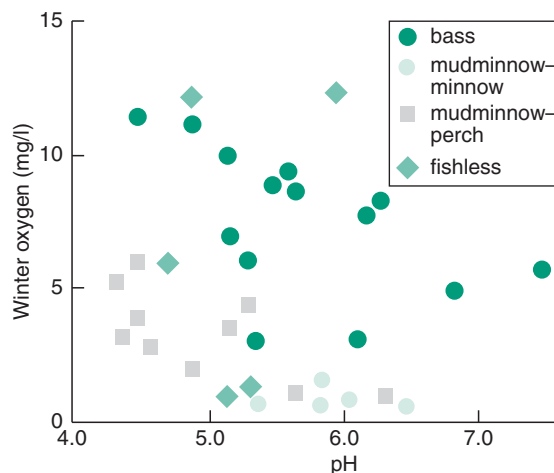


FIGURE 12.7 Winter oxygen levels and pH act as filters to create different fish communities. (From Magnuson *et al.* 1989.)

The *Umbra*–cyprinid lakes also can be sorted into two groups: mudminnow–minnow lakes, and mudminnow–perch lakes (Magnuson *et al.* 1989). Winter oxygen levels and pH largely distinguish these later two groups (Figure 12.7).

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. But it does not explain the reverse. Why do minnows and mudminnows not inhabit the lakes with higher oxygen and pH? Apparently, smaller fish are excluded to lakes from which predators are absent (Magnuson *et al.* 1989).

Sketching this as a series of filters (Figure 12.8), we begin with the pool of fish available to these lakes on the left. Low oxygen and low pH eliminate centrarchid fish from small and shallow lakes. Predation eliminates minnows and mudminnows from the larger lakes.

12.5.4 Coastal wetlands: salinity and frost as filters

Coastal wetlands nicely illustrate the principles of pools and filters. We have already seen how salinity is a strong filter, and how it controls the number of

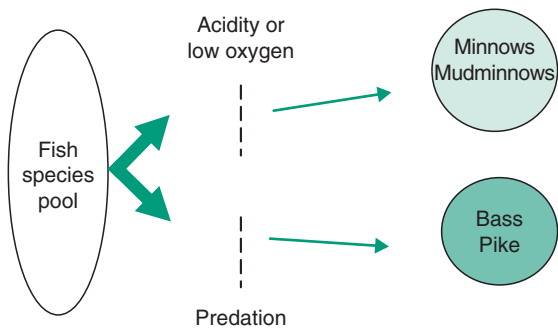


FIGURE 12.8 Different filters create different fish communities from a common pool.

species in coastal wetlands (Section 8.1). In general, higher salinity means fewer species (Figure 8.7). Brief periods of low salinity from spring rain, or spring flooding, may be necessary for many coastal species to germinate and establish at all (Figure 4.23)

Superimposed upon salinity is the factor of cold. We have also seen in Chapter 4 that freezing weather can turn mangrove swamp into salt marsh. Along the northern and southern boundary of mangroves, therefore, a single filter – tolerance to freezing weather – is an important plant trait, and cold weather an important filter (Figure 4.19). But note that it is not the mean temperature that matters. It takes only one northern weather system in a winter to keep coastlines as herbaceous wetlands.

12.5.5 Restoration in coastal wetlands: manipulating salinity and elevation

Many coastal areas are experiencing signs of stress such as loss in land area, conversion of wetland to open water, and declining wildlife production as a consequence. Restoration requires reversing these processes (Lewis 1982; Turner and Streever 2002). You could approach coastal restoration from the point of view of filters and traits. Although the next chapter is devoted to restoration, let us leap ahead a little and look at coastal restoration from the perspective of pools and filters. From this perspective, most coastal problems arise from two factors: increasing salinity and decreasing elevation.

Hence, restoration involves altering these two factors by decreasing salinity and increasing elevation. The most basic restoration techniques will increase inputs of fresh water and silt. Often this involves little more than allowing natural processes, such as spring flooding, to resume. Gaps can be built into the levees to allow fresh water to escape and spread over the marsh surface. Ideally, the control structure should allow both water and sediment to enter.

However, many coastal areas have additional problems, particularly networks of canals. These have arisen from past logging (Figure 4.16), from oil and gas exploration, and from shipping routes. Canals have multiple consequences: the spoil banks from the dredged material obstruct water flow, and tend to develop woody vegetation, often including many exotic species. The dredged canal interferes with movement of fresh water and may allow saline water easy access inland during storms. These canals need to be backfilled to allow normal transport of fresh water and sediment. Figure 12.9 illustrates how canals can be filled to restore normal elevations and allow fresh water to move more naturally through a delta.

Many coastal areas, from Bangladesh to Louisiana, have received both sources of damage: levees and canals. The result has been rapid loss of wetlands and erosion of natural deltas. In extreme cases, where natural forces cannot be harnessed, sediment can be pumped to fill in depressions, or new terraces can be constructed to ensure that marsh plants are not inundated too frequently. In these cases, the research challenge consists of fine-tuning the procedures so that they are as effective as possible in re-establishing wetlands at relatively low cost.

12.5.6 Experimental studies of filters and pools

The application of different filters should allow one to construct many different types of communities from one species pool. It should also allow one to rank filters in order of importance.

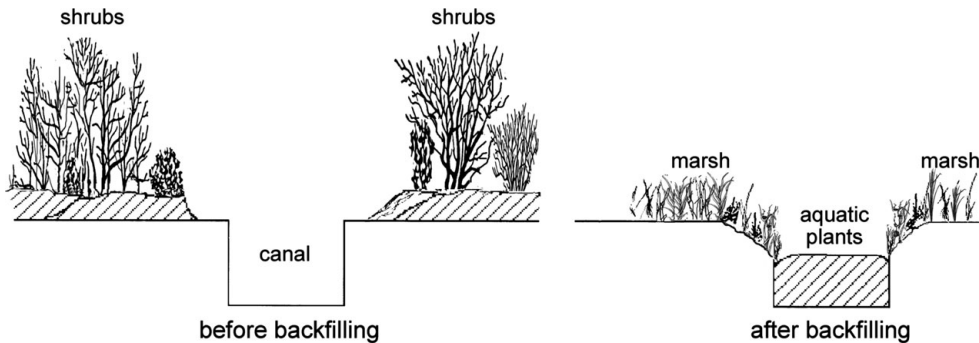


FIGURE 12.9 Canals (left) alter elevation and salinity in coastal wetlands and contribute to loss of these wetlands. Backfilling canals can create more normal elevations and allow flow patterns to re-establish. (After Turner and Streever 2002.)

In one experiment, a standard pool of 20 wetland plant species was sown into 120 containers representing 24 wetland environments (Weiher and Keddy 1995; Weiher *et al.* 1996). The environmental conditions manipulated included most of the major variables thought to influence wetlands: (i) water depth, (ii) timing and duration of flooding, (iii) leaf litter, (iv) soil surface texture, (v) sowing date, and (vi) presence or absence of *Typha*. 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 but water level and fertility were the most important filters. The 24 possible sets of conditions yielded four types of wetland communities (Figure 12.10).

The relative importance of filters can be assayed by exposing species to different filters alone and in combination. In one such study (Geho *et al.* 2007), 16 species of wetland plants were exposed to three different filters alone and in combination: herbivores, competition, and elevation (as added sediments). Herbivores had the largest effect on reducing plant biomass, although it affected only two species significantly. One was bald cypress (*Taxodium distichum*), and the other was cattail (*Typha domingensis*). Without properly designed experiments, the importance of herbivory and competition would not have been obvious. Since the establishment of

coastal cypress forests is an important conservation issue, their sensitivity to herbivores is noteworthy (see also Myers *et al.* 1995). And since *T. domingensis* is able to produce large monospecific stands, the fact that it was apparently limited by herbivores may have important implications for controlling the abundance of *Typha* elsewhere. On a species-by-species basis, however, four of the species – twice as many – were affected by competition. *Pontederia cordata* (one of the species on the book cover) seemed to be the weakest competitor, and it was indeed not present in the natural vegetation. So while we have just made the point that salinity is an overriding factor in coastal wetlands, in this experiment, in which salinity was not modified, competition and herbivory emerged as the two critical factors.

These kinds of experiments are a reminder of the necessity of care in designing experiments. A critic could say that an experiment will usually find what it looks for. If you fertilized, you should not be surprised to find fertility effects. If you manipulate neighbors, you should not be surprised to find competition. If you manipulate salinity, you will likely find that it too has effects. The challenge is to design experiments that combine these in a sensible and meaningful way in order to sort out the relative importance in natural systems. Which, conveniently, brings us to the next topic: how do you simplify nature without losing important information?

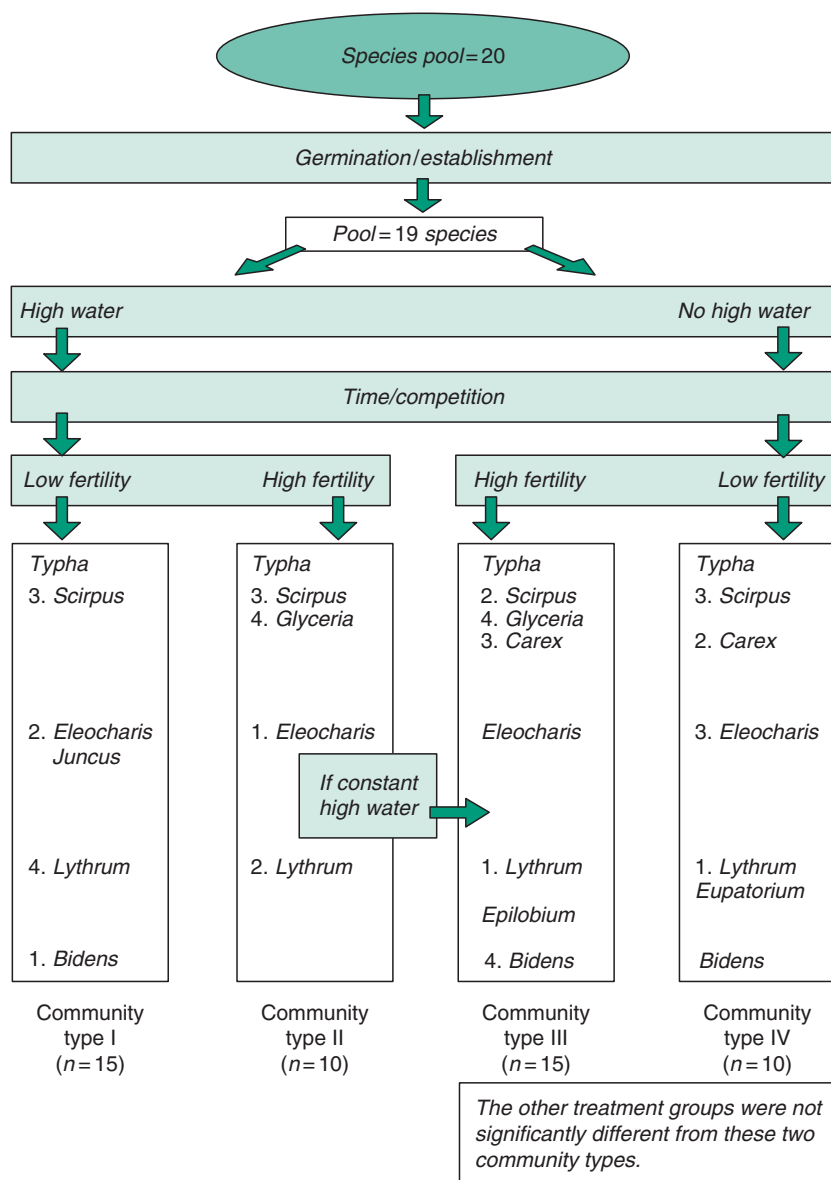


FIGURE 12.10 Twenty-four different environmental conditions, each replicated five times, produced four basic wetland vegetation types from a common species pool. It appears that five filters (colored boxes) can account for the observed patterns. (From Weiher and Keddy 1995.)

12.5.7 Biotic factors as filters

The foregoing examples mostly involve the direct effects of abiotic factors acting as filters. Biotic factors do, of course, have the same potential effects.

Herbivory can be a strong filter, as you saw in Chapter 6. Although coastal marshes are normally

viewed as resulting from salinity and burial, there is a growing body of evidence that grazers such as snails, geese, and mammals can have important effects as filters (Silliman *et al.* 2009). This has further consequences. If grazers can act as filters, then the predators that feed on grazers, say crabs eating snails, or alligators eating nutria, become important. Predation is certainly a strong filter in ponds

(Wilbur 1984; Carpenter *et al.* 1987), which is why ponds without fish are critical for many species of amphibians. Alligators may also have effects on wetlands through controlling the abundance of other prey species such as fish and turtles (Bondavalli and Ulanowicz 1999).

Competition may be an important filter in the sense that weak competitors are excluded from large areas of wetlands. Established plants may also prevent other common species from colonizing apparently appropriate habitat (Figure 5.1). You can think of natural disturbances, or periods of grazing, as factors that temporarily reduce the importance of this filter and allow new species to occupy a wetland.

Finally, if filters like anoxia or salinity are controlling the wetland, then neighboring plants may 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).

Other biotic effects, sometimes termed examples of “ecological engineering” (Jones *et al.* 1994) may be less obvious, but just as important in some wetlands. Beavers, alligators, and elephants are conspicuous examples of species that can engineer habitats. In practice there are many more examples. Even oysters and mussels can act as engineers by shaping the physical conditions of estuaries (Thomas and Nygard 2007), so when humans over-harvest oysters they are in fact reversing this engineering (Kirby 2004). From this perspective, humans are pervasive engineers, with dams, levees, canals, and roads all changing the naturally operating filters in wetlands.

In principle, then, each of these biotic factors could be treated as a separate filter itself – say, elephants as a filter in the Okavanga delta (Mosepele *et al.* 2008), or geese as a filter on the Hudson Bay coastline (Henry and Jeffries 2009).

12.6 Simplification through aggregation into groups

Another approach to dealing with middle-number systems does not have a formal name, but it can be called **simplification**. Instead of trying to deal with a large number of species and their enormous number of interactions, we reduce the number of species to a small number of functional groups. These groups have different names, depending upon the taxa. Zoologists often use the term “guilds,” but the more general term, **functional types**, is more widely used.

12.6.1 What does it mean to simplify? The middle way

Starfield and Bleloch (1991) have written elegantly about the simplification approach, and they admit that learning to compromise is the first step toward building pragmatic models.

Many people, they say, approach ecological modeling in terms of diagrams such as Figure 12.11a. “Their preconception is that ecosystems are made up of components that interact in a complex way and that models should be built to represent their complexity” (p. 14). You can see many such figures in books on wetland ecology. The description of energy flow in coastal wetlands in the preceding chapter (Figure 11.3, top) is an example of how complex studies can become. Consider how much effort is required in measuring each species’ individual contribution. Now consider how each of the species effects may change with location or climate. The task rapidly becomes overwhelming.

But while nature is indeed complex, as Rigler reminded us above, making enormously complex models that represent every species is not feasible, since the number of interactions (not to mention

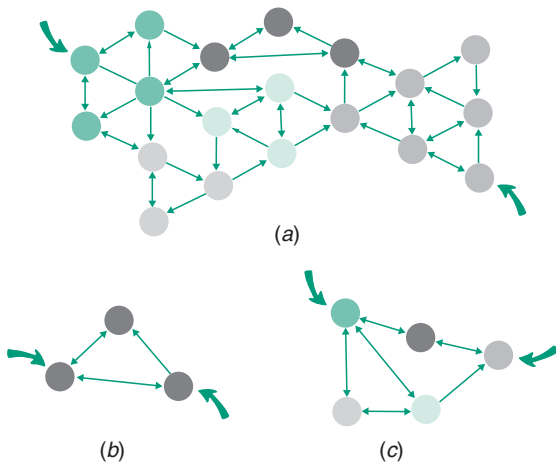


FIGURE 12.11 Representing an ecosystem at three different levels of complexity: (a) a detailed system model, (b) isolating a part of the system, and (c) a less detailed (“lumped”) system model. (From Starfield and Bleloch 1991.)

higher-order interactions) rises as the square of the number of species. Starfield and Bleloch (1991) note, politely, that “often the usefulness of such models, once they have been built, is disappointing.” Our first compromise, they conclude, is simplification. The way to accomplish this is to start with the management problem itself, rather than with a mental picture of the ecosystem. One then searches for the simplification that is most appropriate to solve the problem.

The most obvious approach is to cut out one piece of the system (Figure 12.11b) and treat it in isolation. That is, you make a smaller-number system. You have seen many examples earlier in the book of one or a few species that were studied in depth. These help us understand how species respond to filters, and to each other. But the small piece that has been cut out is artificial. The other factors and species cannot be ignored entirely. As but one example, recall how *Sagittaria lancifolia* was not harmed by flooding or salinity or grazing, in isolation, but it was harmed when they were combined (Figure 8.6).

In some cases, it may be possible to treat the rest of the system as an artificial driving force (thick

arrows). One can think of dealing with wading birds in the Everglades, or frogs in ponds, or mud flat annuals in potholes, where “the rest of the world” might be simplified into a few key factors such as duration of flooding.

An alternative is to combine components that are similar to one another, as indicated by the similarities in shading in Figure 12.11. The most reasonable grounds for combining them would be similarities in function. One then ends up with a complete representation of the system, but one that has been simplified (Figure 12.11c). In fact, this was a decision made by the scientists who produced the energy flow diagram – they chose to combine all the vascular plants into one category labeled “vascular plants” at the upper left of Figure 11.3 (top). Had they tried to measure primary production from each photosynthetic species, and the flow from each of those species to each herbivore and decomposer, the task would have been impossible. So the figure simplifies. On one hand, these sorts of decisions are necessary. On the other hand, they also may hide critical factors – perhaps the distinction between rushes and grasses is critical in this system. Or perhaps diatoms should have been included. The bottom of Figure 11.3 is even more simplified, with energy flow reduced to just five categories. Simplification should always be done as carefully and sensibly as possible. But there are no guarantees. Somewhere between the extremes of measuring everything imaginable and measuring just one thing there is some sort of intermediate. Choosing the appropriate level of simplification is thus “a pragmatic compromise between the complexity of ecosystems on one hand, and the need to solve a problem, with limited data and in a reasonable amount of time on the other” (Starfield and Bleloch 1991, p. 15.)

A further advantage to simplification into functional groups is that it enhances communication among scientists and managers. Taxonomic classification exists to represent the evolutionary relationships of organisms, and the degree to which different kinds interbreed with each other. It did not

originate as a tool to serve the needs of ecologists. When trying to communicate with scientists from other parts of the world, the nomenclature is often an obstacle to exchange of ideas; a different fauna or flora is like a different language. This problem is particularly severe for botanists and entomologists because of the large number of plant and insect species.

Functional groups, therefore, have the dual benefit of providing a naturally simplified approach to wetlands and enhanced communication among ecologists. A third benefit may be that the emphasis upon function provides a natural bridge to those scientists, managers, administrators, and politicians who think in terms of ecological services rather than wetland ecology.

12.6.2 Functional classification for ecological prediction

How do we sort species into types? Let us first remind ourselves of our goals: we want to be able to make predictions about the future states of wetland ecosystems, and particularly to predict changes in services that may result from various human activities. A major obstacle to being able to make such predictions is the large number of species that have to be included in community models. We therefore need to put species into groups.

Classification into groups could have two objectives: (i) forming groups with similar evolutionary histories in order to reconstruct phylogenies, or (ii) forming groups with similar ecological traits for predictive ecology. The former approach has had a major impact upon the historical development of ecology: many of the most high-profile research questions in ecology dealing with diversity (e.g. Hutchinson 1959; May 1986; Connell 1987) can be traced back to the phylogenetic basis of species taxonomy. The recent proliferation of molecular approaches to systematics has greatly reinforced this view of nature, sometimes to the detriment of functional thinking. If we begin with phylogenetic species classifications, we naturally fall

into a certain line of inquiry. The logic appears to go in the following manner. Since there is a large number of species (e.g. May 1988), how did so many species arise? Darwin provided an answer, and stimulated a century of research into the mechanisms and consequences of evolution through natural selection. This led to the second major question: how do all these species coexist (May 1986)? The coexistence of many different species is the great question bequeathed by Darwin. Coexistence has been a central theme of ecology at least since Hutchinson's 1959 paper entitled "Homage to Santa Rosalia" (Jackson 1981; May 1986), but it may have rather little to do with practical questions of ecosystem management.

If, however, we begin with functional classifications, the path of inquiry has a different logic. While there is of course enormous species diversity of the biosphere, there is also obvious repetition of certain themes. Most wetlands have groups of mud flat annuals, floating-leaved aquatics, wading birds, and predatory insects, but the names of the species change with geography. From the functional point of view, the important questions include: (i) What are these major convergent groups and how many are there? (ii) How many do we need for a sufficient level of precision in our models? Growing out of this are other questions. What are the traits which they share? How do we use a knowledge of these traits to predict how a particular functional group will change after an external perturbation? How can we use a knowledge of these traits to predict the group of species that will be present in a specified environment?

Nearly every group of organisms has been explored in this way. Let us look at a few examples.

Birds These are perhaps the easiest to work with because food supply places strong selective pressure upon bill form, and provides a convenient means to sort species into basic feeding groups (Figure 12.12). At the finer scale, bills can vary in other attributes such as densities of comb-like lamellae used for filtering food particles from debris. Other attributes

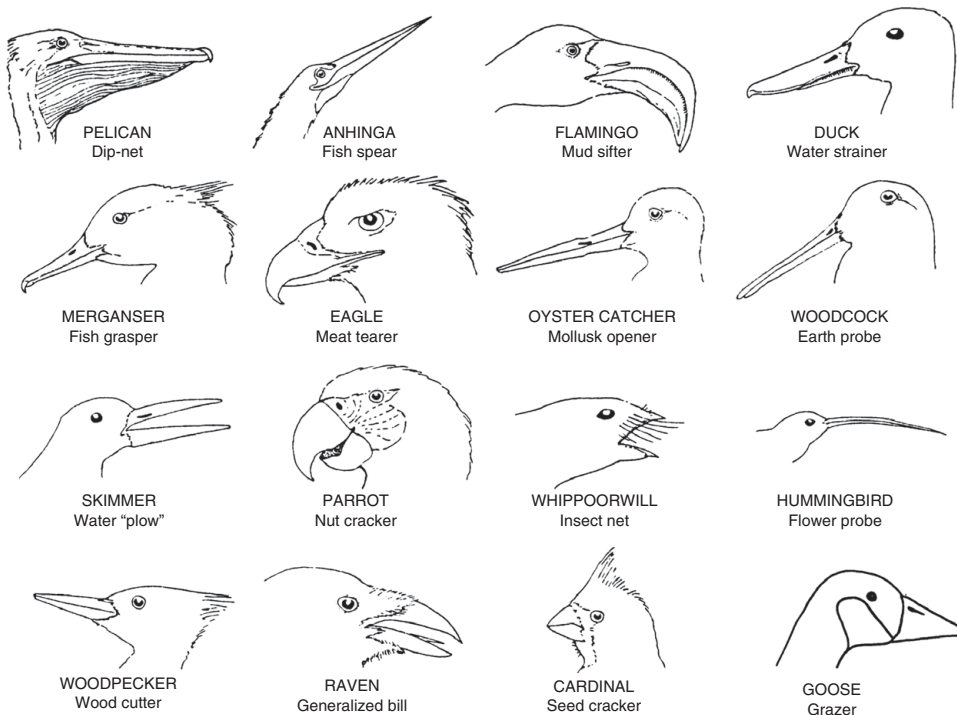


FIGURE 12.12 Birds can be arranged into functional groups based upon their bills, which in turn reflect their food sources. (After Welty 1982.)

such as foraging habitat, nesting habitat, and migration can be used to recognize functional groups (Weller 1999).

Fish Fish too can be classified by feeding strategy (Figure 12.13), with food type being reflected in the characteristics of the feeding apparatus. A still simpler classification, offered by Hoover and Killgore (1998), uses body shape to sort fish into one of four categories (accelerator, station holder, cruiser, and maneuverer), along a morphological gradient running from fusiform and elongated (cigar-shaped) to broad and laterally compressed bodies. Other attributes such as foraging habitat, spawning habitat, and oxygen demands can be used to expand the classification. Diet and body morphology can also be used (Lowe-McConnell 1975; Wikramanayake 1990; Winemiller 1991).

Insects These are frequently classified by their feeding system (Cummins 1973; Cummins and Klug 1979), considering both the dominant food type and the means by which they process it (Figure 12.14). Habitat, dispersal, life cycle, and size can be used to expand the system.

Mammals Mammals can be divided into functional groups based upon size, diet (which can often be inferred from dentition), and habitat type (Figure 12.15). There are 30 types of mammals in North America, according to Severinghaus (1981).

Plants The many types of plants are often classified by growth form (Raunkiaer 1937; Dansereau 1959) with particular emphasis upon woodiness, leaf size, leaf texture, and location of meristems. Life history, propagule type, competitive ability, and seed


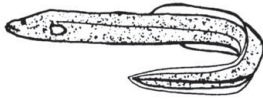
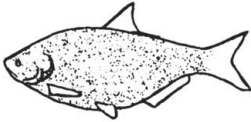
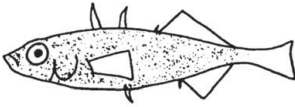
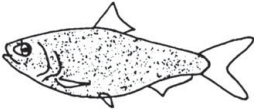
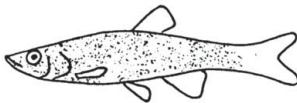
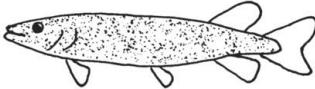
Detritivores	Lake sturgeon	
Scavengers	American eel	
Herbivores	Gizzard shad	
Carnivores		
a. Benthivores	Threespine stickleback	
b. Zooplanktivores	Sardine	
c. Aerial feeders	Redside dace	
d. Piscivores	Pike	

FIGURE 12.13 Fish can be divided into four main functional groups based upon their food sources. (Modified in part from Wootton 1990.)

germination requirements can be used to expand the system (Grime 1979; Weiher *et al.* 1999).

12.6.3 Problems and prospects

Particular functional groups likely have shared sensitivity to particular kinds of environmental stresses (Severinghaus 1981). In his words (using the word functional group rather than guild):

Once the impact on any one species in a functional group is determined, the impact on every other species

in that functional group is known. Furthermore, this information can be applied to any ecosystem within which that functional group is found. If an endangered species is contained in a functional group, it is possible to predict the impact on that species without studying it specifically, which for most endangered species is virtually impossible to do anyway. Economically, the potential cost-savings are tremendous, since only a few species per functional group need to be studied to establish the resulting impacts on all members of the functional group.



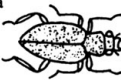

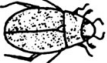


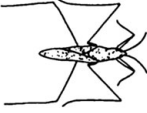

Functional Group	Dominant Food	Feeding Mechanism	Example of Order
Shredders	Living tissue	Herbivore	Lepidoptera 
	Decomposing tissue	Detritivore	Plecoptera 
	Wood	Gouger	Coleoptera 
Collectors	Decomposing organic matter	Detritivore	Collembola 
Scrapers	Periphyton	Herbivore	Coleoptera 
Macrophyte piercers	Living tissue	Herbivore	Neuroptera 
Predators	Living tissue	Engulfer	Megaloptera 
		Piercer	Neuroptera 
Parasites	Living tissue	Internal and external parasite	Hymenoptera 

FIGURE 12.14 There are enormous numbers of insect species, and they process a large portion of the biomass in wetlands. Yet they can be divided into only six functional groups based upon their dominant feeding mechanism. (Modified in part from Merritt and Cummins 1984.)

While there will always, of course, be differences among species within functional groups, this none the less clearly states the potential value of simplification.

The existence of functional groups and their value to science and management is increasingly recognized (e.g. Southwood 1977; Severinghaus 1981; Terborgh and Robinson 1986; Simberloff and Dayan 1991). Still, there is a problem – each group of organisms often has its own nomenclature. Functional groups in birds and mammals are sometimes called “guilds” (Root 1967; Severinghaus

1981), in fish “ecomorphological types” (Winemiller 1991), and in insects “functional feeding groups” (Cummins and Klug 1979). Most animal studies begin with food as the basic resource, and then group species that use a similar food. Terms such as “water strainer” (Figure 12.12), “zooplanktivore” (Figure 12.13), or “macrophyte piercer” (Figure 12.14) clearly delineate groups using the type of resource being consumed. However, such studies retain a taxonomic bias, since the bird that is a “water strainer” may be feeding on the same copepod species as a fish that is a “zooplanktivore.”

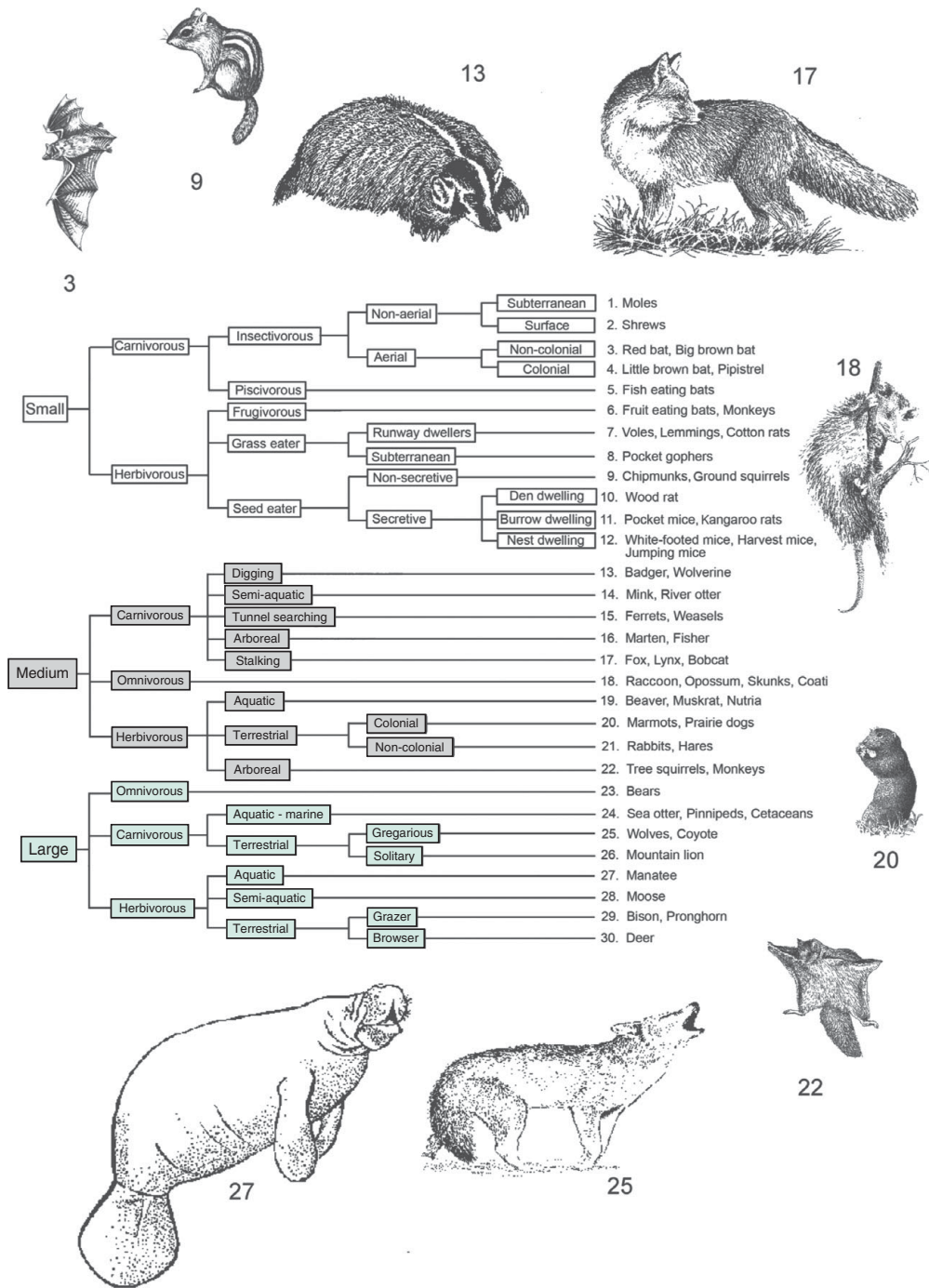


FIGURE 12.15 A functional classification for mammals of temperate regions based upon non-marine mammals inhabiting the continental U.S.A. (From Severinghaus 1981; sketches by R. Savannah, U.S. Fish and Wildlife Service.)

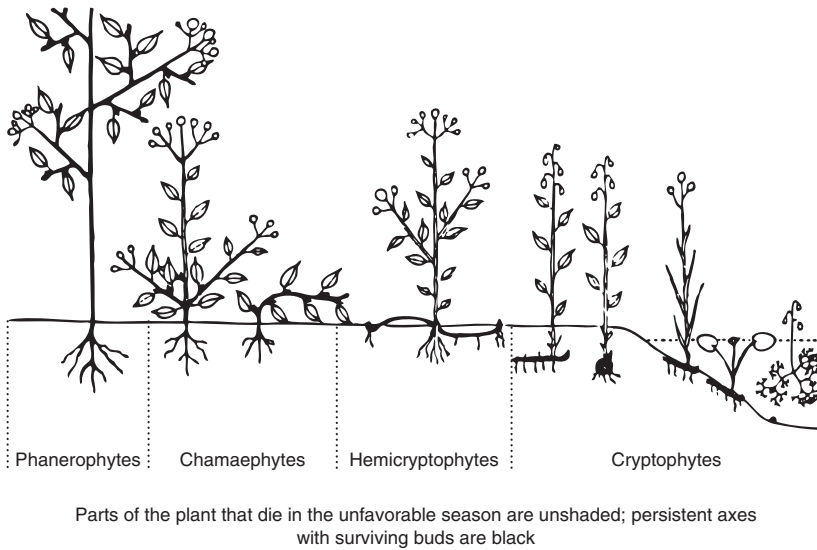


FIGURE 12.16 The Raunkiaer system classifies plants on the basis of location and protection of their meristems. (From Goldsmith and Harrison 1976.)

12.6.4 More on functional classification of wetland plants

There are three reasons for saying more about plants. First, they are particularly difficult to assign to groups. We have seen that animals are often classified by the resources they consume, but plants use so few resources (largely CO_2 , water, N, P, K). Second, because plants provide habitat for everything else, nearly everyone, even zoologists, has to learn something about plant functional types. Third, we can use them to look in more detail at the costs and benefits of making functional groups overall.

One of the most ubiquitous methods of plant classification was proposed by Raunkiaer (1937). His basic theme, paraphrased, is that life is not easy for plants. Unlike animals, they must remain rooted in a site as the environment changes around them. Raunkiaer focused on the most important challenge faced by plants: protecting their meristems during unfavorable periods. Recall that unlike animals, plants have indeterminate growth, directed by defined areas of cell multiplication called the meristems. If these are killed, the plant can neither

grow nor reproduce. Raunkiaer focused our attention on how plants protect their meristems, and erected the categories shown in Figure 12.16.

Raunkiaer's system is excellent for coarse-scale comparison, say for comparing marshes to swamps. It is less useful for more fine-scale work. In a set of marshes, all of the plants may be in only two functional groups: cryptophytes or therophytes (annuals). A finer level of classification may be needed. We must understand that this does not mean there is something wrong with Raunkiaer. Rather, the point is that we need different models to describe or predict at different scales. At the coarse scale, Raunkiaer is excellent. At finer scales, we need more information about the organisms.

Dansereau (1959) developed a more complicated system that uses categories of traits to describe vegetation. His categories were life form, stratification (height), coverage, function (evergreenness), leaf shape, and leaf texture. Any vegetation type can be placed in a reduced number of functional groups.

But here we encounter a new problem: as we reduce scale, the number of groups proliferates. Let us take aquatic plants as a convenient example, in part because we have some large monographs on

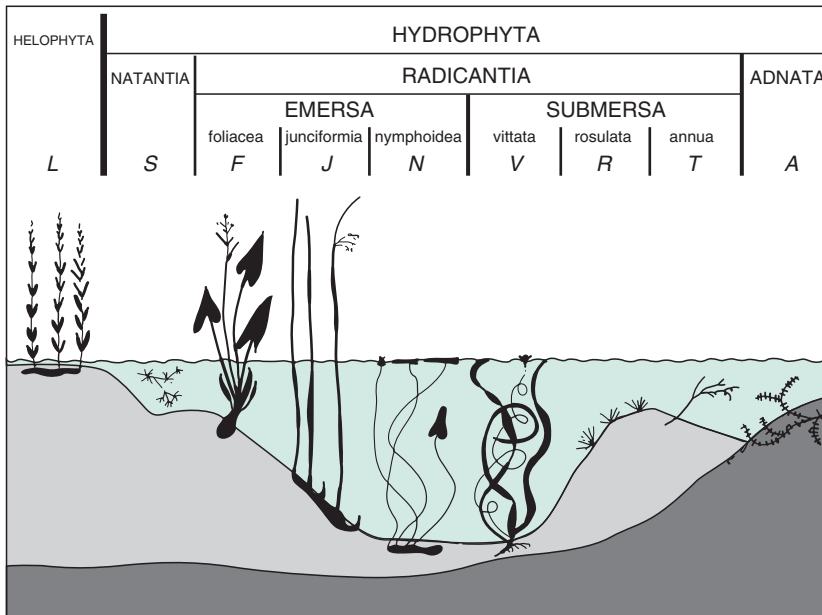


FIGURE 12.17 A classification of aquatic plants based upon their growth form and habitat. (From Dansereau 1959.)

this group (e.g. Sculthorpe 1967; Hutchinson 1975). Dansereau has nine life forms of aquatic plants (Figure 12.17). The principal traits are whether or not the plants are rooted, their relationship with the water surface, and the nature of their leaves (Figure 12.17). Hutchinson (1975) has 22 to 26 groups depending upon how you count them. It is also possible to classify by propagule type (Dansereau 1959). Hence, without caution, trying to simplify the plants into functional groups generates its own styles of confusion. In most cases, the objective is to find the minimum number of groups that allow one to answer the question being asked.

12.6.5 A general procedure for constructing functional groups

There is one general procedure for constructing such functional groups (Figure 12.18). Often, it is done subjectively, but objective approaches can be used too. A key part is the trait matrix. Most traits considered in the above classifications are traits that can be determined by eye, such as life form, lifespan, method of vegetative propagation, and position of

over-wintering shoots. However, it may be preferable to include ecological and physiological properties such as nutrient uptake, competition, and interaction with agents of disturbance or stress. Traits related to these properties may not be obvious upon inspection, but may be none the less closely related to the function of the plant in a community.

Since many of these traits are not obvious upon inspection, we need to apply the process of screening as developed by Grime and Hunt (1975) and Grime *et al.* (1981). The objective of screening is to develop a simple bioassay for a particular attribute, and then apply it systematically to an entire set of species. Shipley *et al.* (1989) created a matrix examining seven juvenile and 13 adult plant traits. The objectives were to explore quantitative relationships among traits to (i) test whether juvenile and adult traits were independent and (ii) explore relationships among the traits. In juveniles, the important traits were variation in seed size, which was inversely correlated with germination rate in light (axis 1), and higher growth rates with reduced germination at constant temperatures (axis 2). More than half the variation in seedling life history traits was accounted

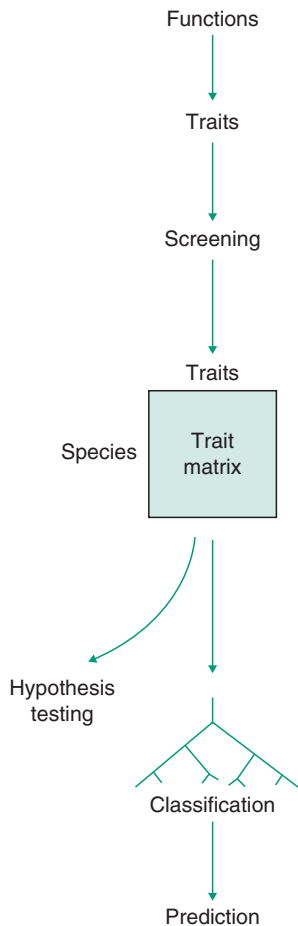


FIGURE 12.18 The process of classifying functional groups based upon a matrix of traits. (From Boutin and Keddy 1993.)

for by these two axes alone. Germination is known to be highly influenced by both light and fluctuating temperatures (Grime 1979; Grime *et al.* 1981) and it appears that wetland plants differ in their response to these two key environmental factors. Since the presence of established plants (shading) is likely to reduce the survival rates of seedlings, seedlings must either be able to escape adult plants by finding gaps, or else resist suppression. These first axes may be interpreted as two evolutionary solutions to this problem: seeds that are large and slow-growing and seeds that are small but rapidly growing. The two key axes in adult plants were the width of the canopy

(axis 1) and the height of the plants (axis 2). This can be interpreted as the importance of holding space and denying it to neighbors.

Perhaps the biggest surprise in the above work was the discovery that juvenile and adult traits were uncoupled. That is to say, the correlation matrices for adult traits showed no association with the correlation matrices for juvenile traits. Perhaps the traits required for regeneration in gaps are fundamentally different from the traits required to hold space as adults. This would mean that two categories, fugitive or stress-tolerant, could be constructed for each of two stages of life history (Figure 12.19). In turn, these four life history combinations can be related to three properties: frequency of gap formation, size of gaps, and soil fertility.

The thought that juveniles are in different functional groups from adults may be unexpected for plants, but there are many examples in the animal kingdom. Young fish may begin as zooplanktivores, but be piscivores as adults. These changes with age are a significant further complication in trying to use species-based approaches to communities and ecosystems. They are also an obstacle to simplification.

12.6.6 Example of functional groups in marsh plants

Another study used a matrix of 43 species by 27 traits. The species were selected to represent wetland habitats and diverse groups from across eastern North America. Species included rare or endangered taxa from infertile lake shores (*Coreopsis rosea*, *Panicum longifolium*), annuals typical of mud flats (*Bidens cernua*, *Cyperus aristatus*), large perennials (*Phalaris arundinacea*, *Typha* × *glaucia*), reeds from river banks (*Scirpus acutus*, *Eleocharis calva*), and an array of other species which represented other life forms and habitats. Traits included: (i) relative growth rate (RGR), which is known to be correlated with rates of resource acquisition (e.g. Grime and Hunt 1975) and seedling stress tolerance (Shipley

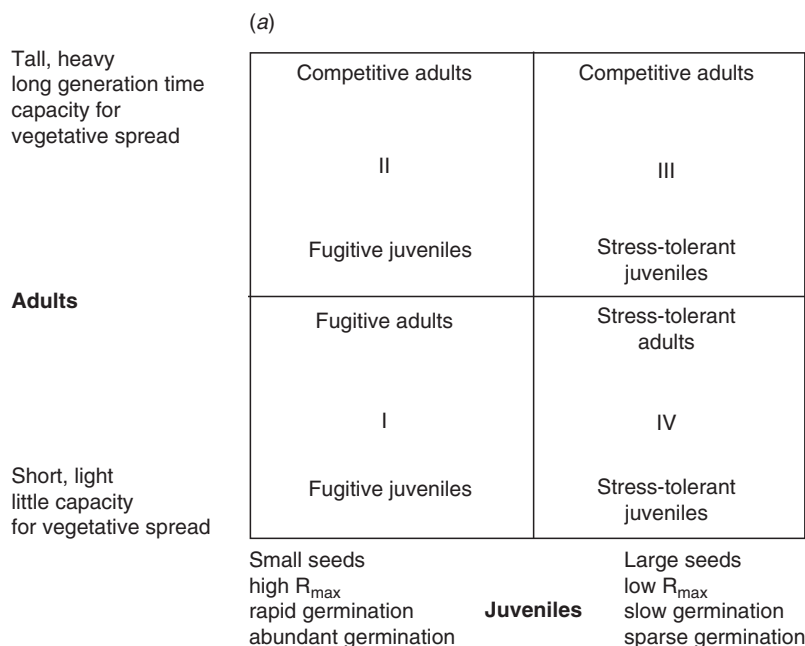
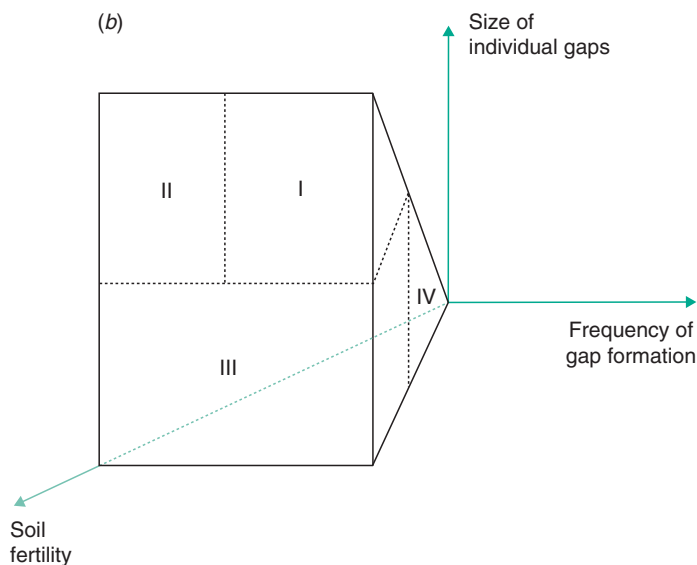


FIGURE 12.19 Four life history types of wetland plants can be constructed by combining seven juvenile traits and 13 adult traits. They appear to differ in tolerance to competition, disturbance, and stress as juveniles or adults. (From Shipley *et al.* 1989.)



and Keddy 1987), (ii) height of juveniles, height of adults, and rates of shoot extension; height is associated with competitive ability for light (e.g. Givnish 1982; Gaudet and Keddy 1988), (iii) above-

and below-ground biomass allocation, as well as photosynthetic area, which are believed to be associated with foraging for different light to nutrient ratios (e.g. Tilman 1982, 1986), and

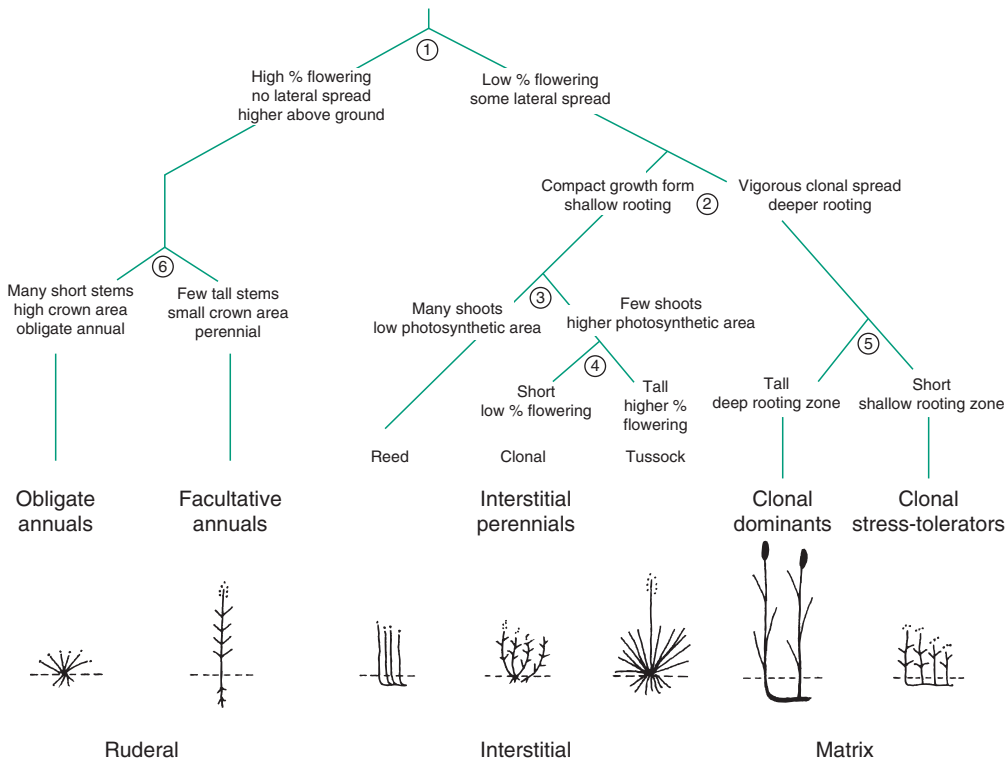


FIGURE 12.20 A dendrogram showing functional types derived through agglomerative clustering of 43 wetland plant species. (From Boutin and Keddy 1993.)

(iv) morphological traits such as shortest and longest distance between aerial shoots as measures of the way in which species held space; such traits are important if, as seems to be the case, plant communities are largely under dominance control (Yodzis 1986).

Figure 12.20 summarizes the results, with the addition of key traits. One main group (left side) had a high percentage of individuals and species flowering in their first growing season, and no lateral spreading of their vegetative growth. In contrast, the other group (right) did not flower much in their first year of growth but they expanded the vegetative parts, especially the below-ground system. These two groups apparently reflect the distinction between “ruderal” (*sensu* Grime 1979) and “perennial” strategies.

The “ruderals” consisted of two further groups. Plants in both groups flowered in the first year, but

one subgroup died at the end of the growing season (“obligate annuals”) whereas the other remained alive (“facultative annuals”).

Within the “perennials,” there was a clear distinction between species that spread clonally and species with a more compact growth form. These two types can be considered “matrix” species and “interstitial” species (*sensu* Grubb 1986).

At a finer scale, the “matrix” species were further composed of two groups. “Clonal dominants” were tall and robust species with vigorous lateral spread that frequently produce monospecific stands in fertile habitats (e.g. *Typha* × *glaucia*). “Clonal stress-tolerators” were much smaller and were more often found on infertile sand and gravel shorelines (e.g. *Scirpus torreyi*).

If such a classification has value, we would expect other traits to be predicted from knowledge of

species membership in these different functional types. Shipley and Parent (1991) tested this by examining three germination attributes: time to germination, maximum germination rate, and proportion of seeds germinating for 64 wetland plant species. Dividing the species into three functional groups (annual, facultative annual, and obligate perennial), they found that the obligate perennials took significantly longer to begin germination, and had significantly smaller maximum germination rates.

12.6.7 Expert systems

The procedure outlined above has the merits of using functional traits that may actually be important to the ecology of the species. Height is related to competitive ability. Relative growth rate is related to stress tolerance. Evergreenness is related to nutrient requirements, and so on. But such work is also extremely labor intensive, since it requires measuring large numbers of traits on large numbers of species, and then combining them all in some meaningful way. That is why simpler systems like the Raunkiaer (Figure 12.16), Dansereau (Figure 12.17), and Hutchinson systems (Table 12.3) continue to be used.

An alternative approach might use the combined expertise of botanists to assign species to groups. Thus, for example, we saw above (Section 12.2.2) that North American plant species have an official wetland indicator status that has been assigned for use in wetland delineation. This is useful for recognizing wetlands and mapping wetland boundaries, but there are not enough groups to discriminate among types of wetlands. Another approach assigns each species an index of conservatism, *C* (Swink and Wilhelm 1994; Nichols 1999; Herman *et al.* 2001), which is intended to indicate how dependent the species is upon natural vegetation types with minimal human alteration. This allows plants to be typically assigned to ten categories. Widespread and common wetland species such as *Phragmites australis* and *Typha*

Table 12.3 A comparison of three schemes of life form classification for aquatic plants

Hutchinson	Fassett-Wilson	Dansereau
A. Natant (Planophyta)		
I. At surface (Pleuston s.s. or Acropleustophyta)	Type 5	Natantia (S)
a. Lemnids		
b. Salviniids		
c. Hydrocharids		
d. Eichhorniids		
e. Stratiotids		
II. At mid-depth (Megaloplankton or Mesopleustophyta)	Type 5	Natantia (S)
a. Wolffliids		
b. Utricularids		
c. Ceratophyllids		
B. Rooted in sediment (Rhizophyta)		
I. Part of vegetative structure above water (Hyperhydrites)	Type 4	Junciformia (J)
a. Graminids		
b. Herbids		
c. Ipomeids		
d. Decodontids		
e. Aeschynomeneids		
f. Sagittariids		Foliacea (F)
g. Nelumbids		Foliacea (F)
II. Leaves mostly floating, not regularly above surface (Ephydates)	Type 3	Nymphoidea (N)
a. Nymphaeids		
b. Natopotamids		
c. Marsileids		
d. Batrachids		
e. Trapids		
III. Leaves entirely submerged or almost so (Hyphydates)		
a. Vittate, with long stem	Type 1	Vittata (V)
1. Magnopotamids		
2. Parvopotamids		
3. Myriophyllids		

Table 12.3 (cont.)

Hutchinson	Fassett-Wilson	Dansereau
b. Rosulate, stem very short	Type 2	Rosulata (R)
1. Vallisneriids		
2. Otteliids		
3. Isoetids		

Source: From Hutchinson (1975).

latifolia receive a score of 1, while species that depend upon small fragments of undisturbed habitat like *Platanthera leucophaea* (Figure 3.4) or *Primula*

mistassinica receive a score of 10. We will return to this topic under wetland indicators (Section 14.8). In Europe, Ellenberg has assigned plants to categories based upon the fertility of their habitats (Figure 3.14).

We can conclude that expert systems work well for describing, delineating, and evaluating wetlands. They therefore have great value for planning and conservation. They do not, however, answer the question of why certain plants behave in similar ways, and why certain species are rare or occupy narrowly restricted sets of conditions. The study of traits and groups of traits may eventually provide the answer and provide more natural functional groups.

12.7 Six tactical guidelines

Money spent on the wrong kind of research is like money spent on buying the wrong kind of habitat – resources that could have been wisely allocated to conservation are lost. We must plan our research with the same dedication and effort as generals like Montgomery or Patton planned their military campaigns. Six guidelines may be of assistance.

12.7.1 Generality

First and foremost, scientific advice must be applicable to a variety of circumstances. Species-specific and site-specific studies are not in themselves a viable approach to managing a global or national system of protected areas. For example, there are over 2000 significant wetlands that have already been identified in just one part of Ontario (Ontario Ministry of Natural Resources 2007). Assume as a first approximation, that each supports 1000 species. If we expect to understand how to manage such wetlands by studying each species, and allocate one year per species, we must allocate 1000 person years per wetland. If we consider the interactions between the organisms (and we must), then 1000 species yields

roughly half a million interactions, which translates into a half million person years per wetland (see also Rigler 1982). It is therefore not possible to study each interaction or even each species to provide management plans for natural areas.

The only way to manage a large collection of wetlands is to look for general principles that apply to numerous sites, or to combine species into groups based on similar ecological properties. Such principles and general models can be applied to many specific sites or species, and refined if necessary. The continuum from general to site-specific models can be represented as a nested hierarchy of models, with the general principles at the top, and the specific site at the bottom (Figure 12.21). One can start at the top and work down to any site, but it is far more difficult to start at the bottom and then extrapolate to the rest of the world.

12.7.2 Explicit constraints

Now let us appear to contradict the first principle. When general principles are established and applied, it is necessary to be aware of constraints to the

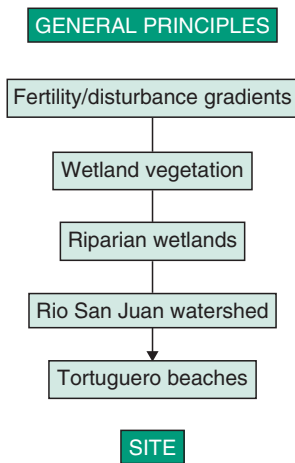


FIGURE 12.21 General principles (top) organize more specific information (bottom) in a hierarchical fashion.

generality. Consider, for example, the seed bank model that was developed for prairie potholes (van der Valk 1981). It now seems that some managers believe that all wetlands must be managed by fluctuating water levels and allowing regeneration from buried seeds. Certainly this model applies to lakeshores (Keddy and Reznicek 1982, 1986) and some ponds (Salisbury 1970; McCarthy 1987). It may apply to many relatively fertile sites with a history of natural disturbance. Other wetland vegetation types, such as bogs and fens, do not rapidly regenerate from seed after periodic disturbance. Such vegetation types could be degraded or destroyed by application of the prairie pothole model. We therefore need guidelines for determining which ecosystem types require which type of management.

This requires careful balance. We cannot, and should not try to, build a new model for every wetland we encounter. Science and management are based upon generalities, upon recurring patterns, upon general principles. Hence, we should start with the broad general principles described in this book, but be prepared when necessary to add constraints. Nutrients may be the overriding factor in the Everglades, while

salinity may be the overriding factor in river deltas, while fire may be the overriding factor in other habitats. Our models, and our indicators, need to specify the habitats to which they apply.

12.7.3 First things first

When we build a house, we normally begin with the major features (foundation, walls) and only then work on the minor ones (door handles, light fixtures). Unfortunately, this perfectly commonsense approach to house building does not seem to carry over into ecology. Sometimes our scholarly journals lead one to believe that some ecologists would pick out door knobs and then be puzzled that they have neither a door nor a house in which to install them. At the risk of restating the obvious, we should start with the most important factors and variables, and then and only then move to the finer ones. To start this discussion, I suggest that (at least in the areas I know) some 50% of the variation in wetland communities is attributable to hydrology. Fertility and salinity probably account for something like a further 15% each. All other factors (e.g. grazing, fire) address only residual variance (recall Table 12.2). We might therefore anticipate that the number one priority of wetland ecologists has been and would be the development of quantitative models linking wetland community structure to hydrological variables.

12.7.4 Description and prediction

Protecting wetlands by zoning or acquisition is only the first step which prevents the obvious threats. Management plans are then required. Management plans require prediction – forecasting the possible effects of human impacts from surrounding activities in the landscape, as well as the consequences of different kinds of management. For example, a management plan will have to consider threats from eutrophication. We have previously seen that the construction of dams produces predictable

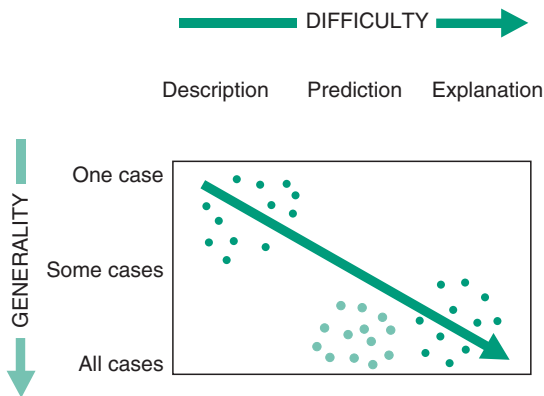


FIGURE 12.22 Descriptive studies of single situations are much easier to do than predictive or explanatory models that apply to many cases or sites. (After Leary 1985.)

consequences for wetlands downstream, as illustrated by the Peace–Athabasca delta. Equally, eutrophication has predictable negative consequences, as we have seen in both the New Jersey Pine Barrens and the Everglades.

No one should therefore build a dam or put nutrients into groundwater without knowing what the result will be. Still, prediction is often far more difficult than description. In his study of kinds of research, Leary (1985) concludes that generality and explanation (Figure 12.22, lower right) are the most difficult, even if they are the most important. They therefore require the most incentive, since all other things being equal, it is tempting to try to solve easy problems. In the case of conservation, it is probably true that we need prediction more than explanation (light dots). Yet it still seems that there is far more scientific activity in description (Figure 12.22, upper left) than in prediction and understanding (Figure 12.22, lower right). This may be fine in the inventory stages of wetland protection, but long-term survival of natural systems requires a change in emphasis toward general predictive models and carefully designed field experiments to unravel

the network of causation that produces ecological patterns.

12.7.5 Attitudinal inertia

Good research addresses important problems in new ways. Traditionally, biologists have focused activities on selected species, particularly those big animals that are favored by hunters. This “moose–goose syndrome” (Keddy 1989a) still colors wetland research and conservation activities. Consider, for example, the effort put into mapping deer habitat as opposed to the effort in mapping turtle nesting beaches, or the number of biologists studying ducks as opposed to invertebrates or plants. This produces inertia in the scientific response to conservation problems. This problem of attitudinal inertia is one of the most expensive and dangerous problems we currently face, since it means that money invested to protect wetlands and wild places is diverted to investigations that are not a priority.

12.7.6 Inner and outer obstacles

A majority of wetland management problems arise because of human actions that have harmed wetlands. One can do the highest quality of science to solve problems, and find it is ignored because people have other priorities. It is not even clear if humans have the ability to make rational decisions about management of their own natural resources. Some examples suggest that humans are very poor judges of the threats posed by their behavior (Tuchman 1984; Slovic 1987). Others suggest that greed and denial lead inevitably to the collapse of civilizations (Diamond 1994, 2005; Wright 2004). This is beyond the scope of this book – except to observe that human psychology has to be considered as an integral part of policy-making (Slovic 1987). In the end, managing wetlands may require considerable attention to managing people, a topic to which we will briefly return in the final chapter.

CONCLUSION

We might begin research in wetland ecology by collecting data on a particular species found in wetlands, or we might begin by picking a wetland and then documenting all the species that are found there. Many people who become wetland ecologists may have started with a favorite species of frog or turtle, or a favorite local wetland. More systematic data from large numbers of species and wetlands allow us to evaluate wetlands for conservation purposes. The Ontario wetland evaluation system provides a useful example that could be extended to other regions of the world with modest effort.

But collecting data on single species and single wetlands can take us only so far. In this chapter, I have addressed the broader issue of how we carry out question-based science and how we build predictive models for wetlands. We will also have to include variables like the key factors that organized this book (hydrology, fertility, disturbance, etc.). In the next chapter we will add the daunting task of adding ecological services to our list of wetland attributes. This adds a whole new class of measurable aspects of wetlands.

Overall, it is safe to conclude that wetland ecology demands a more systematic and thoughtful approach, and a familiarity with an array of scientific methods. Hence this chapter. Species-based approaches are insufficient. There are too many species, too little knowledge about the rest of the system. The alternative, picking one wetland and measuring everything possible, has equal problems. There is no replication, and there are too many variables to measure. This led us to consider three approaches that may have merit for building up general models: (1) empirical ecology, (2) assembly rules based upon filters and traits, or (3) simplification through functional groups. We can think of these as toolboxes that we can draw upon in future studies.

Overall, we need scientists to provide us with more manuals and toolboxes – imagine the difficult task of automobile mechanics if there were no shop manuals and every tool had to be built before they could begin to fix a car. Often, ecologists find themselves in just about this position. In most of the chapters in the book I try provide such a manual and mention the tools that are available, but in this chapter we have had to admit that better manuals and better tools are needed. But again, rather than start from scratch, we could borrow and adapt: the Ontario wetland evaluation system, the U.S. wetland delineation system, and even the Hertzprung–Russell star chart could guide us.

In conclusion, it is relatively easy to visit a wetland and measure something: it is much harder to ask thoughtful questions and answer them in a way that will be generally useful to others.