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## 2

# The Management of Wetlands for Biological Diversity: Four Principles

Paul A. Keddy and Lauchlan H. Fraser

### Wetlands and Gradients

There are vast areas of major kinds of wetlands: swamps, marshes, fens, and bogs (Table 2.1). Because plant and animal species, vegetation, and wetland types are so variable, it may seem difficult to treat all of these together. Far too often, one encounters specialist publications on the plants or animals of a particular bog, fen, marsh, mire, reed swamp or aquatic community; these balkanized treatments detract from the general principles involved in managing wetlands. Furthermore, because so much focus in wetland management is placed on fish and wildlife production this too often takes precedence over other ecological objectives. Large expanses of wetland vegetation are generally ignored or treated in passing as "aquatic plants." Our objective here is to try to pull together all these disparate vegetation types, species, and physiographic types, and present four general principles necessary for managing them to maintain and enhance biological diversity.

From one perspective, referring to wetlands as a whole may appear foolhardy; wetlands appear to have little in common with one another, because one can find so many types of wetlands, from a ombrotrophic peat bog to a wet meadow on a shoreline. However, all types of wetland are, in fact, controlled by only a short list of environmental factors: water levels, soil fertility, disturbance, salinity, grazing, and burial. This is true whether one is talking about the largest tropical floodplain complex in the world, the Amazon basin (Junk, 1983, 1986; Goulding, 1980; Lowe-McConnell, 1975, 1986), or the shorelines of small, temperate zone lakes (Pearsall, 1920; Spence, 1964; Bernatowicz & Zachwieja, 1966; Keddy, 1981, 1983, 1984). Regardless of location, wetlands have

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**Table 2.1. A preliminary list of the world's largest wetlands. At the lower limit of 30,000 km<sup>2</sup> a number of other candidate areas appear possible (after Keddy, 2000).**

Rank	Continent	Wetland	Description	Area (km <sup>2</sup> )*
1/2	Eurasia	West Siberian Lowlands	Peat bogs, boggy forests, meadows	780,000 (up to 1,000,000)
1/2	South America	Amazon River	Large river floodplain 300,000 Small river floodplain > 500,000	> 800,000 > 90,000
3	North America	Hudson Bay Lowlands	Peatlands	> 200,000 320,000
4	South America	Pantanal	Marsh, swamp, floodplain	120,000 140,000 200,000
5/6/7	Africa	Upper Nile Swamps (Sudd)	Swamps and floodplains	90,000 + 50,000
5/6/7	Africa	Chari-Logone (drains into L. Chad)	Seasonal floodplain	90,000
5/6/7	North America	Mississippi River floodplain	Bottomland hardwoods	86,000
8/9	Eurasia	Papua-New Guinea	Swamp, bog	69,000
8/9	Africa	Zaire-Congo system	Riverine swamps and floodplain	40,000 + 80,000
10	North America	Upper Mackenzie River	Marsh, fen, floodplain	60,000
11	South America	Chilean Fjordlands	No published description available	55,000
12	North America	Prairie potholes	Marsh	40,000
13	South America	Orinoco River delta	Floodplain, swamp, marsh	30,000

\*different areas for the same wetland reflect different data sources

gradients of nutrients, soil depth and flooding duration that act like a prism to subdivide them into regions with different abiotic characteristics and corresponding species abundances.

From another perspective, wetlands show differences because each is subject to particular influences such as rates of water level change, waves, fire, and ice scour. In general, these kinds of natural disturbances lead to high biological diversity and many unusual or rare species. Well-studied examples include the wet pine savannas of south-eastern North America (Christensen, 1988) and the rich Atlantic coastal plain communities of the Great Lakes and the eastern seaboard of North America.

In this chapter, we want to combine these two perspectives in order to explore how to manage aquatic ecosystems to maintain the different types of wetlands found in them and, in particular, to protect or create the unusual features that promote high species diversity. A commonsense application of a few general principles provides practical guidelines for the management of aquatic ecosystems.

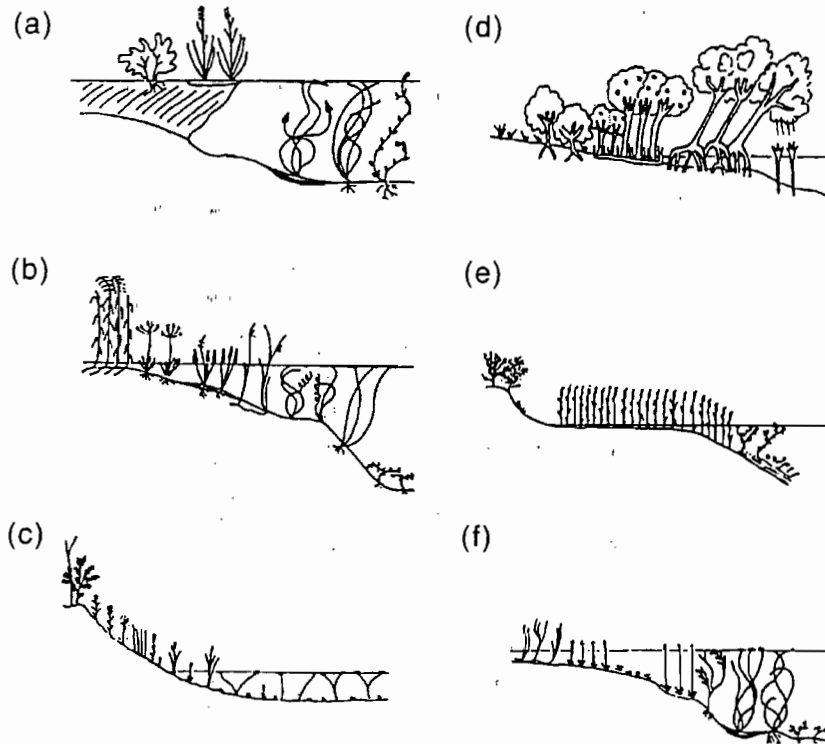
## Four Principles

### Water Level Fluctuations

Whereas all wetlands are associated with flooded soils, the duration of flooding is largely responsible for different vegetation types. This leads to conspicuous vegetation zonation because different species tolerate different degrees of flooding (Figure 2.1). The

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**Figure 2.1.** Some examples of plant zonation: (a) a bog (after Dansereau, 1959); (b) the St. Lawrence River (after Dansereau, 1959); (c) Wilson's Lake, Nova Scotia (after Wisheu & Keddy, 1989); (d) a mangrove swamp of the Caribbean (after Bacon, 1978); (e) the eastern shore of Lake Kisajno, northeastern Poland, a typical small lake phyto littoral (after Bernatowicz & Zachwieja, 1966); (f) a sandy shoreline (after Dansereau, 1959).

relationship between water level and plant species diversity for two types of shoreline wetland are shown in Figure 2.2. This first source of biological variation is so conspicuous that far too many ecologists seem content to profile the vegetation and conclude that they have completed their study of the wetland.

Zonation is a dynamic, not static, property of wetlands. Let us consider two extreme (and limiting) cases to frame the discussion and clarify thinking. If water levels were entirely stable, the result would be a two-zone system (Figure 2.3, bottom). There would be aquatic communities with some emergent species in the water, whereas woody plants would occur above the waterline. If water levels fluctuated widely and wildly, they would frequently exceed the natural tolerance limits of most species, producing habitats devoid of plants, or dominated by only a few weedy species.

Somewhere within these two extremes lies the regimen, then, that promotes maximum ecological diversity. Year-to-year fluctuations are an important factor generating plant diversity. High-water periods kill shrubs that dominate the upper zone, and low water periods allow many other species to regenerate from buried seeds. If mean water levels change from one year to the next, one can then transform the two-phase system to a four-phase system (Figure 2.3, top). In this case, the simple practice of changing water levels from one year to the next doubles the number of vegetation types. It more than doubles the number of plant species, because the new vegetation types, emergent marsh and wet

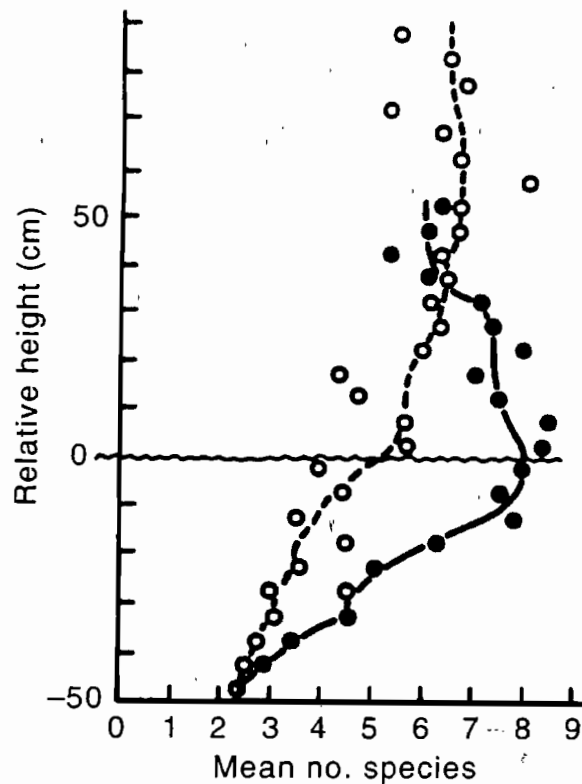


Figure 2.2. The relationship between the mean number of species ( $0.025\text{ m}^2$ ) and the August water level for wetlands on sheltered (solid circles) and exposed (open circles) shores in a Nova Scotia lake (after Keddy, 1984).

meadow, generally support large numbers of plant species. Such diverse plant communities will lead to animal diversity too (Figure 2.4). Furthermore, fluctuations in water level can generate additional levels of biological diversity (Figure 2.5).

How much year-to-year change is enough? This probably varies with climate, but wetland research in the Great Lakes suggests that changes over many meters are required; in smaller inland lakes, this probably drops to less than a meter. Superimposed upon year-to-year variation is variation within a year. This is probably less important for producing rich wetland plant communities, but some seasonal decline in water level is natural and is generally found in species-rich shoreline wetlands. Dropping water levels by roughly one-half meter during the growing season is probably a good first approximation.

#### *A Predictive Model for Changes in Wetland Extent*

Water levels of the Great Lakes have changed over both geological and historical time scales (Figure 2.6), so there is now a rich array of shoreline wetland types. Rich wet meadow flora are particularly well developed on gently sloping sandy shorelines (Reznicek & Catling, 1989). Great Lakes wetlands provide important habitats for fish, waterfowl, and rare plant species (Smith et al., 1991). Large areas of these wetlands have been drained, and humans have also already reduced the amplitude of water level fluctuations. More

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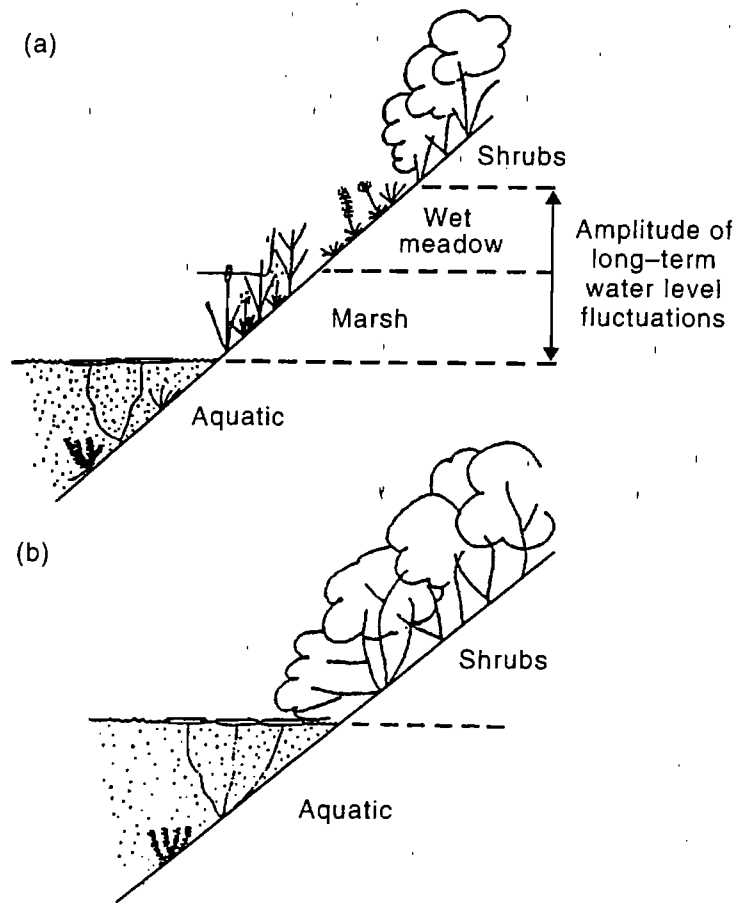


Figure 2.3. The constriction of water level fluctuations reduces wetland habitats from four zones (a) to two zones (b) (from Keddy, 1991).

recently, there has been added pressure to control fluctuations further. Quinlan and Mulamootil (1987) report that around the shore of Lake Ontario, wet meadows accounted for a staggering 65.4% of the wetlands in 1927, and only 22.1% in 1978. Figure 2.7 provides preliminary estimates of the probable effects of water level fluctuation on wetland area based on a model that predicted the upper boundary of wet meadows and the lower boundary of the marsh.

To model the landward edge of the wet meadow, it was necessary to consider the dieback and recolonization by woody plants. Two assumptions were made. The first was that the dieback of woody plants was directly related to high water levels during the growing season; secondly, woody plants reinvaded according to an exponential model. This allowed predictions of the lower limit of woody plants from projected water levels (Figure 2.7, top line). Lag times of 15, 18, or 20 years, made little difference.

To model the lower boundary of the marsh required the assumption that marsh plants move downslope the same year that water levels fall; this would most likely be the result of germination from buried seeds. As water levels rose, the marsh plants would die back over several years (Figure 2.7, bottom line). Lag times of 2, 3, or 4 years made little difference.

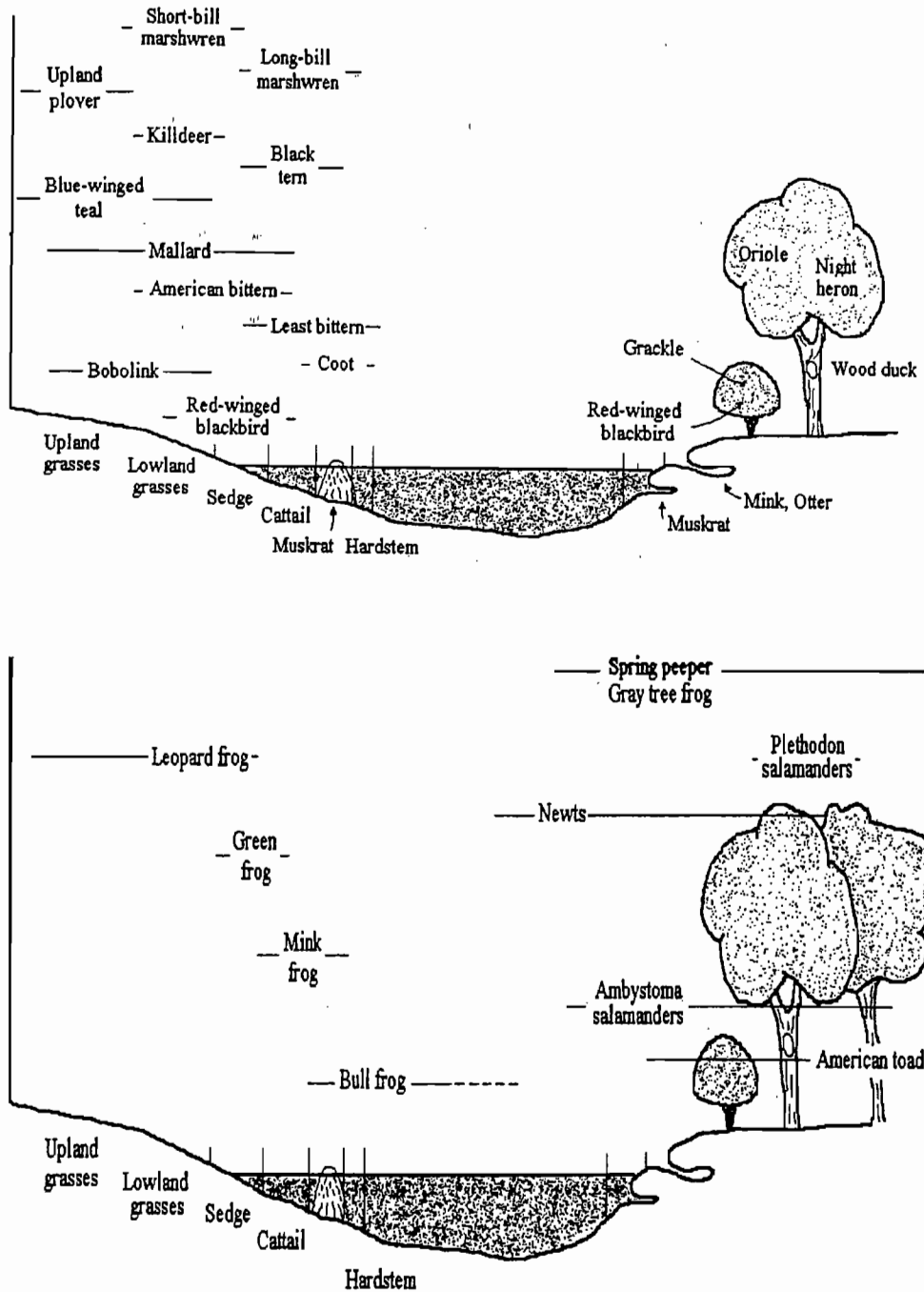


Figure 2.4. Zonation in some birds and mammals (top) and amphibians (bottom) in relation to water level and vegetation (after Weller, 1994).

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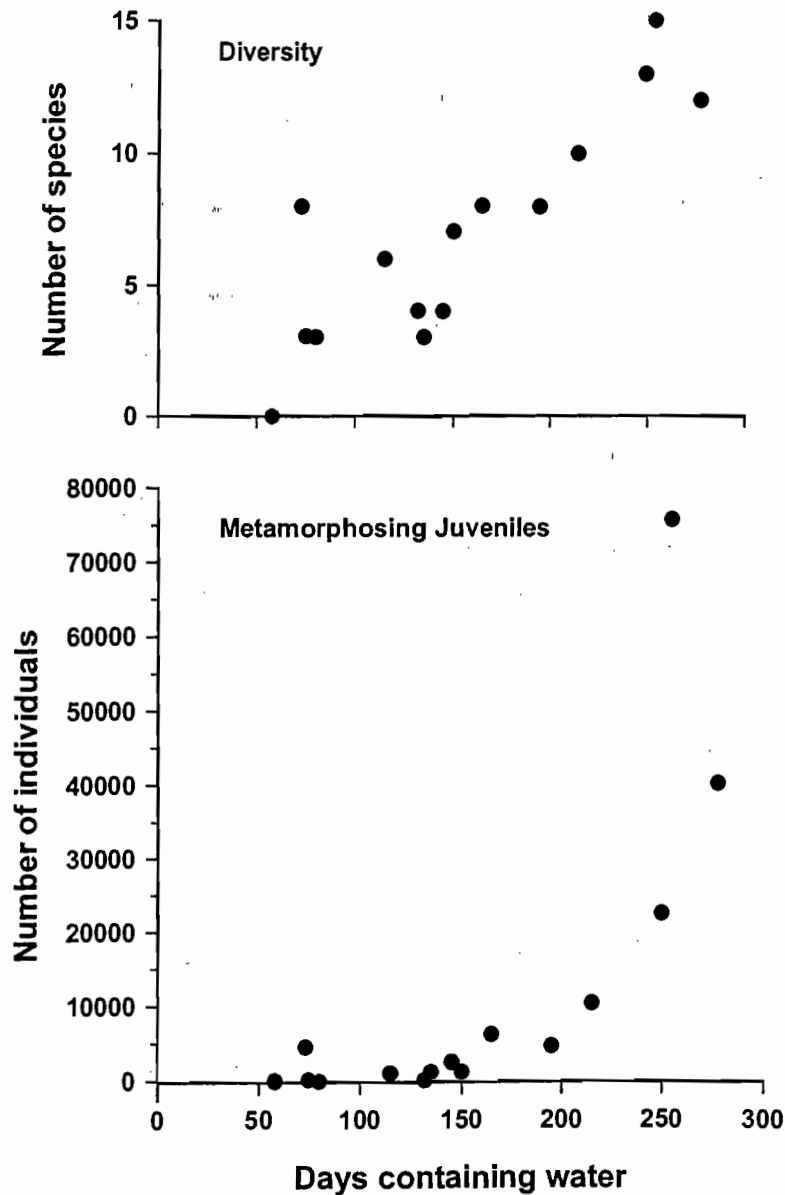


Figure 2.5. Relationship between water level and amphibian species diversity (top) and number of metamorphosing juvenile amphibians (bottom) (after Pechmann et al., 1989).

The area between these lines is then the area of wet meadow and marsh as a function of time. Figure 2.7 shows, for example, the great areas of wetland that occurred during the low water period of the mid-1930s. This model was then used on projected water level scenarios to forecast the effects on wet meadow/marsh area in the Great Lakes. If further reductions in amplitude occurred as opposed the model predicted losses approximating 30% of the wetlands in Lake Ontario alone.

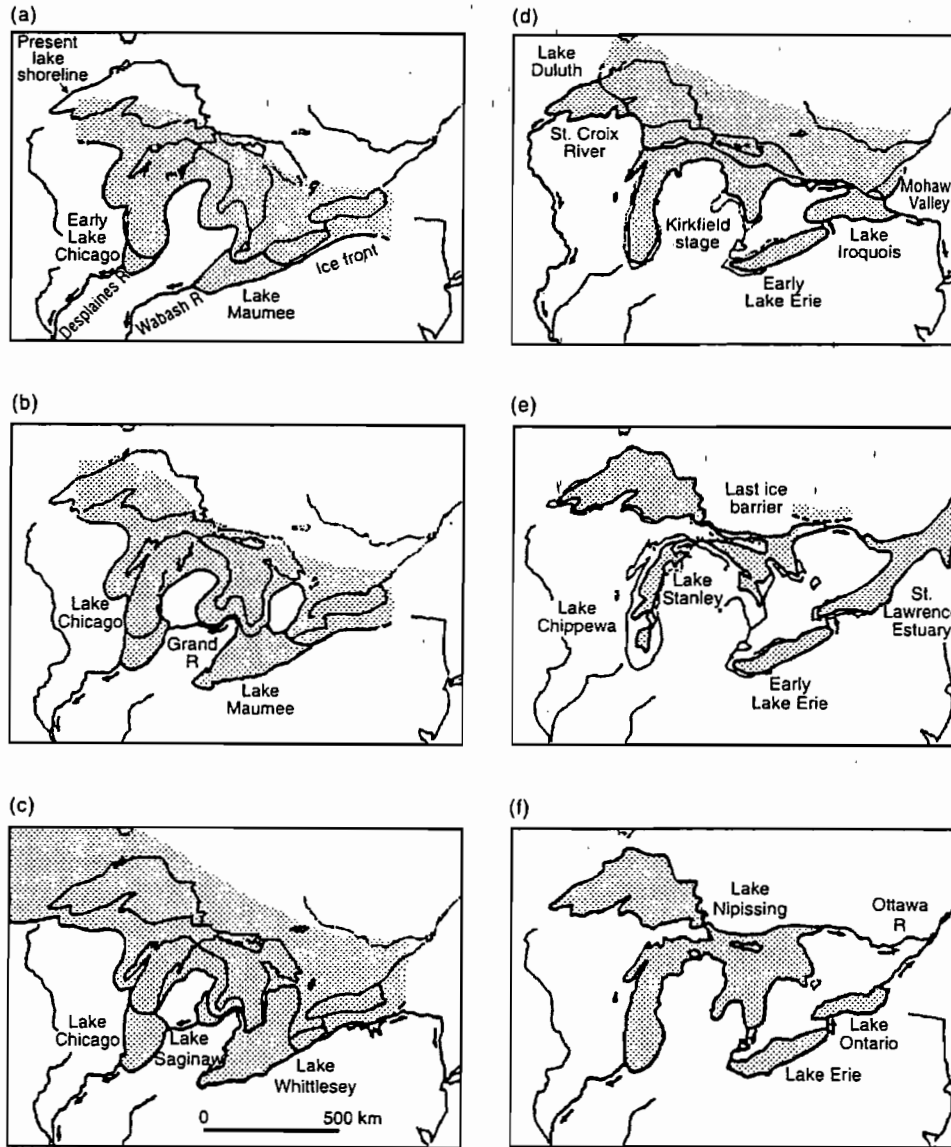


Figure 2.6. Changes in the water levels of the Great Lakes over millennia (after Strahler, 1971).

*A Descriptive Model for Frequency and Intensity of Flooding*

Two of the most important components of flooding, frequency and intensity, can be plotted on orthogonal axes to represent all possible pairwise combinations. We can then plot, for many sites, the frequency of flooding against the depth of flooding, or perhaps more conveniently, the frequency of flooding and amplitude of water level changes. There are several important properties that could then be plotted for sites located in relation to these axes. One could plot the many reservoirs or wetlands of the world in order to explore patterns. Are there, for example, certain combinations that are rare and others that are

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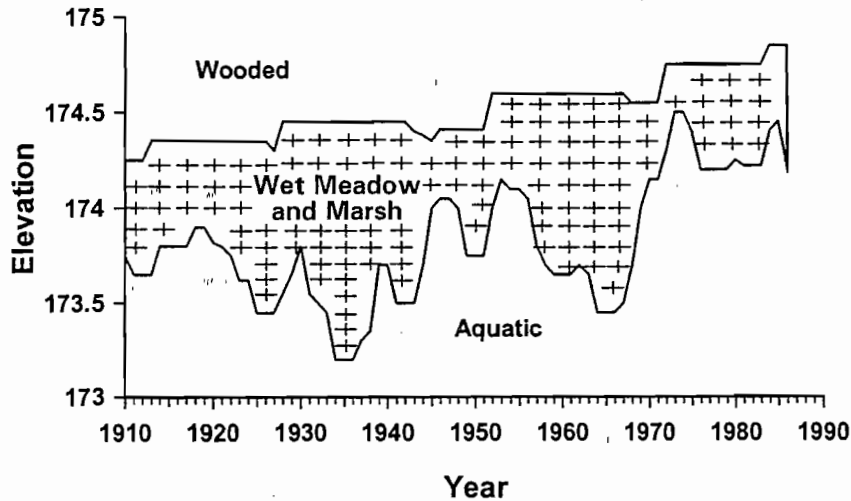


Figure 2.7. A simple simulation model showing how wetland vegetation changes with water levels in the Great Lakes (after Painter & Keddy, 1992). The upper line is the woody plant boundary (18 yr lag), whereas the lower line is the lower marsh boundary (3 yr lag). Note that the area of wet meadow and marsh varies with water level history.

common? One could plot important properties such as productivity or wildlife diversity, and explore how they are related to water levels. Unfortunately, the required data on water levels are scattered through a broad literature describing individual cases, and buried in reams of unpublished reports. Often the data are not quite comparable. As a first step in this direction, Figure 2.8 shows such a plot for a few lakes, and identifies a corridor of high plant species richness. This is based upon a set of lakes in eastern North America, and there is currently no way to know how well we can extrapolate from this geographic region or to other properties.

### Fertility

Variation in fertility occurs among and within wetlands. In wetlands exposed to waves and ice scour, silt and clay are constantly eroded and exported, so these areas tend to be infertile and support distinctive plant species. In contrast, silt and clay are deposited in bays, and these wetlands tend to be dominated by few large clonal species with dense canopies. Fertility gradients are therefore an important feature in producing different plant communities in all wetlands. The greater the array of fertility levels, the greater will be the array of vegetation types and plant species (Pearsall, 1920; Spence, 1964; Bernatowicz & Zachwieja, 1966; Auclair et al., 1972). This is most easily illustrated by use of the biomass of plant communities as a measure of their location along the fertility gradient. Figure 2.9 plots the total number of plant species and rare plant species against biomass for wetlands. The diversity of plant species is highest at intermediate levels of biomass (fertility), and the number of rare species is greatest at the lowest levels of biomass (lowest fertility).

Eutrophication will reduce the length of this fertility gradient and slowly cause more areas of a wetland to converge on the high biomass vegetation type. In one experiment, 12 different habitat types were created in plastic containers (Weiher & Keddy, 1995; Weiher et

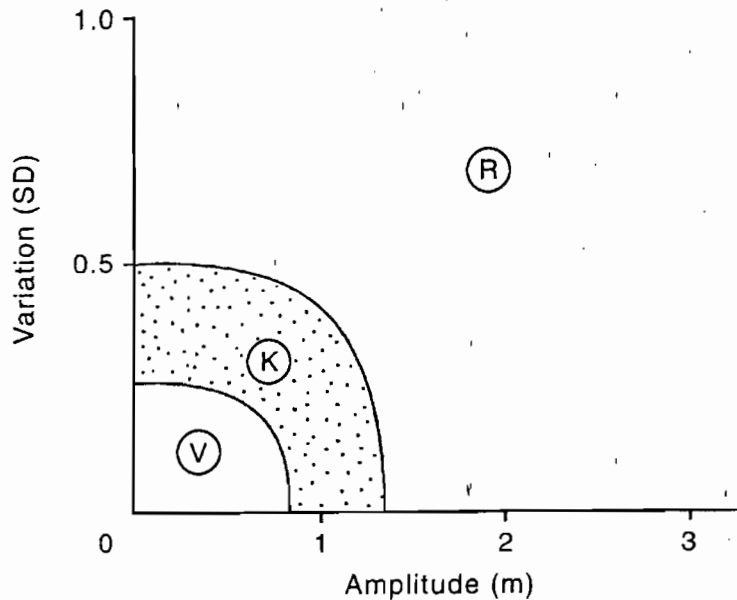


Figure 2.8. A corridor of high species richness (stippled region) is associated with yearly water level amplitudes of roughly 1 m and standard deviations of roughly 0.5 m. The circles indicate three representative lakes from Nova Scotia: V, Vaughan; K, Kejimikujik; R, Rossignal (from Hill et al., 1998).

al., 1996). These habitats included sand, gravel, cobbles, and stable and fluctuating water levels, each replicated 10 times. Half of these wetland types received additional NPK fertilizer and, as shown in Figure 2.10, in every case, the number of plant species was lower in the fertilized plant communities.

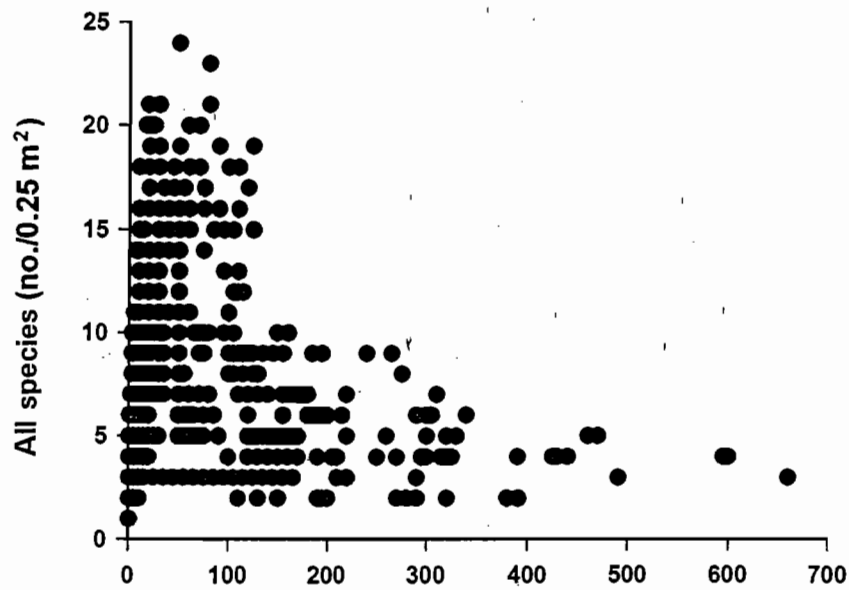
#### *A Mathematical Model for the Prediction of Maximum Potential Species Richness*

The relationship between diversity and productivity is well documented and applies to both plant and animal distributions (see Tilman & Pacala, 1993; Rosenzweig & Abramsky, 1993; Keddy & Fraser, 1999, for overviews). One promising general model for the prediction of herbaceous plant diversity is the standing crop–species richness relationship (“hump-backed model”) first proposed by Grime (1973a, 1973b, 1979), which states that species richness reaches a maximum at intermediate standing crop. Grime suggests that species richness is limited at low standing crop by minimal availability of mineral nutrients and, in some cases, high levels of disturbance, whereas at high standing crop, interspecific competition limits the number of species. We investigated the general applicability of the “hump-backed model” in herbaceous wetlands by searching the literature for all studies that presented species richness as a function of biomass. Our objective was to explore both the generality and the potential limitations of the model. We also wanted to predict quantitatively the decline in species richness with increasing biomass using known biological parameters and equations. In particular, we wanted to determine the maximum species richness we would expect to find at any given standing crop in a herbaceous wetland.

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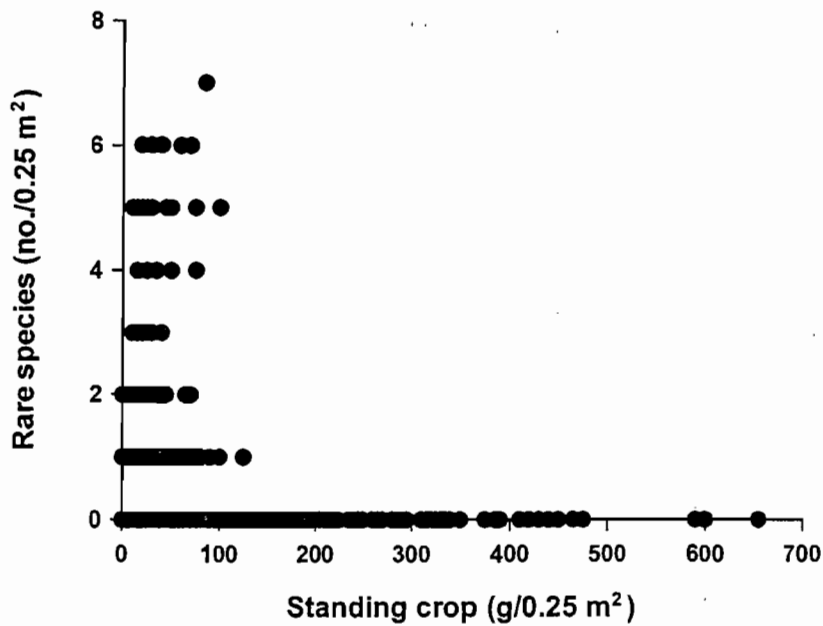


Figure 2.9. Plant species richness along gradients of standing crop (a) for 401 0.25 m<sup>2</sup> quadrats in eastern North America and (b) same quadrats, but nationally rare species only (from Moore et al., 1989).

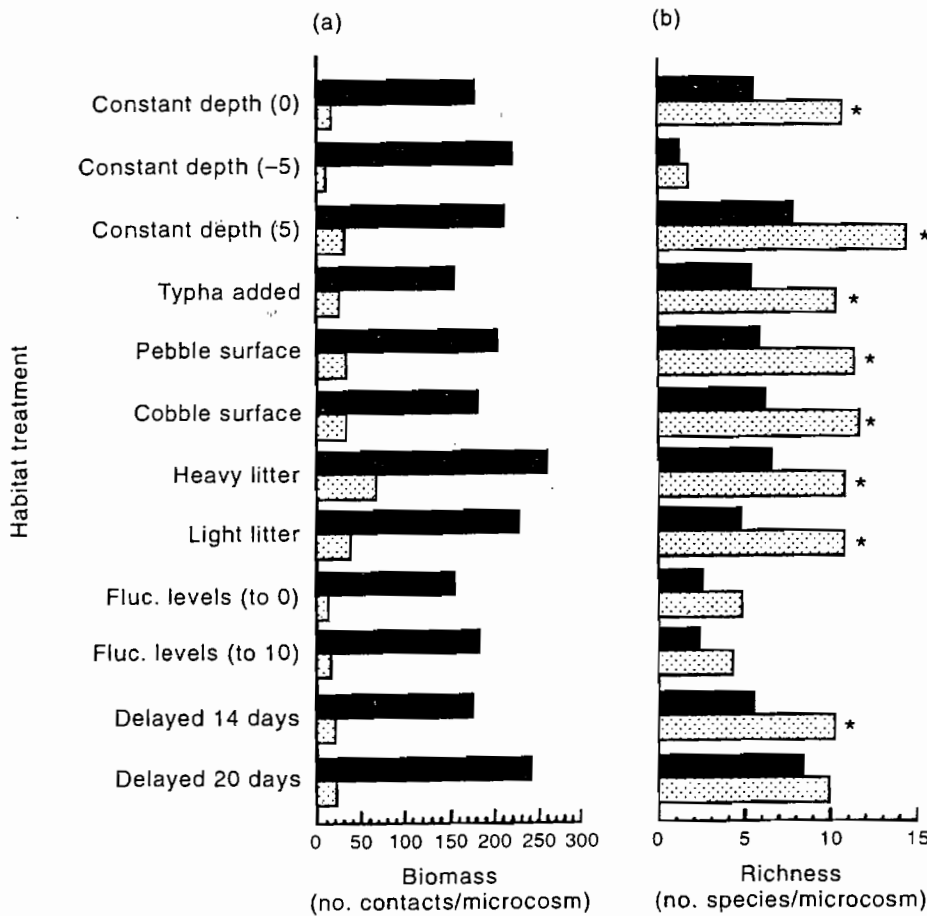


Figure 2.10. The effect of fertilization on biomass and species richness of wetland plants in 12 artificially created habitats (from Wisheu et al., 1991). Stippling represents the infertile treatment, whereas solid bars are the fertilized plants. \* $P < .001$ .

We found 22 published studies that measured both standing crop and species richness, totalling 1,367 data points, from fresh- and saltwater marshes, bogs, fens, and wet meadows around the world, varying in sample size from 0.20 to 50 m<sup>2</sup>. In order to standardize the scale of sample size to 1 m<sup>2</sup>, we generated a species richness versus log area linear regression from the data. This regression line was:  $S^A = 3.42 \ln A + 13.28$ , where  $S^A$  = species richness per unit area of measurement ( $A$ ), and  $A$  = area (m<sup>2</sup>) (F ratio = 77.42;  $df = 1,909$ ;  $P < .001$ ) (see Connor & McCoy, 1979; Palmer & White, 1994, for further discussion of species-area relationships). We then standardized the scale to 1 m<sup>2</sup> by applying the equation:  $S = S^0/S^A$ , where  $S$  = species richness m<sup>-2</sup>, and  $S^0$  = observed species richness.

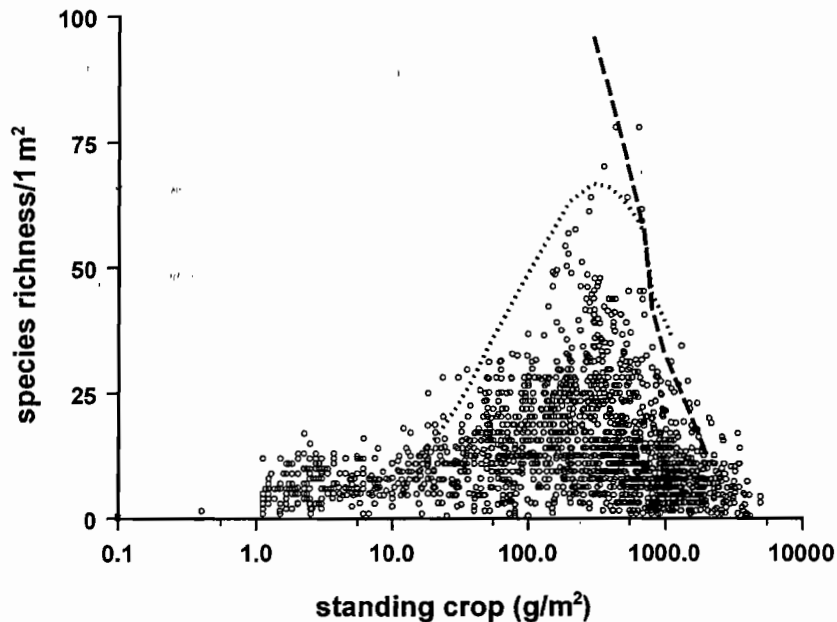
The data display the classic "hump-backed" shape, with richness reaching a maximum at about 500 g m<sup>-2</sup> (Figure 2.11). There have been previous attempts to fit polynomial regressions through biomass-richness data sets with varying degrees of success (Wisheu & Keddy, 1989; Puerto et al., 1990; Garcia et al., 1993; Muotka & Virtanen,

Figure 2.11. Lines show biomass and species richness from 1972; Day & Klinkhamer, 1991; Wilson, 1991; Snow, 1984; Keddy, 1984

1995). Wetland and stand factors have been studied (Vitt, 1994) and salinity (disturbance) variance.

Despite not following a curve, there could be a correlation for emergent vegetation points are

Both statistical analyses have suggested by a regression



**Figure 2.11.** The relationship between species richness and aboveground biomass in herbaceous wetlands. The lines shown, equations 2 (dots) and 3 (dashes), represent the maximum species richness possible as a function of biomass and are explained in the text. The data represent 1,367 points from 22 published studies (Auclair et al., 1972; Day et al., 1988; Forrest & Smith, 1975; Garcia et al., 1993; Gough et al., 1994; Grace & Pugsek, 1997; Klinkhamer & de Jong, 1985; Lambert, 1976; Moore & Keddy, 1989; Muotka & Virtanen, 1995; Partridge & Wilson, 1987; Puerto et al., 1990; Rejmankova et al., 1995; Vermeer, 1986; Vermeer & Verhoeven, 1987; Vince & Snow, 1984; Vitt, 1990; Wheeler & Giller, 1982; Wheeler & Shaw, 1991; Wilson & Keddy, 1986a; Wilson & Keddy, 1988; Zobel & Liira, 1997).

1995). We found a significant nonlinear parabolic relationship between species richness and standing crop, but it explained only 13.5% of the variance in richness. Many other factors have been shown to influence plant species richness in wetlands, including climate (Vitt, 1990), pH (Gough et al., 1994), soil nutrients (Willis, 1963; Verhoeven et al., 1996), salinity (Partridge & Wilson, 1987; Grace & Pugsek, 1997; Keogh et al., 1999), abiotic disturbance (Keddy, 1983), and herbivory (Lubchenko, 1978), which may explain the large variance.

Despite a statistically significant relationship, the biomass–richness relationship did not follow a specific statistical pattern that could be described by any one line. The data could certainly be hiding families of lines and curves. Our intention, though, was to look for emergent patterns from the 1,367 data points in order to make general predictions (e.g., Brown, 1995). We found that richness varied from 0 to 75  $m^{-2}$ , with a clear maximum occurring in the range of 300–600  $g\ m^{-2}$ . Although collected from a wide array of vegetation types and geographic locales, and corrected for differences in sample area, the points are clearly consistent with Grime's model.

Boundaries (as opposed to means) are difficult, if not impossible, to define statistically (but see Scharf et al., 1998). Nevertheless, Brown and Maurer (1987, 1989) have suggested that many relationships between ecological variables are not characterized by a regression line through the data, but fall instead within a region to which lines set

boundaries. For example, the range of trees is limited along an altitudinal gradient by frost, which forms a boundary condition. Applying a similar approach to the standing crop–richness relationship, traditional regression lines may simply not be appropriate; indeed, as originally formulated (Grime, 1973a, 1973b), the relationship is a boundary condition (maximum rather than mean richness) that is specified as the dependent variable (see also Marrs et al., 1996). It is clear that the data follow a pattern, and that the greatest species richness occurs between 300 and 600 g/m<sup>-2</sup>. Here, we examine a quantitative method of estimating an upper boundary to species richness.

To estimate this boundary, the first step was to calculate  $N$  (the estimated number of shoots in a quadrat), and then to calculate  $S$  (species number) for the given  $N$ . Because we used the same procedure to calculate  $S$  from  $N$  in both the upslope and downslope equations, we begin by describing the technique to calculate  $S$ . We used the so-called “collector’s curve” (Pielou, 1977) to predict species richness from the number of individuals (shoots, ramets, rosettes, etc.):  $S = S^*[1 - (1 + N/kS^*)^{-k}]$ , where  $S$  is species number,  $S^*$  is species pool,  $N$  is number of individuals (shoots), and  $k$  is a constant describing the slope (generally, the larger the  $k$  value, the greater number of rare species in the community). The collector’s curve describes a relationship in which  $S$  approaches  $S^*$  asymptotically. The model has two parameters:  $S^*$  and  $k$ .

In nature, the species pool,  $S^*$ , varies between communities. Species pool is a measure of the total set of species that are potentially capable of coexisting in a particular community (Partel et al., 1996). There is evidence of a positive correlation between the species pool of a particular area and species richness measurements at the smaller scale (Wisheu & Keddy, 1996; Partel et al., 1996; reviewed by Zobel, 1997). Therefore, if the species pool is large, all things considered, there will be a greater chance that richness will be higher in, say, a 1 m<sup>2</sup> area. In this case, we used data from Wisheu and Keddy (1996) to determine, via polynomial regression, that  $S^*$  could be expressed as a function of biomass between 12 and 1680 g m<sup>-2</sup>, such that  $S^* = -9.56 \ln B^2 + 86.21 \ln B - 76.49$ , where  $B =$  standing crop (m<sup>-2</sup>) ( $F = 67.356$ ;  $df = 25$ ;  $P < .0001$ ).

We acknowledge that  $k$ , like  $S^*$ , also varies between communities. We have given  $k$  a value of 1, but if  $k$  is varied, the shape of the slope stays approximately constant. Most of the difference, though slight, occurs in the tail of the curve. Given  $S^*$  and  $k$ , our provisional formula for the calculation of  $S$  for both the upslope and the downslope is as follows:

$$S = (-9.56 \ln B^2 + 86.21 \ln B - 76.49) \times [1 - (1 + N/(-9.56 \ln B^2 + 86.21 \ln B - 76.49))^{-1}] \quad (1)$$

The calculation of the number of individual shoots,  $N$ , required different methods and data for the upslope and downslope.

*Upslope.* At any standing crop,  $N$  can be calculated by dividing standing crop ( $B$ ) by the mean individual weight ( $C$ ). The problem is that  $C$  does not remain constant with increasing biomass. Consider, for example, the small rosette species such as *Isoetes* or *Lobellia* on gravel shores compared with large shoots of *Typha* or *Phragmites*. One way we can estimate  $C$  requires us to know total biomass,  $B$ , and the number of shoots. Consequently, Auclair et al. (1972) measured both numbers of individuals and total aboveground biomass. Using the field data from Auclair et al., we established through polynomial regression that mean individual weight could be expressed as a function of

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standing crop between 20 and 1100 g m<sup>-2</sup>, such that  $C = 3.54 \times 10^{-6}B^2 + 6.81 \times 10^{-4}B + 1.10$  ( $F = 9.64$ ;  $df = 104$ ;  $P < .001$ ). Therefore, using our "working formula" (equation 1), the final equation for the upslope (over the range of 20–1100 g m<sup>-2</sup>) can be written as follows:

$$\begin{aligned} S &= (-9.56 \ln B^2 + 86.21 \ln B - 76.49) \\ &\times [1 - (1 + B/(-9.56 \ln B^2 + 86.21 \ln B - 76.49)) \\ &\times (3.54 \times 10^6 B^2 + 6.81 \times 10^4 B + 1.10)^{-1}]. \end{aligned} \quad (2)$$

*Downslope.*  $N$  was calculated by applying the self-thinning rule for plants (Yoda et al., 1963), which has been shown to apply for almost any fully occupied plant stand dominated by a single species such that:  $\omega = 9670d^{1.49}$ , where  $\omega$  = shoot dry weight (g), and  $d$  = density (m<sup>-2</sup>) (Gorham, 1979). Since  $\omega d = B$ , and  $d = N$ , we can rewrite the self-thinning equation as  $N = (9,670/B)^{2.04}$ . Therefore, by using equation 1, the final equation for the downslope (between 12 and 1,680 g m<sup>-2</sup>) is as follows:

$$\begin{aligned} S &= (-9.56 \ln B^2 + 86.21 \ln B - 76.49) \\ &\times [1 - (1 + (9,670/B)^{2.04}/(-9.56 \ln B^2 + 86.21 \ln B - 76.49))^{-1}]. \end{aligned} \quad (3)$$

Figure 2.11 shows that these two simple equations, one relating plant size to standing crop, and one relating shoot density to standing crop, when combined with the standard collector's curve, can set upper limits to species richness. Furthermore, when superimposed on our data from 1,367 samples in 22 published studies, a close fit is apparent. Similar to Oksanen's (1996) "no-interaction" model, the number of shoots determines the upper limits to species richness. Points may, of course, fall well below these lines, but our objective was to define upper limits rather than account for diversity on a quadrat by quadrat basis.

### Competitive Hierarchies

Over the last few decades, it has become apparent that most plant communities are organized by competitive hierarchies (Keddy, 2001); a small number of strong competitors tend to make up most of the biomass in a wetland, whereas larger numbers of weak competitors use the remaining space. The stronger competitors occupy the fertile sites and exclude the weaker competitors to infertile areas. Furthermore, increasing soil fertility increases the ability of these few species to dominate a wetland and exclude neighbors (Keddy et al., 2000). The dominance achieved by *Typha* or *Phragmites* in fertile soils can be compared to the rich array of plant types in interdunal meadows, wet prairies, or fens. The competitive ability of seven wetland plant species measured in an experiment was able to predict their field distributions along the shoreline; the large leafy plants occupied the fertile sites, and small rosette species were excluded to the sandy shores (Wilson & Keddy, 1986a, b). This experiment was repeated with a much larger sample of species and the same result was found (Gaudet & Keddy, 1995). This merges with the work on fertility, because it is well established that fertilization enhances the competitive performance of the large leafy species. The more eutrophic a site, the greater the likelihood of dominance by a few aggressive wetland species such as *Typha*, *Phragmites*, or *Phalaris*.

**Centrifugal Organization**

The same species usually prosper in the fertile and sheltered sites within a wetland, but different species can occur on other sites depending on the constraints. Shallowly sloping sands may develop fens, gravel shorelines may have isoetid plants, wet prairies may occur where fire or water level fluctuations kill woody plants, pannes may develop between alkaline sand dunes, and so on. The benign ends of many gradients are similar enough that we can describe them as a "core" habitat that can be dominated by the same species. At the peripheral end of each gradient, however, species with specific adaptations to particular sources of adversity occur. This pattern is termed *centrifugal organization* (Figure 2.12). Many peripheral habitats radiate outwards from the single, central core habitat.

The core habitat has low disturbance and high fertility, and is dominated by large leafy species capable of forming dense canopies. In northeastern North America, *Typha* dominates the core region. In other climatic regions, herbaceous perennials in the genera *Papyrus*, *Phragmites*, *Phalaris*, *Calamagrostis*, or *Rhynchospora* may play a similar role. Outside the core, different constraints create radiating axes along which different groups of species and vegetation types are arrayed. Along an axis of soil phosphorus, for example, the community composition changes from a high biomass *Typha*-dominated wetland to sparse vegetation dominated by isoetid and insectivorous species (Moore et al., 1989), two

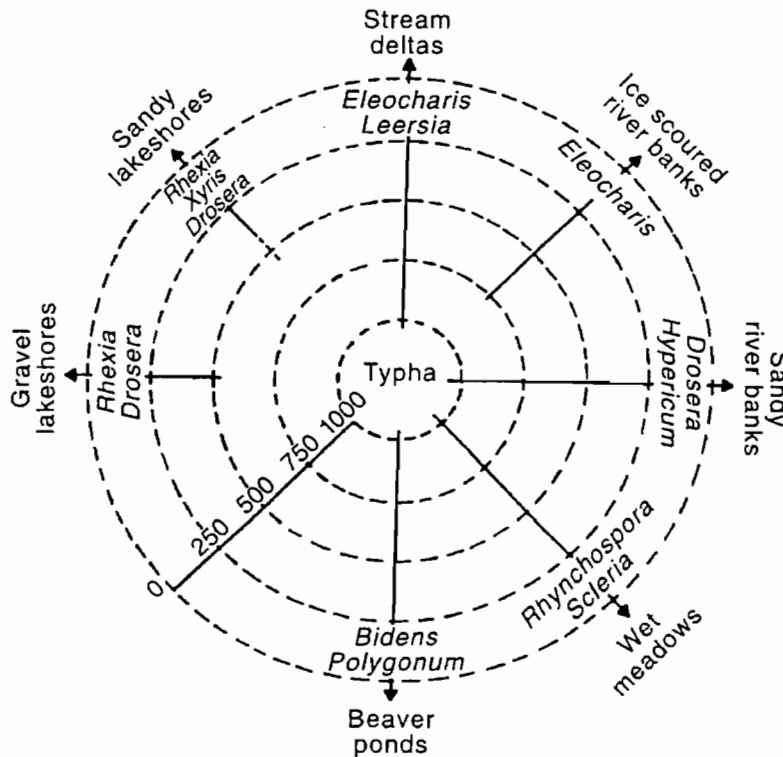


Figure 2.12. When many gradients radiate outward from a shared core habitat, the pattern is termed *centrifugal organization* (from Wisheu & Keddy, 1992).

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groups of plants indicative of infertile conditions (Boston, 1986; Givnish, 1988). Furthermore, the shortage of phosphorus, as opposed to nitrogen, creates rather different plant communities (Verhoeven et al., 1993, 1996).

Nutrient concentrations, however, are only some of the many gradients that occur in wetlands. Another gradient is disturbance, and the species found along these gradients differ from those found along gradients of fertility. *Typha* would again occupy fertile, protected areas, but where ice scour or severe flooding occur, either reeds or annual species would be abundant (Day et al., 1988; Moore et al., 1989). The deeply buried rhizomes of reeds protect them from moderate ice scour, while fast-growing annuals are able to set seed between periods of mud deposition (Grubb, 1985; Day et al., 1988). Peripheral habitats formed by different kinds and combinations of infertility and disturbance support distinctive floras that reflect differing environmental conditions [e.g., shoreline fens (Charlton & Hiltz, 1989; Yabe, 1993; Yabe & Onimaru, 1997), interdunal swales and sand spits (Willis, 1963; Reznicek & Catling, 1989), coastal plain wetlands (Keddy & Wisheu, 1989), river banks (Brunton & Di Labio, 1989; Nilsson et al., 1989), bottomland swamps (Penfound & Hathaway, 1938; White, 1983), and floodplains (Salo et al., 1986; Duncan, 1993)].

Our objective here is to introduce this model and stress its value in creating biologically diverse wetlands. The postulated mechanisms that produce this arrangement of vegetation, and tests of these postulates, are discussed elsewhere (Keddy, 1990, 2000, 2001; Wisheu & Keddy, 1992; Gaudet & Keddy, 1995).

### Management Guidelines

The following guidelines apply to all wetland types. The numbers given are drawn from temperate zone lakes and will have to be calibrated for other wetland types. Tropical floodplains, for example, may have much larger seasonal variation than temperate lakes.

1. Water levels should change from year to year. A 10-year cycle with changes of 1–4 m is probably typical of smaller lakes, with greater fluctuations in larger lakes. The highest water levels will determine the area of herbaceous wetlands by setting the lower limit of trees and shrubs.
2. Within years, high water levels in spring will further retard invasion by shrubs and trees.
3. During the growing season, water levels should fall approximately 0.5 to 1.0 m.
4. The gradient(s) from infertile to fertile sites greatly increase the number of ecological communities that can arise.
5. The more kinds of infertile and otherwise constrained habitats available, the more kinds of plants that can coexist in a lake, reservoir, or wetland.
6. Eutrophication usually reduces both the number of species at individual sites and the total number found in a lake, reservoir, or wetland.

### Wetland Management for Water Resources

The supply of renewable freshwater for human use is limited. Postel et al. (1996) estimated that by the year 2025, humans will appropriate over 70% of the total renewable

runoff of freshwater. Many regions of the globe are already experiencing severe water shortages or unsanitary water (Gleick, 2000). Due to their location between terrestrial and aquatic communities, wetlands form an important component of the hydrological cycle. Most surface waters originating from terrestrial systems must pass through wetlands in order to reach their aquatic outlet. Because these waters can contain an array of dissolved substances, wetlands receive and collect many different compounds. Consequently, wetlands can potentially play an important role in the transformation and reduction of these compounds. Constructed wetlands for the purpose of treating wastewater may therefore play a very important role in cleaning freshwater and water recycling for human use. These so-called "treatment" wetlands (Kadlec & Knight, 1996) can be applied to a number of different management situations, including agricultural runoff, human waste, and acid-mine drainage. Treatment wetlands vary in size from a few square meters to many acres. Some treatment wetlands are designed with water flowing above the soil surface, whereas others have a subsurface flow of water (Kadlec & Knight, 1996). It is very difficult to prescribe general design criteria for treatment wetlands because of the vast diversity of types that are found and the conditions under which they are applied. The listed management suggestions are for natural wetland systems and do not necessarily apply to treatment wetlands. Treatment wetlands are not designed to maximize diversity, but to treat wastewater. The high nutrient conditions commonly found in treatment wetlands for agricultural runoff would tend to reduce plant species diversity by increasing biomass and interspecific competition.

Nevertheless, the four major principles should not be ignored when considering the management of treatment wetlands. Water level fluctuations are important for all wetlands and therefore should be considered for treatment wetlands. It may be possible to include nutrient gradients within treatment wetlands by increasing the size of the wetland and introducing heterogeneity of the substrate, for example, soil depth and the size of soil particles. It may also be useful to consider constructing treatment wetlands at the head of threatened natural wetlands to act as preliminary sieves, thereby reducing the detrimental effects of eutrophication.

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# 3

## Use of Meta

Brian A.

### Introduction

There have been a number of studies in the last few quarters of a century. Whitehead and others have located uranium pollution and field results show phosphate-rich conditions of metal could be used of radionuclides in the 1960s, but such literature is not (1970b, 1980). plants for monitoring (see Onianwa awareness of

Since the use of heavy metals for convenience, proposed and use for broad studies have, the researcher

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