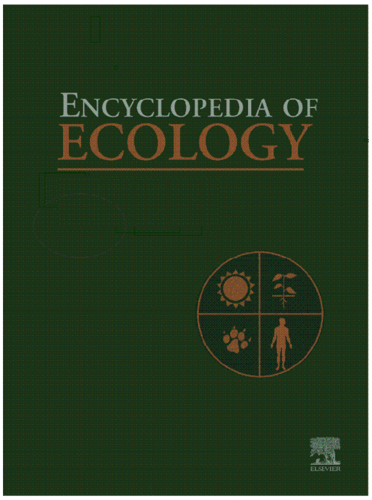

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See also: Invasive Plants; Matrix Models; Plant Competition.

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Wetland Models

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Introduction

Wetlands encompass a variety of ecological characteristics, distributed across a wide range of climates. Ecological models of wetlands are likewise a diverse assemblage of tools for better understanding each particular ecosystem. However, these models generally share a common characteristic: a method to consider the responses of some part of the ecosystem to varying magnitudes and frequencies of flooding. For some purposes, this may be as simple as an assessment of the suitability of specific ranges of water levels for different biological communities. More complex ecological modeling tools may investigate biogeochemical dynamics under varying interactions between surface and ground water flows. A model of further ecosystem integration couples these hydrologic and biogeochemical processes to those of plants and higher trophic levels within a wetland.

Regardless of the objectives and the level of model complexity, a principal driver of wetland models involves the hydrology of flooding and associated surficial soil/sediment saturation. These wetland physics influence the selection of the implicit or explicit ecological processes to be considered in model development. Important modeling topics such as algorithm formulation (e.g., biogeochemical process equations) and model analysis (e.g., uncertainty) are specified in other articles. Moreover, other articles consider ecological models of a separate class of wetlands that are engineered or 'constructed' for mitigation of anthropogenic disturbances. This article emphasizes the selection of appropriate model processes relative to the defining characteristics of 'natural' wetland ecology. In particular, intermittent flooding is a definitive characteristic of wetlands, and is an important consideration in modeling those systems.

Model Objectives

Defining the objectives is an important first step in modeling of any system, wetlands or otherwise. Often the (real or perceived) failure of models is a disconnect between two model 'niche' spaces: (1) the expectations of the users for model application and (2) the original intent of the model design. The utility of a model lies in the intersection of expectations and design intent – a basic point that is sometimes lost in practice as a result of inadequate communication. For example, a model that is designed to explore alternative hypotheses of the effects of climatic disturbances on vegetative succession can enhance understanding of potential responses to infrequent events. Particularly if supporting data for the model are sparse, such a model may not necessarily be the most appropriate tool to use in predicting the 10–20-year ecosystem responses to managed water flows into a relict wetland. Conceptual models serve an important role in this process. The simple conceptual models of wetland ecology that are summarized here can serve to organize information on scientific knowns and unknowns for a particular (set of) objective(s), and thus be useful ecological models as such. However, the primary intent of their presentation is to highlight the important wetland dynamics that are implemented as mathematical simulation models at various scales of space, time, and process complexity.

For the conceptualization step, it is convenient to separately consider hydrology, biogeochemistry, and the biology of plant and animal components – or modules in a simulation model. The interaction of these organisms and their environment (i.e., ecology) can be considered either implicitly within any of these modules, or explicitly within an integrated model framework of interacting modules. Conceptually, many different ecological models of wetlands can be summarized as different trophic level responses to a hydrologic 'driver' (**Figure 1a**). The water levels or flows drive the response of the ecological component of interest, with no feedbacks from those dynamics that affect the hydrology. For example, some wetland nutrient models are as simple as employing a first-order equation that describes nutrient loss from surface water when it is present. Alligators have specific hydrologic requirements for nesting and other activities in order to maintain a viable population. A simple alligator model driven by changing surface water depths can investigate the long-term population sustainability under different scenarios of hydrologic perturbations. Both of these examples focus on the influence of water levels on ecosystem properties, but do not consider how those properties may in turn affect water levels (i.e., through changes in vegetative resistance to flow, or altered microtopography). Such simple modeling frameworks can extrapolate spatial and/or temporal trends, aiding the understanding of wetland component of interest.

There are varying degrees of aggregation in such models of trophic level responses to hydrology, with an increasing total number of aggregated processes with increasing trophic level. (Network or energy analyses of ecosystems point to this increased complexity with trophic level.) A simple model of habitat responses to decreased water levels may assume that limiting nutrients do not increase with soil oxidation over time. Similarly, a model abstraction of a herbivore population response to changing wetland hydrology may make the basic assumption that the freshwater marsh habitat does not change to an upland during the simulation. Each of these broad assumptions actually implies a suite of more detailed assumptions regarding the actual interactions that occur in the actual wetland system. The broad assumptions make use of observed correlations between an altered input (water flow) and an altered ecosystem property, but generally mask the underlying causal processes behind the resulting ecosystem change(s). While simplifying the mathematical equations of model structure, simple assumptions still must be verified for the conditions being considered. Nevertheless, such broad assumptions can be very reasonable in the correct context of model application, and they provide the framework for simple, successful simulation to better understand a part of the wetland

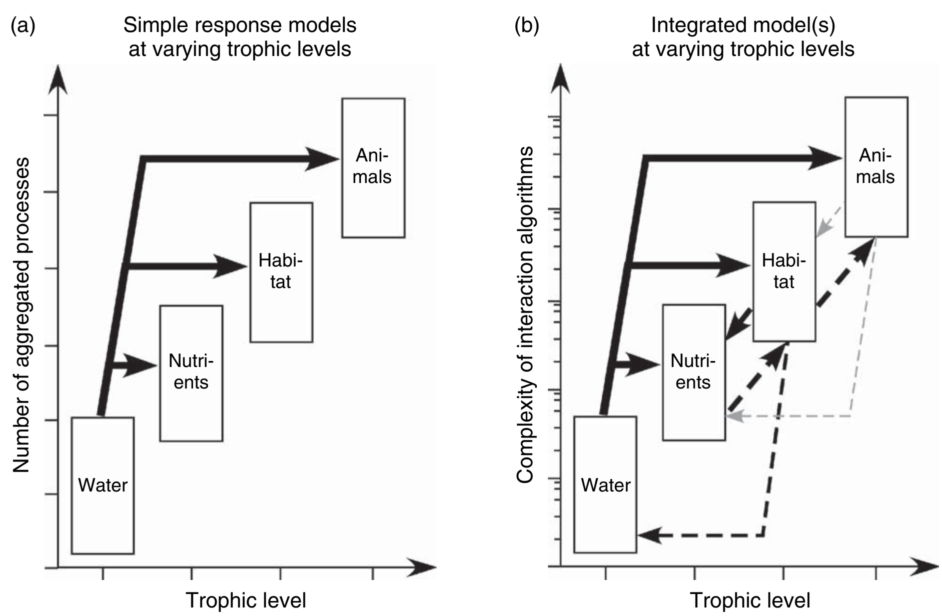

Figure 1 Trophic level and aggregation of different models. (a) As simple (nutrient, or habitat, or animal) models of ecological responses to hydrology incorporate higher trophic levels, the number of (implicit) aggregated processes increases. (b) With increased explicit integration among trophic levels, the complexity of interacting equations may increase geometrically.

ecosystem. A point to keep in mind is that simple ecological models tend to make complex assumptions in aggregating complex system dynamics.

While simpler models of a wetland habitat may aggregate the effects of processes such as nutrient cycling and plant herbivory, more complex integrated approaches include some explicit level of those lower and higher trophic level interactions (**Figure 1b**). The algorithms rapidly become more complex with those interactions, with the intent of the design presumably to increase the realism as constraining assumptions are lifted. In the simple models of trophic response to hydrology, the developer has a few large opportunities to misrepresent the actual wetland dynamics. Alternatively, as the numbers of interactions are increased in an attempt at greater 'realism', the developer increases the number of ways to produce a simulation that fails to characterize the targeted components of a wetland system. A cornerstone of model conceptual and mathematical development is assessing the most effective tradeoff between two factors: model complexity and predictability. At some point, an increase in model 'reality' of simulating complex interactions is (usually) associated with a decrease in accurately tracking all of the observed behaviors of the system (i.e., model predictability) – largely due to incomplete scientific understanding. Ecosystems are notoriously complex systems, with significant data requirements in order to parametrize an 'entire' suite of interactions for a given ecosystem. To meet the objectives of a modeling exercise, a fundamental step is to determine the ecological processes that are important to the wetland dynamics of interest – and what processes are supported with sufficient observational rigor relative to the overall modeling goals. The important or unique processes of wetlands that are considered in ecological models are summarized in a hierarchy of trophic levels below.

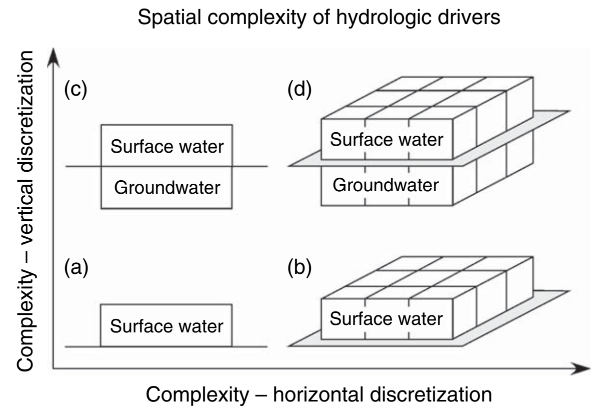

Figure 2 Spatial discretization of the hydrologic component of wetland models largely determines the questions that can be addressed. (a) Simplest case, with ponded surface water depths of a single unit area; (b) horizontal extension of surface water across multiple spatial units; (c) vertical stratification of surface and ground water storages; and (d) complex case of both vertical and horizontal spatial discretization.

Model Design

Water

'Getting the water right' is a primary consideration in understanding the dynamics of wetlands, and the phrase is a driving principle behind an ambitious restoration effort in the remnants of the vast Everglades wetlands of North America. The hydrologic 'engine' of ecological models of wetlands is the foundation of the spatial and temporal scales of the other ecological components of the model. The science of hydrologic modeling is extensive, and here we simply touch upon some of the important considerations for supporting ecological models of wetlands.

At the simplest level, the hydrologic driver of a wetland model may consider surface water alone as a single unit (**Figure 2a**). While this concept may be useful in modeling a component such as fish survival in a homogenous area, it can be extended to consider spatial variation in topography and water depths, employing a two-dimensional (2D) surface water model. Alternatively, the more important physical driver of an ecological component (e.g., for a rooted macrophyte community) may be temporal transitions among ponded, saturated, and unsaturated sediments within a unit area, in which case the spatial discretization lies in the vertical zonation among surface and ground water storages. In one of the more comprehensive spatial frameworks (**Figure 2d**), both horizontal spatial heterogeneity and changes among vertical storages are important to the objectives, leading to a layered 2D or fully 3D dynamic model. While the physics of any of these implementations are well understood, the most complex discretizations require increasingly extensive data and computing resources to implement. Additionally, because of the special expertise that may be needed, it is common for ecological models of wetlands to employ some degree of indirect or direct linkage to existing hydrologic models of the system being considered.

Concomitant with the spatial considerations are those of the hydrologic processes (**Figure 3**) that are important to the ecological dynamics – hydrologic drivers that operate at timescales of minutes to days. When the water table (or stage) height is below ground surface, the distance from ground surface to the saturated water table is a zone of potential unsaturated storage within the pore spaces of the sediment. Ponded surface water generally denotes an underlying saturated ground water storage, with the water table above ground surface. Spatially distributed differences among water table heights present hydraulic head gradients. Resultant surface and ground

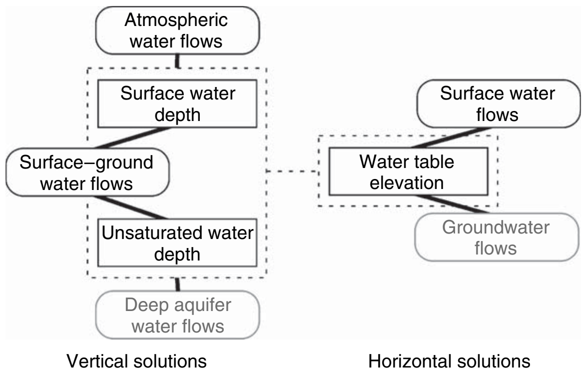

Figure 3 Hydrologic processes that influence ecological dynamics. Exchanges between surface waters and the surficial zone of the subsurface groundwater storages become particularly important in wetlands, with highly dynamic water tables relative to land surface. Rectangles denote attributes such as storage or height of water; flow processes are shown in rounded rectangles. Flow algorithms are distinguished here between their vertical vs. horizontal components. Flows that often are assumed to be of relatively minor importance in direct ecological responses are in lighter font.

water flows are modeled using a variety of computational methods. These horizontal flow calculations are dependent on the sediment and vegetation resistance associated with surface waters, and the hydraulic conductivity of the subsurface aquifer, respectively. Such overland and groundwater flow computations establish the basis for much of the other physical characteristics of a wetland model.

Other important design considerations for any wetland hydrologic model are the atmospheric exchanges. An elementary model of an isolated wetland may be primarily driven by estimates of net rainfall, which is the difference between vertical inflows of precipitation and losses to the atmosphere by evapotranspiration. Precipitation is most often a forcing function that is input to ecological models, as are a variety of other meteorological observations that are used to determine potential and actual evaporation and transpiration (combined into evapotranspiration, or ET). While the mechanistic detail is relatively complex, potential ET is a function of the net energy gradient between the wetland and atmospheric storages of water. Actual ET is largely determined by the available water storages in the wetland, and is influenced by emergent vegetation. In the absence of ponded surface water, actual ET rates are largely driven by plant transpiration and the depth of the unsaturated zone of storage in the soil relative to root depth. This biological effect is often simply determined through the use of static model parameters relating to land use or habitat type. These ET losses are withdrawn from surface and subsurface water storages, and are a principal component of the hydrologic budget. In particular, depth variations in ponded surface and unsaturated zones have significant repercussions in modeling ecological responses of wetlands.

Hydrologic linkages among the subsurface and surface storages are a defining characteristic of wetlands. They also can present relatively complex modeling problems, particularly in the presence of spatially distributed hydraulic gradients. In the presence of an unsaturated zone of water storage, surface water (from rainfall or local runoff) infiltrates into the pore spaces of the subsurface sediments. In fully saturated media overlain by ponded surface water, transpiration by rooted macrophytes withdraws water from subsurface storage, advecting water from surface to subsurface storages. Differences in the heights of the water table induce hydraulic gradients across space, leading to horizontal flows in the groundwater and the surface water. Depending on the changes in local storage capacities, these flow dynamics can result in vertical upflows or downflows among the surface and subsurface storages. Integrated hydrologic modeling of such surface and groundwater dynamics has been accomplished at a variety of levels of mechanistic detail. Ultimately, the importance of the detail in modeling these changes in surface – ground water storages and flows – depends on the objectives of the modeling effort.

One of the more common design constraints for wetland ecological models is that of matching spatiotemporal scales of the hydrologic and biological processes. Water flows are usually considered at scales of minutes to days, whereas upper trophic level responses of plant and animal communities operate at timescales that are orders of magnitude greater. With models specific to hydrology often tending to emphasize fine temporal response algorithms, the computational requirements for hydrologic flows tend to reduce the model time domain, and tend to use spatial resolutions that are coarser than optimal for understanding spatial heterogeneity of ecological dynamics over annual to decadal timescales. Thus, the selection of the hydrologic characteristics to drive wetland ecological models can become a crucial factor in the endeavor's scope and objectives.

Nutrients

Wetland modeling of nutrients not only involves a strong degree of coupling to hydrologic flows for nutrient transport, but is highly dependent on biological transformations. This dependence, however, again is directly related to the hydrology via intermittent flooding or saturation of the wetland soil and sediments, which largely determines the relative degree to which aerobic or anaerobic rates and processes are operative. Rarely is surface water very deep, if present at all in a generalized wetland. This results in a high surface area of (soil/sediment and vegetative) biological interaction relative to water volume. In parallel with water levels, nutrient availability to macrophytic, algal, and microbial communities becomes an important driver in the development of plant communities and organic soil accretion. Chemical sorption and precipitation mechanisms exert an influence in the wetland biogeochemistry that varies among systems, often dependent on the mineral content of underlying sediments. Modeling wetland nutrients involves determining the most useful combination of the physical hydrologic drivers and the biological mediation of nutrient transformations.

Transport of nutrients and other constituents (e.g., salts) in the vertical and horizontal dimensions (**Figure 4**) is directly linked to hydrology. In most spatially distributed models, calculations of water advection in the horizontal dimension are coupled in some direct fashion to transport of nutrients that are dissolved and/or in suspended particulate forms. In addition to this transport mechanism, dispersive flux (i.e., a case of diffusion in turbulent flow regimes) further propagates constituents across space. This becomes important primarily in surface flows, rather than in the slower subsurface flows through a sediment zone. Because of the spatial and temporal variability in topography and vegetative resistance in these very shallow flow regimes, the relative contribution of dispersion to total nutrient transport remains difficult to accurately quantify. Instantaneous water velocity measurements at different locations in the water column, in combination with dispersion of dye tracers, provide some of the more useful, if still uncertain, understanding of this transport process across a wetland region.

As noted in the hydrologic discussion, water flows involving the subsurface groundwater storages can lead to vertical gradients of flow between subsurface and surface waters. Mass balance dictates that dissolved nutrient constituents are advected with those vertical flows, including surface to subsurface flows induced by withdrawal of subsurface water by rooted macrophyte transpiration. Particularly in regions where transpiration is a major component of the hydrologic budget, this plant 'pump' has the potential to mix water and nutrients among the surface and subsurface storages, albeit over a short distance approximating the root zone depth. Dissolved constituents also move across diffusion gradients between the surface and subsurface storages, though rates across very short diffusion lengths are usually low relative to other potential biological and physical flux mechanisms. The surficial sediments associated with the root zone are often modeled as the most 'active zone' for biogeochemical dynamics of uptake and mineralization. As emphasized in a later section, dynamic water tables in this sediment zone establish a range of potential trajectories in nutrient and habitat status.

Phosphorus and nitrogen are the primary nutrients that are usually considered in wetland models, as one or the other are typically understood to be a limiting factor of wetland productivity. Nitrogen cycling is conceptually (and mathematically) more complex than that of phosphorus, principally because of the presence of atmospheric exchanges (nitrification and denitrification), and the more involved suite of oxidation–reduction reactions that transform nitrogen into inorganic forms of different bioavailability. Beyond nutrients that potentially limit biological reactions, modeling salinity in relation to hydrologic flows is a major component of coastal wetland models.

Boundary condition inflows of these nutrients from the atmosphere and from overland or groundwater sources are often a significant source of uncertainty in biogeochemical components of an ecological model. Wet and dry atmospheric deposition of nutrients such as nitrogen and phosphorus are difficult to measure in the field, and usually are assumed to represent minimal contributions to any external load to a wetland. Nevertheless, these atmospheric inputs may be the only external load to some systems. Most other wetlands have the added complexity of horizontal inflows. Even in the cases where overland and groundwater flows are measured or inferred with relative accuracy, nutrient concentrations associated with those flows are seldom monitored or understood at the relatively short timescales associated with the sometimes rapid changes in water flows.

Because of the potential assimilative capacity of wetlands for nutrients, 'water quality' modeling in these systems has been of interest in a variety of nutrient management contexts. The efficiency of engineered, or constructed, wetlands in assimilating anthropogenically derived nutrients in surface waters has been investigated

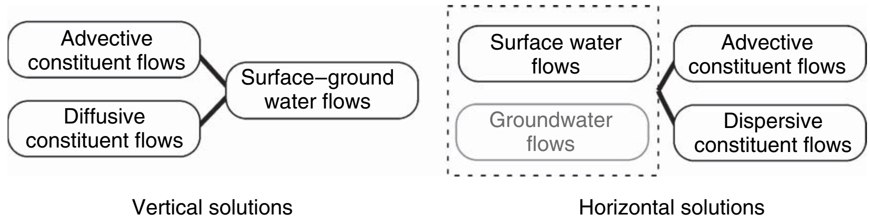

Figure 4 Transport processes of nutrients and other waterborne constituents. Beyond transport shown here, the fate of nutrients is highly dependent on biological activity in shallow surface waters and the upper sediment zone. Flows that often are assumed to be of relatively minor importance in direct ecological responses are in lighter font.

using a range of modeling techniques. Some of these efforts are based on first-order equations of highly aggregated nutrient losses from surface water storages, taking advantage of the simplifications possible through constructed wetland design and relatively predictable, managed water levels and flows. Physical entrainment and settling of suspended particulate matter, with associated nutrients, is combined with all other water column nutrient losses into parameters that aggregate the net nutrient assimilation by the biological and physical components of the wetland. The residence time of a water parcel as it flows through the wetland parcel becomes a primary consideration in determining nutrient assimilation of the wetland.

Ecological models associated with biogeochemical transformations in natural wetlands may start with a similar, simple suite of assumptions of relatively controlled physics and biology. The objectives of ecological modeling projects typically extend these modeling concepts to incorporate an increasingly broad suite of biogeochemical interactions. Because of the potential prevalence of microbial- and plant-based uptake and release of nutrients in wetlands, an important step in wetland nutrient modeling is an estimation of these biological contributions to total wetland nutrient budgets. Understanding these contributions becomes complex in wetland models due to the frequency with which the system is alternately wetter and drier, with resulting changes in primary nutrient controls.

The regular (often diel) fluctuations in flooding of tidal wetlands greatly contrast with isolated peat bogs that are dominated by seasonal or interannual cycles of net precipitation. These physical drivers are a major influence on the ecosystem type and landscape pattern that develops over long timescales, and thus the resulting biological processes that influence nutrient chemistry. For example, algae or periphyton (a composite of algal and microbial communities) are of relatively low importance in carbon production and nutrient uptake in an isolated wetland with infrequent flooding, while they can be the major nutrient uptake mechanism in a model of a freshwater wetland with extended hydroperiods (i.e., flooding duration). The methods for simulating nutrient processes associated with algal, gramminoid, and forested plant communities take on a wide range of process complexity, and are generally not unique to wetland models. As in other ecosystems, a primary consideration in modeling these biological effects in wetlands is understanding the spatial and temporal variations in biomass, productivity, and mortality of these biotic variables, including their relative nutrient uptake affinities.

Production and mortality of plants (and, to a much lesser extent, animals) establishes the source of organic material that may accumulate as part of the sediments of a wetland. Much of the complexity of wetland nutrient modeling stems from the variations of a water table level relative to land surface, affecting the extent to which the sediments are sources or sinks for nutrients. At a simple conceptual level, prolonged flooding or saturation of sediments tends to lead to anaerobic conditions in the sediments, with resulting lowered rates of organic decomposition compared to unflooded, more oxygenated zones.

Microbially driven mineralization of organic detrital storages of phosphorus and nitrogen makes them available for plant uptake, or to be precipitated or sorbed back into the sediment/detrital storage complex. Laboratory isolation of specific flux paths such as sorption and desorption provides baseline rates of nutrient dynamics. However, the presence of interactions among biotic, chemical, and physical potential fluxes leads to a significantly more complex modeling problem. With fluctuating water tables around the sediment and surface water interface, and varying biological activity, discerning the (importance of) rates of the alternative pathways of nutrient flux is an ongoing topic of research. Model hypotheses can explore the repercussions of varying the magnitudes of such alternative paths, providing insight that may guide research goals.

Habitat

Habitats of wetlands have various operational definitions, and wetland habitat delineation is the subject of significant scientific and regulatory efforts. For the purposes of this modeling overview, habitats are simply considered to be combinations of soil/sediment and plant community characteristics. Principal characteristics of a generalized wetland habitat are the function of sediment accretion, and the related structure of the macrophyte and/or algal communities. Some of the more important applications of ecological models in wetlands involve understanding the processes that lead to alternative trajectories of habitat types – which support animal populations of interest. This leads to significant modeling challenges: understanding and quantifying the rates of sediment accretion and plant succession, under baseline and altered conditions, and generally across a long time domain.

Water and nutrients are two primary drivers of the development of wetland habitats. Modeling those dynamics over short timescales of months to years provides a snapshot of insight into the ecological interactions within given habitat types. However, the development and maintenance of habitats involve cumulative interactions over much longer timescales. A myriad of biological, chemical, and physical interactions can lead to changes in habitats. The succession of macrophyte communities, and accretion of sediments, become observable at multiyear or decadal time periods, with infrequent disturbances being a third major driver of the long-term habitat trajectories.

The frequency and magnitude of events such as prolonged drought or severe storms has the potential to significantly modify ecological processes, and thus the status of habitat types in a modeled wetland. Major disturbances including fire and hurricanes are specific to particular wetlands, and can directly modify the habitat structure and underlying ecological processes, as seen in examples of coastal and freshwater wetlands of southeastern North America.

Rather than considering all of the potential ecological interactions, models of habitat changes usually simplify the objectives to focus on more specific processes that are understood to be most important to the system of interest. While periphyton community dynamics may be modeled as an important habitat characteristic in the Everglades wetlands, sediments, and macrophytes are typically the focus of models of wetland habitat change.

Some of the simplest such models involve dimensionless habitat suitability (0–1) indices, reflecting assumptions of the suitability of particular environmental conditions to maintain or establish some desirable habitat type. Hydrologic data and best professional judgments are typically the primary drivers of the suitability index. Models of this type serve to organize available (usually limited) information on the ecosystem requirements into a framework for discerning the relative benefits of alternative scenarios of wetland management.

With more advanced knowledge of the environmental drivers and biological responses, more of the causal factors for habitat change can be incorporated into an ecological model. Plant communities are a conspicuous component of wetland habitat structure, and processes associated with their population dynamics comprise an important part of wetland function. Ecological modeling of plant production and mortality has a long and diverse history. Terrestrial, marine, and lake literature provides a rich background for understanding the methods available for macrophyte and algal simulations, for a range of scales and objectives. Associated with the wetland hydrology, coastal wetland models often incorporate flow-induced salinity stressors on production or respiration/mortality. The extent to which nutrient biogeochemical processes interact to limit plant growth varies widely among model objectives. One of the more characteristic components of wetland plant models involve the need to develop response mechanisms for hydrology that may range from flooded to very dry, multiple times within a plant generation.

Dynamics of plant populations comprise an important component of wetland habitat modeling. Extending this, models of wetland vegetative succession provide insight into long-term habitat trajectories. The most appropriate timescales range across multiple decades (to perhaps centuries), particularly for long-lived trees in mangrove, cypress, or riparian bottomland forests. Depending on the objectives, these models vary along a continuum of spatial and ecological-process complexity. Implied or explicit equations of competition for space and/or resources are commonly employed. However, compared to the number of models involving ecological processes at shorter timescales, there are relatively few succession-oriented wetland models.

Succession models of canopy gap dynamics in mangrove or other forested wetlands tend to synthesize physical and biogeochemical processes that influence individual trees and their canopy interactions. Simulation of the succession of species or specific community types is generally targeted to local plots that are sized on the order of tens of meters. Those dynamics can potentially be scaled up to apply across multiple plots within a larger regional landscape model. However, in the case of large spatial domains where water and constituent (nutrient and/or salt) flows are considered important, century-long simulations can become constrained by the data and computational complexity of the combination of spatially distributed gap dynamics plus hydrologic and constituent drivers.

Models of the pattern of long-term vegetation succession dynamics in gramminoid wetlands tend to encompass a slightly shorter, but still multi-decadal, timescale that is associated with higher turnover rates of these plants compared to trees. While forest models may consider vertical spatial gradients within the understory and canopy, reduced-statured gramminoid succession has less of a vertical spatial dimension. Models of transition probabilities among habitats have provided the basis for understanding the principal variables associated with habitat changes, and such efforts tend to drive further research into causal factors underlying the change. Beyond the wetland hydrologic processes, gradients of stressors such as salinity or subsidies such as nutrient loads can be used to drive the relative success (or switching) of plant communities.

Whether via direct simulation of population processes, or indirectly via suitability indices, habitat change in wetlands is strongly affected by the cumulative effects of water depth and duration – which is directly coupled to changes in land surface elevation. With such interactions among biological and physical processes, which is of primary importance: the sediments or the vegetation component of habitat? That sometimes depends on whether the modeler is a soil or a plant ecologist! More precisely, it depends on how the physical hydrology interacts with the biological and chemical dynamics of the wetland over long timescales.

Land elevation patterns are modified by water velocity and associated erosion or deposition (**Figure 5**). These sedimentary processes shape creek geomorphology in tidal marshes that are largely high in mineral content. The organic soils of the Everglades have directional

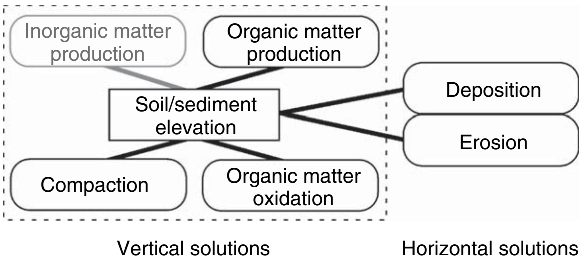

Figure 5 Processes that affect the sediments of a habitat. Patterns of land surface elevation are developed and maintained by the interactions among a variety of hydrologic and biological processes. Flows that often are assumed to be of relatively minor importance in direct ecological responses are in lighter font.

patterns that are clearly modified by water flows; the degree to which erosion and deposition of very fine flocculent detritus particles shape these patterns is a priority research topic in that wetland restoration effort. Hydrodynamic algorithms that use first principles of conservation of both mass and energetic momentum are frequently used in engineering applications to understand sheer stresses on sediment particles. With such physical dynamics operating at very short timescales, further challenges remain in effectively aggregating their effects within models that consider multidecadal sedimentation dynamics.

A significant component of elevation changes in wetlands is due to positive feedbacks from accumulation of above- and belowground plant detritus. Root growth and mortality accumulate organic matter in the soils, and aboveground plant dynamics add to that elevation potential. Countering this potential rise is the oxidation of the soil organic matter. Rates of this microbially mediated decomposition are dependent on the quality of carbon (e.g., the refractory carbon content), available nutrients, and the degree of oxygenation of the soil matrix. Flooded sediments typically are characterized by anaerobic pathways of microbial metabolism, though different wetland macrophyte species have varying capabilities of maintaining increased oxygen in their root zone. Lowered water tables expose the sediment to increased oxygen availability and increased oxidation rates. The mineral content and the soil bulk density impact the relative magnitude of soil height that is lost with the decomposition. Due largely to the long timescales required for accurate measurement, supporting models of change in land surface elevation is difficult. However, research that better defines decomposition under varying environmental conditions is providing a useful basis for modeling a principal wetland process, and permanent sampling devices (such as Sedimentation–Erosion Tables) can monitor long-term changes in sediment heights.

With direct effects of water levels, water flows (erosion and deposition), and plant dynamics (growth and mortality), sediments are integrated indicators of the relative 'health' of wetlands: modeling these sediment/soil dynamics is a valuable approach to understanding long-term, integrated wetland function. Perhaps because of the complexity of these multiple interacting processes, and long observational timescales, such all-encompassing simulations of wetlands are relatively uncommon.

Animals

Nutrient and habitat modules typically involve at least an aggregated level of direct linkages with horizontal flows and vertical surface-water to sediment interactions. Most wetland ecological models that focus on upper trophic level dynamics tend to be less directly coupled to those wetland physical interactions. Rather, the simulated animal dynamics typically respond to the resulting resource availability within habitats. Some wetland animals (e.g., fish) are restricted to habitats with ponded water levels. In turn, avian predators respond to potential concentration of prey in the small-scale pools of a marsh. Thus, beyond their effect on habitat and resource structure itself, water level fluctuations are a fundamental determinant of the temporal and spatial availability of habitat. The periodicity of this availability ranges from daily flooding of intertidal wetlands, to annual recession of water levels in flooded wetlands with the onset of a dry season. Particularly in wetlands, the challenge of modeling animal trophic dynamics becomes one of representing the interactions within and among populations, in the context of habitats that may be dynamically varying with hydrology.

Much of early ecological science focused on animal population and community dynamics, with a rich literature on the associated modeling theory and practice. Trophic dynamic modeling becomes highly specific to the system of interest, relative to the particular scientific or management objectives. At a minimum, it may be generalized that many wetlands have detrital-based food webs. Those lower trophic level resources become the base for more complex predator–prey interactions. Simple equations of such interaction have been explored at many levels of modeling, along with associated energetics of foraging and resource assimilation. In understanding and modeling animal dynamics in wetlands, it appears that an ongoing challenge is that of sampling motile populations in a fluctuating environment.

Animal dispersal is complex in both time and space. For example, fish and invertebrates moving onto and off intertidal marsh habitats are difficult to sample in a quantitative fashion. The density of emergent wetland vegetation, which serves as refugia for prey, also hinders estimates of motile animal densities needed for modeling. Nevertheless, data from innovative sampling devices and mark-recapture methods have been used to parametrize some models. Simulations of resource limitations and animal movements provide a context for generating hypotheses of the key regulators of animal interactions in a dynamic environment.

A modeling approach that is increasingly being used for such purposes is that of individual-based models (IBMs). As with simulations of forest succession due to interactions among individual trees, IBMs of animals incorporate individual variation in the quest for understanding dynamics of larger populations (or interacting populations). Relaxing some of the broader assumptions of population homogeneity, these modeling approaches explicitly incorporate some aspect of how individuals respond to dynamics of biological and/or physical changes in their environment. In such a model framework, multiple avian predators can be 'rewarded' energetically by finding assemblages of fish prey individuals, which have responded to dry season recessions of wetland water levels and become concentrated in isolated pools of surface water. In understanding such potential interactions through the collective response of individuals, potential emergent properties of the population(s) can be explored in a highly dynamic wetland environment.

Integrated Ecosystem

An integrated simulation model can take on a range of definitions. Largely dependent on the specific objectives, this may involve the interplay among physical, chemical, biological, and socioeconomic sciences. As apparent in the discussion of each trophic module above, a comprehensive understanding of wetland structure and function involves a rather complex suite of ecosystem properties. Integral with these 'natural' properties are the effects of anthropogenic drivers – human degradation or restoration of wetland systems. Moreover, specific land-use requirements may frame the possible trajectories of wetland change, all within the context of the human values ascribed to the function of the system. In planning for projects involving wetland modifications, there typically are limited data available on the specific system of interest. Comprehensive understanding of long-term, fully integrated wetland dynamics is elusive.

Relatively simple modeling tools may be the best available to forecast the scenarios of wetland change. Statistically oriented models based on past wetland behavior may serve to guide initial plans for such wetland management. However, such relatively simple models tend to make complex assumptions regarding long-term wetland landscape trajectories. Outside of the envelope of past observations, uncertainty of such models becomes problematic, and the models tend to lack explanatory power. Given a general framework of socioeconomic drivers, it is desirable to determine the minimum set of ecosystem properties that will interact to lead to long-term trajectories of wetland structure and function. Understanding the fundamental physical, chemical, and biological interactions – at some minimal level – becomes a goal for ecological simulations of wetland dynamics in this context.

The majority of current wetland ecological models focus on hydrologic and plant dynamics (Table 1), usually associated with freshwater systems dominated by emergent graminoid macrophytes. Nutrients, animal, or soil components are each represented in about one-third of the published models, while relatively high levels of ecosystem integration among (at least four of) these ecosystem components is not commonly modeled (i.e., in less than 20% of the published models).

Integrating the full ecosystem dynamics across a heterogeneous wetland landscape is a daunting goal. Given the current depth and breadth of our ecological understanding of any specific wetland, that goal would likely

Table 1 Number of published wetland ecological modeling articles, classified into five general wetland types, and the number of those articles that considered each of five generalized classes of ecosystem component(s)

Wetland type			*Ecosystem component*					
Salinity	*Vegetation*	*N*	*Water*	*Nutrients*	*Habitat-soil*	*Habitat-plant*	*Animals*	*Integrated*[a]
Fresh	Forested	9	7	2	2	3	5	1
Fresh	Graminoid	48	33	21	14	29	19	9
Fresh	Bog/fen	7	2	2	5	5	1	0
Saline	Forested	6	2	2	4	6	4	2
Saline	Graminoid	15	9	8	3	14	4	3
Total		85	53	35	28	57	33	15

[a]A model was classified as Integrated if it included at least four of the five ecosystem components. Between 1997 and 2006, 85 wetland ecological modeling articles were published in selected ecologically oriented journals. Each of a model's explanatory or state variable(s) was classified into one of the five ecosystem components; external factors that were assumed to be constant or certain were not included (e.g., if water was assumed invariant without effect). (The query used in the Web of Science (http://www.isiknowledge.com), *Science Citation Index Expanded*, for 1997–2006 was: ''TS = (wetland* OR mangrove* OR bog* OR fen* OR marsh* OR swamp*) AND TS = (model*) AND SO = (ecological modelling OR ecology OR ecological applications)''. During that time period, 189 articles that were published in the journals *Ecology, Ecological Applications*, or *Ecological Modelling* had some apparent reference to wetland modeling. Of those, 85 articles met the criteria for use in this table. For an article to be used: 1) some form of wetland had to be explicitly incorporated into the model (e.g., instead of a peripheral area mentioned in text); 2) the model had to explain or predict some ecological characteristic(s) of a wetland (e.g., instead of a statistical model summarizing an isolated experimental treatment-effect). If a model considered more than one wetland type, one primary type was assumed and used here.)

not result in analyses with significant forecasting utility. However, such model integration serves to highlight the missing information, and thus is a useful heuristic tool for advancing the state of knowledge. Moreover, there are varying degrees of scientific integration. Integrated ecosystem models, at some scales, can provide enhanced understanding of the potential trajectories of wetlands.

Such an incompletely integrated model is necessarily specific to the wetland and objectives of the particular project. Certain environmental or biological drivers may be assumed constant; others may be fundamental to understand potential scenarios of change. While there are innovative attempts to integrate terrestrial ecological models with long-term meteorological models, the effects of global sea level rise on coastal marshes can assume a suite of increasing water heights to understand habitat trajectories – without necessarily incorporating feedbacks from changing vegetation on local climate. On the other hand, major shifts in habitat may have important repercussions to surface water hydrology, through feedbacks of vegetative resistance to flow, local ET demands, or organic sediment accumulation and topographic patterns.

There is a core suite of variables and processes whose integration may provide insight into understanding long-term wetland dynamics. The preceding overviews of the modeling at varying trophic levels outline the basic nature of some desirable levels of integration, shown in conceptual form in Figure 6. The emergent characteristics of this potential integration reflect the unique character of wetland dynamics: understanding the physical drivers of intermittent flooding, and the biogeochemical and biological responses of the habitats to those dynamics. While not comprehensive, such integration within a simulation model is still difficult to parametrize for most wetlands, particularly over large spatiotemporal scales. Few wetlands in the world are studied adequately to implement such a complex model with significant certainty for forecasting. One of the most comprehensively studied wetland in the world is the Everglades of North America. A range of hydrologic, statistical, and ecological models are in use, or are under development, in order to better understand how to manage and restore the Everglades landscape (Figure 7). Considering more than 10 000 km^2 of coastal mangroves, freshwater marshes, and upland ecosystems, some of the ecological models attempt to integrate components of the ecosystems throughout the region. None of these modeling tools provides sufficient understanding to be confident of projected results even a mere 50 years from now. Hand in hand with simulation tools that make relative assessments of future scenarios, comprehensive monitoring is being implemented – to adaptively assess and modify plans as the landscape responds along unforeseen trajectories. As scientific understanding evolves, so do the models that assimilate that knowledge. Uncertainties in how major disturbances will affect these dynamics over long timescales become some of the interesting topics that can be explored with ecological models.

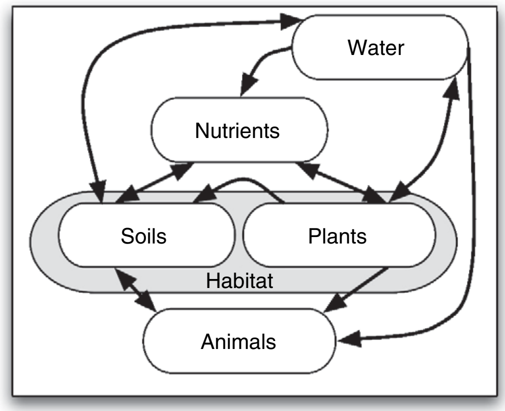

Figure 6 The process-oriented feedbacks among the biotic and abiotic components of an integrated wetland model. Dynamics of macrophytic plants alter surface water runoff through changes in structure and thus surface roughness. Water losses via transpiration vary with changes in biomass and canopy structure, while the availability of water is one control of plant growth and mortality. Hydrologic algorithms also transport nutrients and are a control on their mineralization rates, while nutrient availability and uptake kinetics affect plant growth (and soil decomposition). Mortality of plants and animals accumulate soils, but soil decomposition offsets that trend and decreases land surface elevation, which is an important hydrologic driver. Animals respond to habitat availability, and sequester plant and detrital (soil) biomass that may modify the turnover rates of those components.

Figure 7 *Nymphaea* in an experimental mesocosm, and emergent *Cladium* near monitoring boardwalks (background), within a periphyton-dominated, open water slough habitat of the Everglades in South Florida, USA. In parallel with long-term synoptic monitoring and field experiments, numerous models of ecological dynamics have been developed for this impounded wetland, in order to better understand and restore the highly managed, regional Everglades wetland mosaic. Photo courtesy of Everglades Division, South Florida Water Management District.

See also: Biogeochemical Models; Marine Models.

Further Reading

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Relevant Website

http://www.evergladesplan.org – USACE and SFWMD. Comprehensive Everglades Restoration Plan.

Wildlife Ecology

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Introduction

This article introduces the discipline of wildlife ecology, which forms the scientific foundation for conservation and management of wildlife species. Development of the discipline is briefly reviewed. Central interrelated themes in wildlife ecology are presented, and application of wildlife ecology to management and conservation of wildlife species is discussed.

Wildlife ecology is the application of ecological principles to the study of wildlife species. The term wildlife, however, lacks a universally accepted definition. Common use of the term changed during the 1900s in association with development of the profession of wildlife management. Historically, wildlife management focused on hunted or harvested birds and mammals that were collectively referred to as game species. Since the 1960s, the focus of wildlife management activities has broadened to encompass species that are not hunted or harvested (i.e., non-game species) and to include conservation of rare or endangered taxa. Today, the term wildlife commonly refers to all terrestrial vertebrates (birds, mammals, reptiles, and amphibians), but can also include invertebrates (**Figure 1**). Fish (both freshwater and marine) and other aquatic species generally are not considered wildlife, and, in many nations, fish and wildlife species are managed under different regulations by separate agencies.

Wildlife ecology as a field of study emerged following the rise of ecology in the 1900s, and, as such, represents a subdiscipline of ecology. Aldo Leopold is credited with formalizing the study of wildlife ecology and management in North America by publishing the first text on game management in 1933 and establishing the first university curriculum in wildlife ecology and management.

Wildlife ecology typically encompasses multiple levels of biological organization, including individual organisms and their relationship with the environment, interactions among individuals within a population (e.g., sociality, intraspecific competition), dynamics of populations, interactions among species (e.g., competition, predation, parasitism, disease), and dynamics and structure of communities. More recently, these levels have been expanded in each direction to formally include the interactions of wildlife with ecosystem processes and genetics of wildlife populations.

Central Themes in Wildlife Ecology

Habitat

Habitat is a core concept in wildlife ecology. The term habitat has been used in both an organism-specific context (e.g., elk habitat) and also in a land-based context (e.g., riparian habitat). More commonly, wildlife ecologists define habitat as the area where an animal lives, including all resources (both biotic and abiotic) that affect survival and reproduction. This operational definition is similar to the Grinnellian niche of a species. Use of geographic information systems (GIS) to map distributions of wildlife species and their habitats has made it possible to analyze multiple habitat variables simultaneously (e.g., vegetation,