MODELS OF REGENERATION, TREE GROWTH, AND CURRENT AND POTENTIAL RANGES OF TREE AND MAMMAL SPECIES IN THE EASTERN U.S.

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We are developing a multi-phase set of models that simulate tree and mammal migration in response to global change. The phases involve:

1. Tree regeneration processes
2. Tree growth and development
3. Potential tree migration rates across a fragmented landscape
4. Current and potential distributions of tree species
5. Current and potential distributions of selected animal species
6. Predicted distribution of tree and selected animal species under global change

TREE REGENERATION PROCESSES

An environmentally responsive, mechanistic regeneration simulator should simulate important ecological relationships and disturbance effects. Development of such a regeneration simulator is complex because of the many attributes that characterize reproductive strategies and the importance of forest history and disturbance in determining the composition of the next forest. We are constructing a model of tree regeneration based on the requirements of different tree species and the potential pathways by which available species might regenerate. This rule-based Mechanistic Origination Model (MOM) combined with a gap-phase model that includes disturbance processes (Phase 2) will be used to predict the migration of tree species for the central hardwood region of the United States, and we will progressively apply the same techniques to other regions (eg., northern hardwoods).

We synthesized information from the forest biology and ecological literature to determine a set of tree-regeneration attributes that would be applicable to a wide range of forest types. These attributes are important in the colonization or revegetation of forests during the gap phase of forest development. Twenty attributes representing flowering, seed production, seed dispersal, seed dormancy, germination, and survival were used to create a matrix of categorical data suitable for classification analysis. We evaluated these attributes for 62 tree species in the central hardwood region of the eastern deciduous forest of North America. We used classification analysis to delineate guilds of species with similar regeneration attributes over a wide range of categories. The guilds represent niches in the central hardwood forests; species within the guilds have similar regeneration attributes such as dispersal mechanisms, time of flowering, and requirements for germination.

We expected that species within guilds would exhibit similar regeneration behavior and that a guild would have a common pathway through the regeneration process. However, this was not the case. Although species within guilds do have similar regeneration attributes, the regeneration behavior or pathway of a species at a given place and time depends on forest history and type of disturbance that incites a regeneration event. For example, a species may respond differently to overstory removal than to a ground fire. The common element here is not the nature of the species but the characteristics of the disturbance. Stated another way, common pathways by which regeneration occur depend on the disturbance (its effect and scale) and the conditions at the time of disturbance. The pathway by which regeneration and recruitment occur depends on both species attributes and the nature of the disturbance.

The needs of the model were defined by our understanding that common pathways driven by disturbance determine regeneration outcomes. First, we are defining the potential pathways. Then, for each pathway, we are determining the attribute thresholds for species that could follow that pathway. Examples of attribute thresholds include the amount of light at the forest floor and soil and moisture requirements. Finally, to model regeneration, we also must model disturbances since these alter site attributes. In Phase 2, plot status information that MOM requires (eg., quantity of light on the forest floor, seedbed condition, number and species of seed producing trees and number and species of sprouting-capable trees) will be calculated at least each year and after each disturbance event.

TREE GROWTH AND DEVELOPMENT

Phase 1 and Phase 2 are highly interactive, and Phase 2 simulates the growth and development of trees. Several models were evaluated on the basis of whether they were parameterized for the entire United States, their sensitivity to climate change and the ability to predict annual diameter growth and mortality of each tree. The gap model ZELIG was chosen, which relies heavily on monthly climatic conditions and may be easily modified for site specificity. ZELIG has been streamlined by eliminating many of the diagnostic print and screen displays, which will allow the program to update the many thousands of Forest Inventory Analysis (FIA) plots efficiently in Phase 6. We are replacing the REGEN subroutine of ZELIG with MOM to create MOM/Z (Figure 1). For MOM to work in this context, disturbance routines are being added to ZELIG to provide simulations of the many conditions that can stimulate regeneration. Parameters controlling the probable frequencies and intensities of these disturbances are easily modified to simulate different

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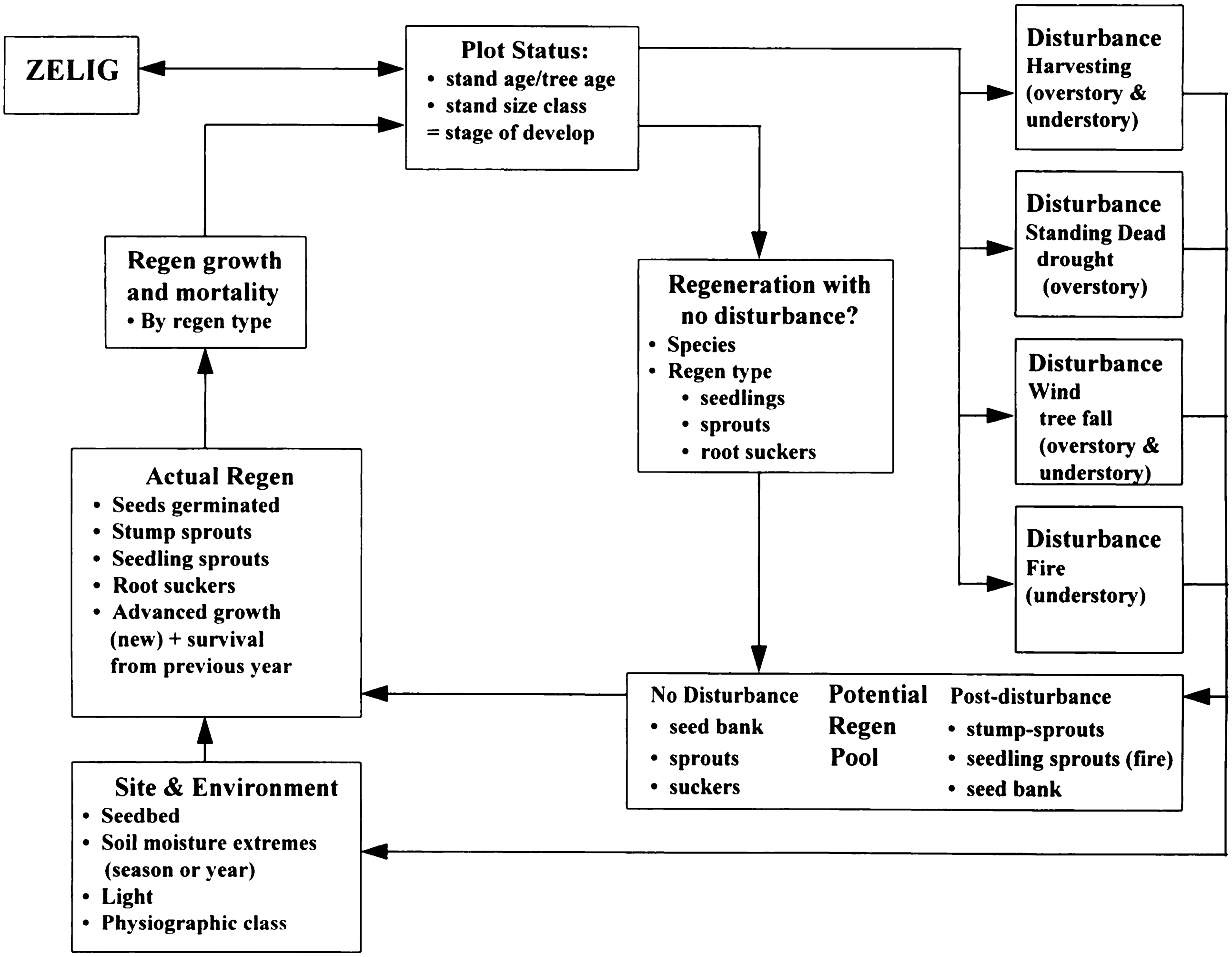

Figure 1.—Flow diagram of the Mechanistic Origination Model (MOM) to be used with the ZELIG gap-phase model modified to simulate disturbance events. ZELIG will provide plot status information that MOM requires (eg., quantity of light on the forest floor, seedbed condition, seed producing trees, sprouting-capable trees) at least each year and also after each disturbance event.

management strategies. We are in the process of adding harvesting, fire, and windthrow disturbance algorithms to the model which are regionally specific. This will facilitate the replacement of ZELIG's recruitment algorithm with the MOM regeneration algorithms. The use of MOM will avoid the unrealistic assumption of gap models that all species are able to regenerate on each site.

POTENTIAL TREE MIGRATION RATES ACROSS A FRAGMENTED LANDSCAPE

In Phase 3, or MYGREAT, we determine maximum tree migration rates in response to a changed climate. Examinations of the relationship between current plant distributions and climate suggest that a northward distributional shift of 400-800 km will be required for many species. Holocene reconstructions of past tree migrations provide a model for how fast trees may be able to respond to climatic change. These historical studies suggest that trees will not respond at rates of more than 50 km per century, or about an order of magnitude slower than may be required to keep pace with future warming. The historical model, however, may not represent an accurate prediction of future response, because the data generally record trees moving across a mostly forested landscape. The current landscape is much more fragmented, with environmental barriers and a matrix of low quality habitat reducing potential migration rates. We use a simulation model to predict the ability of trees to migrate in response to climatic change under various conditions of habitat availability. The model uses Holocene tree migration rates to approximate maximum migration rates in a forested landscape. Habitat availability and local population size are varied systematically under two dispersal and colonization models. The underlying dispersal models varied in the likelihood of long-distance dispersal. The results of the first model indicate that migration rates could decline

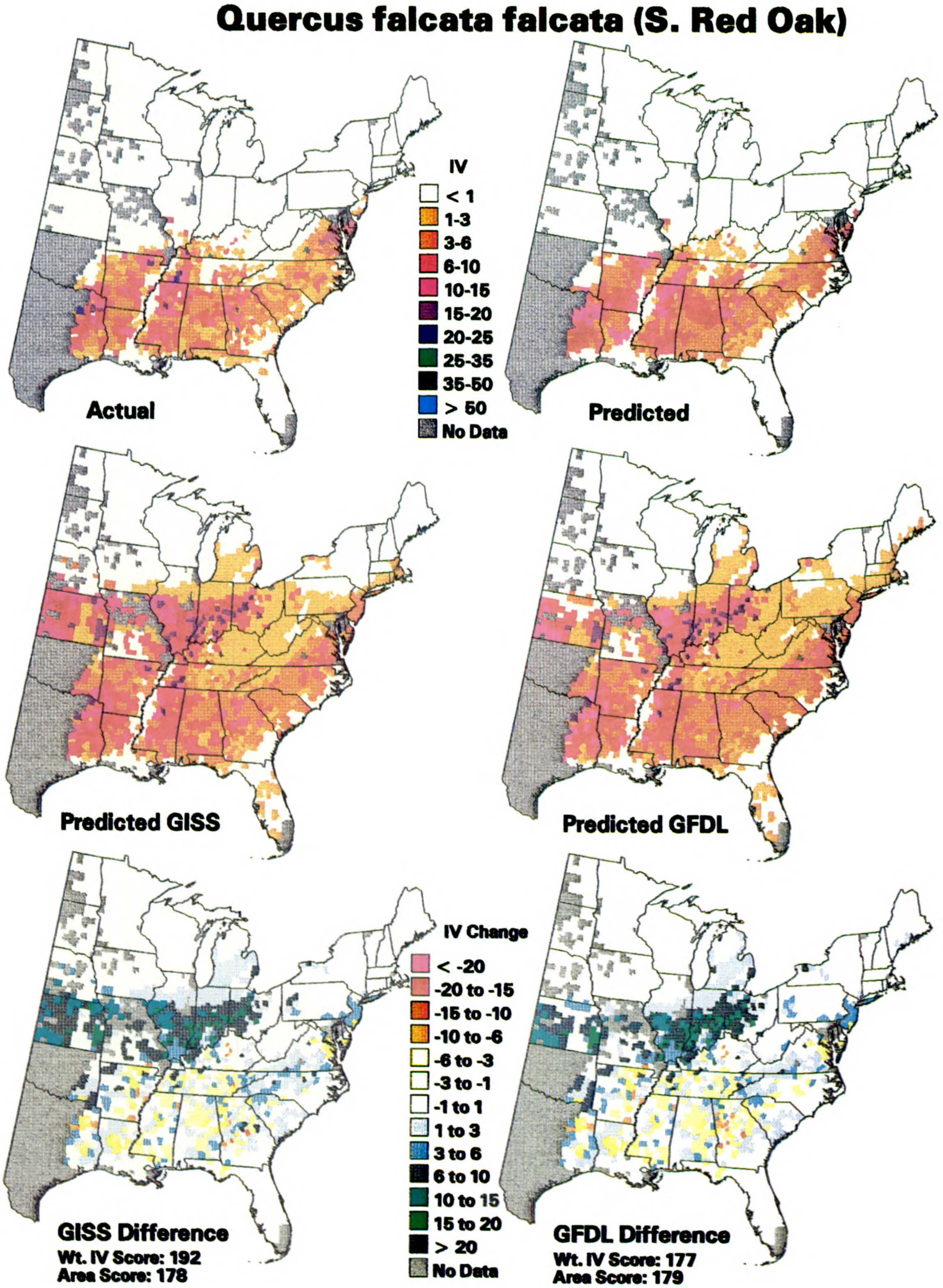
Quercus falcata falcata (S. Red Oak)

Figure 2.—Example model outputs for *Quercus falcata* var. *falcata* (southern red oak), including: a) actual county importance values as calculated from FIA data; b) predicted current importance values from the RTA model; c) predicted potential future importance values after climate change according to the GISS GCM; d) predicted potential future importance values after climate change according to the GFDL GCM; e) and f) difference maps showing potential change in importance values for the GISS and GFDL maps, respectively.

by an order of magnitude where habitat availability is reduced from 80% to 20% of the landscape. The second model, using an inverse power function, carried a higher probability of long-distance dispersal events. The results from this model predict relatively small declines in migration rates when habitat availability is reduced to 50% of the landscape, but mean migration rates for lesser forest areas are similar to those of the first model. Initial results predict maximum migration rates of 1-10 km per century when habitat availability is less than 30%.

We now are refining the model to run on a real landscape, the state of Ohio, with a cell resolution of 1 km by 1 km. We have computed the percent forest cover by cell with classified Landsat TM data (overall forest cover = 30%), and used this as an indicator of habitat availability for the model. For comparison, we ran the same model with the Ohio landscape as it existed prior to European colonization (overall forest cover > 95%). The model has been run for four species that have their northern limits in Ohio: yellow buckeye, southern red oak, Virginia pine, and persimmon. The fragmented nature of today's forest significantly slows the migration potential, according to the model outputs. The next phase is to revise the model to run at the scale of the Eastern United States.

CURRENT AND POTENTIAL DISTRIBUTIONS OF TREE SPECIES

An envelope analysis of current tree species ranges with environmental variables was needed to establish bounds on the migration and regeneration potentials mentioned above. In Phase 4, the DISTRIB component, we relate current tree distributions to associated environmental variables, and then change the climate to model the potential future tree distributions. Two main assumptions are made for this model: (1) the tree will get there if conditions are suitable, i.e., there are no barriers to migration, and (2) the current distribution defines the range of conditions possible for the species to grow. We have collected, summarized, and analyzed data for climate, soils, land use (including the spatial configuration among land use types), socio-economic factors, and species assemblages for over 2,100 counties east of the 100th meridian. FIA data for over 100,000 forested plots in the East provided the tree species range and importance values information for 103 species of trees. Regression tree analysis (RTA) is being used to devise prediction rules from current species-environment relationships, which are then used to replicate the current distribution as well as predict the future potential distributions under two scenarios of climate change with 2xCO_2 (Figure 2). Validation measures prove the utility of the RTA modeling approach for mapping current tree importance values across large areas, leading to increased confidence in the future predictions. Although these future predictions do not address the fate of species migrating through fragmented landscapes, they do give an idea of the basic envelope to which the species may be adapted should no restrictions to migration apply. Graphical outputs from RTA, combined with the predicted tree species distribution maps in GIS, provide a powerful means of understanding the relationships among various factors associated with tree species distributions.

CURRENT AND POTENTIAL DISTRIBUTIONS OF SELECTED ANIMAL SPECIES

Paleontologists have dated the presence and location of certain mammal species back to the Pleistocene Epoch (approximately 10,000 - 11,000 years ago). Distribution ranges of species have been formed from this and other paleoenvironmental data to demonstrate range changes using the geologic clock. In Phase 5, habitats are being characterized for 10 of the mammals that have exhibited range changes due to historical changes in the environment and that currently populate OH, KY, IN, and IL. At the county level of scale, we are evaluating relationships between current distribution ranges of the mammals and the current environmental picture which includes the derived importance values of tree species as developed in phase 4. Land use and human population density will be evaluated for spatial patterns across the region that will help to geographically characterize mammal habitat. In an attempt to relate the habitat characterizations of current mammal ranges with historical and potential ranges, we will also factor temperature and precipitation into the analyses. Canonical correspondence analysis was used to relate mammal presence or absence data with the derived environmental factors since no single environmental factor has been shown to characterize mammal habitat.

PREDICTED DISTRIBUTION OF TREE AND SELECTED ANIMAL SPECIES UNDER GLOBAL CHANGE

In Phase 6, the general approach will be to initiate MOM/Z using Forest Inventory Analysis (FIA) plots, and run simulations using local climate estimates derived from mesoscale climate models of 2xCO_2 GCMs. Using these simulations, we will evaluate potential species shifts for each county. This effort, in conjunction with the effort to understand the role of fragmented habitats and potential distributions, will help elucidate likely patterns in tree species migration and associated ranges of mammal species.