ecological interactions. Some combined models evaluate consequences of particular foraging preferences or functional responses. Other models assume that foragers respond optimally to varying prey density, to predict effects of adaptive behavior on community stability. The body of results is complex; this section lists only a few prominent lessons.

Suppose that an individual forager's effect on the prey population's growth declines as prey density increases. The consequent decelerating functional response does not tend to reduce density fluctuations in a consumer–resource interaction. However, a sigmoid functional response accelerates at intermediate prey densities, so that the prey mortality imposed by each forager increases with the density of prey. Hence, at some prey densities a sigmoid functional response can stabilize population dynamics. When a consumer population preys on two species, a sigmoid functional response can arise if foragers switch between resources and so concentrate predation on the more common prey. Predator switching can, therefore, stabilize the three-species interaction. When a switching predator prevents one prey species from excluding another competitively, the predator's impact is termed a keystone effect.

Dynamical consequences of foraging preference, and its impact on details of the functional response, have been deduced in analyses of three-species food chains. A resource is exploited by a consumer that, in turn, is exploited by a third species. The third species might be an omnivore (exploiting both the resource and the consumer) or a top predator specializing on the consumer; omnivory should exert the greater stabilizing influence on density fluctuations.

Parasitoids often exploit a host population with a highly clumped spatial distribution; many patches contain few hosts, and some patches contain many hosts. An inefficient forager fails to respond to host spatial heterogeneity, while an optimal forager searches patches with the greatest host density. In models of this interaction, optimal patch use by the parasitoid tends to stabilize the densities of the two species. Finally, consider a predator with access to two prey species of differing profitabilities. Suppose that the contingency model's average rate of energy gain enters the dynamics as a component of both prey mortality rates and the predator's birth rate. The predator always includes the prey of higher profitability in its diet. It adds or drops the second prey as the density of the preferred prey changes, according to the optimal diet's choice criterion. The resulting pattern of prey consumption does not tend to stabilize the dynamics,

and it can be destabilizing. In general, adaptive foraging may or may not promote stable ecological interaction; predictions—not surprisingly—depend on model details.

SEE ALSO THE FOLLOWING ARTICLES

Behavioral Ecology / Energy Budgets / Evolutionarily Stable Strategies / Predator–Prey Models

FURTHER READING

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FOREST SIMULATORS

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Forest simulators are computer models used to predict the state and dynamics of a forest. As such, forest simulators are on the more complex end of ecological models, both because of the inherent complexity of forest communities and because these models are typically focused on predicting real assemblages of trees, not abstract "forest vegetation." Diverse motivations have driven the development of forest simulators, but the objectives fall into two general classes: (1) to test and extend ecological theory and (2) to predict responses to management action and environmental change. Increasing scientific concern with climate change and the role of forests in global C and N cycles, together with advances in computational power and modeling, are increasing the importance of forest simulators as predictors of forest responses.

OBJECTIVES OF FOREST SIMULATORS

Forest simulators serve to synthesize our reductionist information about how forests work into a coherent,

quantitative framework that can predict mechanistically based on first principles and permit us to verify that inclusion of all the "parts" we study in detail allows us to reconstruct the "whole." In this regard, forest simulation can drive theory by forcing us to codify our assumptions, allowing data–model mismatch to identify false assumptions or understudied processes. A related goal has been to test theoretical predictions about forest dynamics with data from specific systems. Examples include investigating different theories of species coexistence and the roles of disturbance and site history in forest dynamics.

Beyond theory, forest simulators also play an important role in management and policy. A number of applied forest simulators are routinely used to predict growth and yields, such as the U.S. Forest Vegetation Simulator (FVS) and the Canadian Tree and Stand Simulator (TASS). These tend to be far ahead of most ecological models in terms of the diversity of factors they include that impact forest growth, but they also suffer the problem of overparameterization, which leads to high forecast uncertainty. The incredibly high data demands for fully calibrating such models means that they are regularly used with default parameters that may not be appropriate for a given site or situation. In the last few decades, there has also been an explosion of forest simulation research focused on global change issues. The goal here is to make projections that help clarify the potential impacts of global change on forests, such as the change in ecosystem services or the loss of biodiversity, and equally importantly to characterize feedbacks from forests to the climate system via energy, water, and carbon fluxes. These global change applications share the goals of informing policy and management and prioritizing directions for further research. Finally, a more recent application of forest simulators has been in data assimilation, where the goal is to estimate the current state of the forest, rather than some future state, given the constraint of incomplete data. For example, a forest simulator might be used to estimate the structure of a forest that would be compatible with an observed lidar profile and then to make inferences about the likely range of values for other stand properties.

CLASSES OF FOREST SIMULATORS

Forest simulators encompass a wide range of models dealing with different ecological processes and operating across a large range of spatial and temporal scales. While there are exceptions, most forest simulators can be divided into two groups, one that is focused on community ecology and the other on ecosystem ecology.

Within the first group, forest simulation is dominated by a class of models generally referred to as gap models because of their origin in simulating forest gap dynamics, the dominant disturbance for many forest types. Gap models originated in the early 1970s with patch-based models such as JABOWA and FORET that accounted for the height-based competition for light among trees of different sizes and species. These models generally predict dynamics driven by growth rate and shade tolerance, with fast-growing but shade-intolerant early successional species giving way over time to slower-growing but shade-tolerant late successional species. The 1990s saw the development of truly spatially explicit, individual-based forest simulators such as SORTIE. In these models, the crowns of individual trees interact with each other in three dimensions and the understory light environment is more heterogeneous, driven by the overlap of the shadows cast by each individual tree. Similarly, in these spatial individual-level models, seed dispersal becomes an explicit two-dimensional process, with models differing as to whether they treat dispersal from a Lagrangian (individual seed, e.g., SORTIE) vs. Eulerian (seed density, e.g., SLIP) viewpoint. In addition to the spatially explicit IBMs, there are also a number of landscape patch models, such as LANDIS, that take a simpler representation of each individual patch but which represent the broader scale interactions of vegetation with the abiotic environment and which are often focused on broad-scale spatial-pattern and disturbance feedbacks.

In contrast with community-focused gap models are ecosystem-focused forest simulation models. These models are focused primarily on fluxes and pools of carbon but may represent other biologically important cycles as well, most commonly water and nitrogen. Forest ecosystem models tend to be much simpler in terms of their representation of interactions among individuals but more complicated in their representation of physiological processes, such as photosynthesis, carbon allocation, and respiration. These models are also more likely to represent belowground processes such as rooting, soil moisture, and soil biogeochemical cycles. There is a much wider range of spatial and temporal scales represented in forest ecosystem models than in forest community models, from individual trees up to the globe and from near instantaneous in time to millennial. That said, the biological processes involved tend to have particular scales they operate at, and thus models are generally built around specific spatial and temporal scales. Indeed, some of the major remaining challenges in forest modeling—both conceptually and computationally—revolve around scaling.
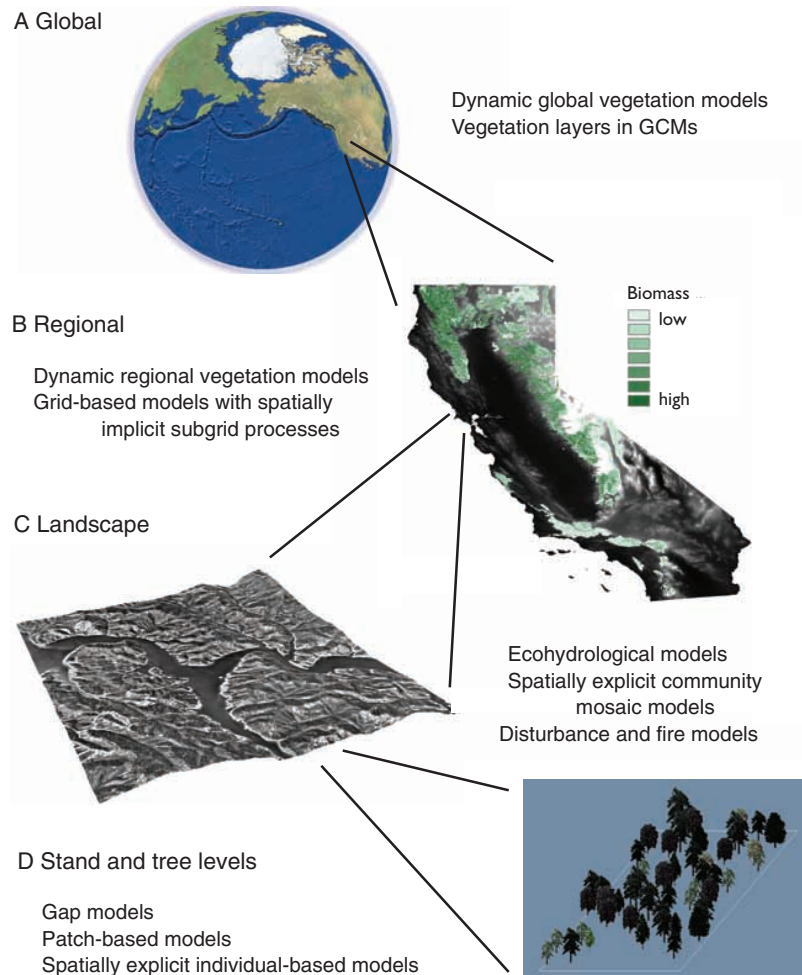
SPATIAL SCALES

Individual Scale

The spatial scales represented explicitly by forest models range from <1 m to global (Fig. 1). At the finest spatial scales are the spatially explicit individual-based models, such as SLIP and SORTIE, that represent the exact location of individual trees and the spatial interactions between trees. The primary focus of these models is competition for light, which is the limiting resource in most forests and which drives interspecific and intraspecific interactions, tree growth patterns, and demography. Fine-scale processes include the 3D representation of light based on ray-tracing algorithms, which are particularly important for capturing the high degree of heterogeneity in the light environment of forest gaps (Fig. 2). Also occurring at a fine scale is crown competition, 2D seed dispersal, and density-dependent interactions in the youngest life history stages
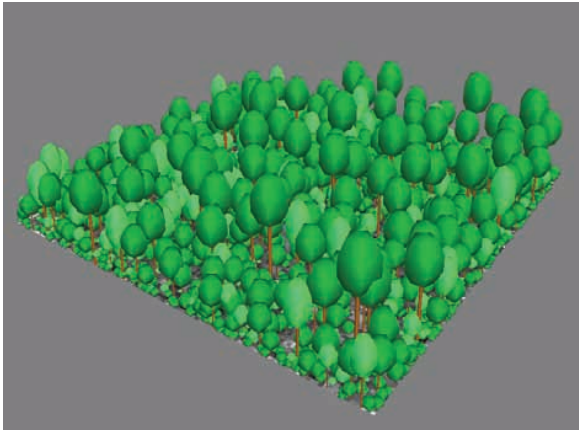
(e.g., seed bank, seedlings). The focus of these models has thus far been on autogenic fine-scale heterogeneity, rather than fine-scale exogenous heterogeneity in soils or topography, as a mechanism for promoting coexistence.

Patch Scale

The next spatial scale represented by forest models is the "patch" scale, which is on the order of 10–30m in diameter depending on the model, thus encompassing several to dozens of individuals in what is assumed to be a locally homogeneous, common environment. Patch-based models average over the fine-scale variability of spatially explicit models, and the size of patches are set assuming that every individual within a patch is able to compete with every other and that the mortality of the dominant canopy tree is sufficient to convert a patch to a forest gap. Light within a patch-based model is usually represented by a vertical

A Global

Dynamic global vegetation models
Vegetation layers in GCMs

B Regional

Dynamic regional vegetation models
Grid-based models with spatially
implicit subgrid processes

Biomass
low
high

C Landscape

Ecohydrological models
Spatially explicit community
mosaic models
Disturbance and fire models

D Stand and tree levels

Gap models
Patch-based models
Spatially explicit individual-based models

FIGURE 1 Spatial scales addressed by different classes of forest simulators: (A) global vegetation; (B) regional vegetation or forest; (C) landscapes; and (D) forest stands and individual trees.

FIGURE 2 Visual representation of forest dynamics in the spatially explicit forest simulator SLIP.

gradient, in which case these models tend to overestimate light levels in gaps, though some models do consider the shadow cast by each patch onto neighboring patches.

The patch is the fundamental scale for a large fraction of models from both the community and ecosystem perspectives, with one key difference: community models are still individual based and thus include multiple trees of multiple sizes and species within a single patch, whereas ecosystem models are based on aggregate carbon pools of a single plant functional type. One ramification of this difference is that while community models will have multiple canopy layers, ecosystem models typically have either a single layer of foliage, often referred to as the "big leaf," or two layers of foliage, representing the functional difference in leaf structural and photosynthetic properties between sun-leaves and shade-leaves. Another key difference in the two modeling approaches at this scale is that because community models are individual based they are focused on the demography of individuals. This means that the fundamental dynamics are conceived in terms of individual demographic responses: the growth rate of a tree based on its size, species, and light environment, the fecundity of individual trees as a function of size and sometimes growth, and the mortality of whole individual trees as a function of growth rate. The inclusion of individual mortality means that almost all forest community models are stochastic, while ecosystem models are almost all deterministic. A consequence of this is that community modelers usually analyze models based on runs with large numbers of patches to average over stochastic dynamics, whereas ecosystem models usually have just one patch in which mortality is simply a deterministic "coarse litter" flux term.

Landscape Scale

The next scale up above patches is the landscape scale (Table 1). The spatial extent of landscapes can vary considerably, from hundreds of meters to tens of kilometers or more. The critical feature of landscape-scale models is not their absolute geographical extent but rather the fact that they account for environmental heterogeneity among patches and aim to provide insight into the effects of such heterogeneity on community or ecosystem dynamics. This heterogeneity can be in terms of the physical template of the landscape itself (e.g., topography, soils, hydrology, microclimate), anthropogenic heterogeneity in the landscape due to land use and fragmentation, or autogenic heterogeneity generated by large-scale disturbances. There is a greater emphasis in landscape modeling on real landscapes rather than on conceptual ones, which are common in gap models that are often focusing on more theoretical questions about the process of succession and community assembly. With this focus on real landscapes also comes a greater emphasis on applied problems and management. A frequent "natural" extent for landscape models is the watershed. Landscape-scale models are most often community focused (e.g., LANDIS, MetaFor), though there are also a number of landscape-scale ecosystem models (e.g., RHESSYS, ForClim), the majority of which are coupled to watershed hydrology models to address ecohydrological questions. Another common feature of landscape models is that there is greater emphasis on spatially contagious processes such as disturbance and dispersal. The most studied of these processes is fire; there are many forest landscape models coupled to fire models that range in complexity from simple "contagious" process models to very detailed mechanistic models of fire spread and intensity (e.g., BEHAVE, FIRE-BGC). While the fundamental unit in landscape models is the patch, the representation of processes within each patch is often simplified compared with patch-scale models. Landscape-scale models are often operating at a spatial scale that encompasses thousands or more patches and necessarily focuses on the distribution of vegetation types and stand ages across patches, rather than the states and dynamics of individual patches. In applying landscape models, users typically assume that they are large enough that the states of constituent patches reach a steady-state distribution (i.e., Watt's patch mosaic) despite the fact that individual patches are far from equilibrium.

Regional to Global Scale

Above the landscape scale are models that take a regional to global perspective on forest dynamics. The questions driving research at this scale primarily surround climate

TABLE 1
Classification of models discussed in the text

Model	Spatial Scale	Temporal Scale	Phenom. or Mechanistic	Descriptive or Predictive	Deterministic or Stochastic	Point or Areal
SLIP (Scaleable Landscape Inference and Prediction)	Individual	Annual	Phenom.	Proscr.	Stochastic	Area
SORTIE	Individual	>Annual	Phenom.	Proscr.	Stochastic	Area
TASS (Tree and Stand Simulator)	Individual	Annual	Phenom.	Proscr.	Stochastic	Area
JABOWA (concatenation of authors Janak, Botkin, Wallis)	Patch	Annual	Phenom.	Proscr.	Stochastic	Point
FORET (Forests of Eastern Tennessee)	Patch	Annual	Phenom.	Proscr.	Stochastic	Area
FVS (Forest Vegetation Simulator)	Patch	>Annual	Phenom.	Proscr.	Stochastic	Point
LANDIS (Forest Landscape Disturbance and Succession)	Landscape	>Annual	Phenom.	Proscr.	Stochastic	Area
MetaFor (Forest Meta-model)	Landscape	Annual	Phenom.	Proscr.	Stochastic	Area
RHESSYS (Regional Hydro-Ecologic Simulation System)	Landscape	Daily	Mech.	Proscr.	Determ.	Area
ForClim (Forests in a changing Climate)	Landscape	Monthly	Phenom.	Proscr.	Stochastic	Point
LPJ-GUESS (Lund-Postdam-Jena General Ecosystem Simulator)	Globe	Daily	Mixed	Proscr.	Stochastic	Avg. point
Hybrid	Globe	Daily	Mech.	Proscr.	Stochastic	Avg. point
ED (Ecosystem Demography)	Globe	Subdaily	Mech.	Proscr.	Determ.	Area
CLM (Community Land Model)	Globe	Subdaily	Mech.	Proscr.	Determ.	Wt. point
Sheffield DGVM (Dynamic Global Vegetation Model)	Globe	Daily	Mech.	Proscr.	Determ.	Wt. point
Orchidee (Organizing C & Hydrology in Dynamic Ecosys.)	Globe	Subdaily	Mech.	Proscr.	Determ.	Wt. point
LPJ (Lund-Potsdam-Jena)	Globe	Daily	Mech.	Proscr.	Determ.	Wt. point
Biome-BGC (Biome BioGeochemical Cycles)	Globe	Daily	Mech.	Proscr.	Determ.	Point
CASA (Carnegie-Ames-Stanford-Approach)	Globe	Monthly	Mech.	Descr.	Determ.	Point

NOTE: Many additional excellent models exist in every category. Spatial scale generally refers to the broadest spatial extent the model is designed to run at, though the individual-based models (IBM) typically function at the scale between patch and landscape. Temporal scale refers to the time step of the model. For point vs. area, wt. point refers to models that have multiple points within a grid cell that are weighted by their proportional area while avg. point refers to models that have multiple stochastic replicates within each grid cell that are averaged. See the text section "Process Representation in Forest Simulators" for discussion of other groupings.

change impacts on the carbon cycle and to a lesser extent on biogeographic/biodiversity issues, though these are usually resolved only to the level of biome or plant functional type rather than to species (e.g., Community Land Model, Sheffield DGVM, Orchidee, LPJ). These models all have an ecosystem component, and only a small subset considers community processes (e.g., ED, LPJ-GUESS). However, there is a growing recognition that disturbance history and successional processes can strongly influence the carbon cycle. These models are typically run on a grid where the grid cells are often much larger in extent than the landscapes in the landscape models. When these models include processes at individual through landscape scales, they must represent them as spatially implicit subgrid processes. For example, in the Ecosystem Demography (ED) model forest stands of different ages are not given spatial locations but are represented by the proportion of the landscape that is in each age class.

Since most global models are based on deterministic ecosystem models, the dynamics of these grid cells are essentially identical to that of a single patch or a weighted average of noninteracting patches representing different plant functional types. Models at this scale include the dynamic global vegetation models (DGVMs) that represent the terrestrial ecosystems in general circulation models (GCMs). While these global models are no longer strictly forest models, almost all originated as forest models (e.g., Forest–BGC evolved into Biome–BGC) and were later modified to incorporate other vegetation types. Because of the emphasis on global change within this research community, there have been a much larger number of model intercomparison projects focused on these models than on other classes of forest models. These include early efforts such as VEMAP (Vegetation/Ecosystem Modeling and Analysis Project) and VEMAP2 focused on the continental United States as well as more recent intercomparisons such as the global scale C4MIP (Coupled Carbon Cycle Climate Model Intercomparison Project), the LBA (Large Scale Biosphere Atmosphere) focused on Amazonia, and the two NACP (North American Carbon Program) intercomparison projects, one focused on the continental scale and the other on site-level comparisons to the Ameriflux network.

TEMPORAL SCALES

Forest models resolve processes that range in temporal scale from the near instantaneous to the millennial. Because the

processes involved in community models are essentially demographic, they tend to focus on a narrower range of time scales, from annual to centennial. In contrast, all ecosystem models resolve intra-annual dynamics and some resolve subdaily processes down to a very fine scale. There are two reasons for forest models to resolve processes at subdaily scale. The first reason is to capture the diurnal cycle of photosynthesis using mechanistic photosynthesis models that are driven by instantaneous values of light, temperature, humidity, CO_2, and wind speed. Since these mechanistic models are nonlinear, photosynthesis models operating at a coarser time step either have to make approximations based on an "average" day or use more empirical relationships. The second reason for subdaily modeling is to explicitly resolve the mass and energy budgets of the land surface. These budgets are calculated using a class of process models referred to as land surface models that include a large number of environmental processes beyond the strictly ecological (e.g., boundary layer mixing, snow physics, hydrology, and so on). The primary motivation for including a land surface submodel within a forest ecosystem model is to be able to couple the ecosystem model with an atmospheric model, which requires a lower boundary condition for the land surface. By operating at fine temporal scale and by including atmospheric, vegetation, and hydrological processes, land surface models aim to capture the turbulent mixing and other energy flows that mediate feedbacks among the soil, vegetation, and the atmosphere that are vital to climate projections and to understanding the role of forests in global climate.

At daily to monthly time scales, the processes resolved by forest models are ecophysiological in nature, such as photosynthesis, respiration, carbon allocation, phenology, decomposition, and biogeochemical cycling. Models that have a daily or monthly time scale as their smallest time step typically resolve an explicit mass balance but assume that the energy budget is controlled by some external meteorological driver. At annual to multiannual time steps, forest models typically resolve growth, mortality, reproduction, and disturbance. For most ecosystem models these processes are not resolved explicitly, while for most forest community models this represents the fundamental time step and these processes are the basis for their dynamics. Since most community models ignore intra-annual processes, their calculations for demography are typically based on data-driven empirical relationships rather than physiology. As such, community models are often more constrained to field data, especially with respect to long-term dynamics, but because they generally rely on correlations rather than well-defined mechanisms,

they are less suitable for extrapolating responses to novel changes in the environment drivers or novel combinations of environment variables. In contrast, mechanistic ecosystem models are more robust to extrapolation to different conditions, but they often fail to represent long-term dynamics both because they do not include the successional processes that dominate long-term dynamics and because they are often only calibrated to short-term data.

PROCESS REPRESENTATION IN FOREST SIMULATORS

Beyond space and time, forest models can also be classified by how they represent different processes. Below are presented four important contrasts in model dynamics: phenomenological vs. mechanistic, descriptive vs. predictive, stochastic vs. deterministic, and point-based vs. area-based.

Phenomenological vs. Mechanistic

As alluded to above, the phenomenological/statistical versus mechanistic/physiological dichotomy in many ways reflects the community/ecosystem distinction, but it is more useful to view this as a continuum because at some scale of biological organization all our ecological models are phenomenological and within ecosystem models there is a good bit of variability in how different processes are represented. However, the crux of the distinction lies in whether tree growth is based on correlations with environmental variables or on mechanistic representations of NPP/photosynthesis because this distinction largely determines our degree of belief in extrapolating to novel conditions. In principle, other demographic transitions might also be modeled mechanistically, but in fact mechanistic models for mortality simply do not exist, and those for fecundity are rare and difficult to parameterize. The link between growth and productivity is largely one of mass balance—a given amount of net carbon uptake translates into a given amount of growth, and the only real issue is allocation. Mortality, on the other hand, is a complex and multifaceted phenomenon that is often gradual, with many drivers, feedbacks, and lags. Typically, forest gap models assume that mortality is a function of growth rate and disturbance, while in ecosystem models mortality can be as simple as assuming some constant background rate. Beyond mortality and growth, fecundity can be either phenomenological or mechanistic (usually some fixed fraction of NPP), but in either case it is usually poorly constrained to data.

In theory, dispersal can be either phenomenological or mechanistic, though in practice we are unaware of a

forest model that has been coupled to a mechanistic dispersal model, but this is bound to happen soon due to their increasing popularity. Mechanistic dispersal models are of varying complexity, but all are fundamentally based on wind speed and seed drag or on movement patterns of animal dispersers. Phenomenological dispersal models, on the other hand, are all based on dispersal kernels, which are probability density functions that give the probability a seed will travel a given radial distance from the parent. Either way, data and theory suggest long-distance dispersal (LDD) is a highly stochastic and inherently unpredictable process. One reason for the use of mechanistic dispersal is that LDD is almost impossible to determine from seed trap data. While the role of LDD in community dynamics is well recognized, its importance for ecosystem responses is less well understood—most large-scale models lack explicit dispersal but instead assume one of two extreme cases that define the endpoints in LDD: (i) new seed is available at all places at all times and thus dispersal is not limiting or (ii) all seed rain is local.

Descriptive vs. Predictive

Another important dichotomy is between models that are descriptive versus predictive. Predictive models attempt to predict biotic responses given a set of initial conditions and meteorological drivers and thus can be run into the future conditioned on meteorological scenarios. Descriptive models, on the other hand, typically require other biotic variables to be specified as drivers. Most commonly these are remotely sensed data, such as LAI, fAPAR, albedo, and the like. Because these models are more constrained by data, they are expected to do a better job of diagnosing unobserved biotic variables. For example, atmospheric inversion models such as the CarbonTracker typically base their continental-scale ecosystem carbon fluxes on descriptive models such as CASA. The tradeoff is that such models cannot be run into the future, and thus climate change forecasts are all based on predictive models.

Stochastic vs. Deterministic

A third contrast is between stochastic and deterministic models. As mentioned above, most ecosystem models are deterministic and most community models are stochastic. This difference is due to mortality and the spatial scales of the models. In fine-scale models, the death of an individual tree is an all-or-nothing event and has a large impact on the microenvironment, and thus these deaths are represented stochastically. In broad-scale models, in contrast, mortality is often modeled as a carbon flux term. Since the fine-scale dynamics of individual tree mortality and gap dynamics are thought to play a large role in overall forest structure and composition, the failure to represent these gaps is one of the main limitations of deterministic ecosystem models at long time scales. The approaches to accommodate this scaling problem can be divided into two categories. First, there are ecosystem models, such as LPJ-GUESS and Hybrid, that are coupled with stochastic gap models and scale up by sampling (i.e., running a large number of replicate stochastic patches). Second, there is the Ecosystem Demography model (ED) and models derived from the ED that treat mortality as a deterministic process and accommodate this by explicitly modeling the distribution of stand ages across the landscape. In essence, mortality is thought of as affecting some fraction of each patch in each year, which is reset to a stand age of 0, while the remainder of the patch does not experience mortality. Simulations with a stochastic version of ED show that the deterministic approach accurately captures the mean of the stochastic version and also is more efficient and tractable, as demonstrated in work by Moorcroft and collaborators (2001).

Point-Based vs. Area-Based

The final contrast considered here is between point-based and area-based models and has to do with how models represent space. Most regional/global models are actually point or patch models that are 0D or 1D (vertically structured) and are simply run on a grid (models represent the nodes on the grid). A few contain spatially implicit subgrid processes, where different patches within a grid cell represent different fractional areas, and thus could be considered to be quasi-area-based. Stand level models are area based in terms of a grid of patches (where each patch truly fills the area allocated to it) or are IBM that are spatially explicit and represent area in 2D or 3D. Landscape models fall in between in that they are explicitly based on a map of polygons or grid cells but these grid cells can start to get too big to represent every tree in them or to safely assume all trees within a cell are interacting. Understanding how a model represents space affects how processes scale in the models, what data can be used to calibrate or test the model, and how we interpret model parameters and model dynamics. For example, a leaf property such as maximum photosynthetic rate means very different things if it is referring to an individual leaf on a tree, the whole forest canopy within a patch, or the aggregate carbon uptake across a 1×1 degree lat/lon grid cell.

DISTURBANCE AND STEADY STATES

A number of disturbances have been included in forest models, the most common being gap phase disturbance, from which gap models derive their name, and fire. Gap phase disturbance can either be autogenic, driven by the mortality of a large adult tree, or externally generated by windthrow or ice storms. As mentioned above, fire models vary enormously in their complexity from simple contagious processes to complex simulations. A number of other disturbances are also included sporadically in different models, such as land-use/land-change, droughts, insects, and pathogens, but overall these have received far less attention than fire and gaps.

One of the reasons the representation of disturbance is so critically important to forest models is that they have such a large impact on if and when an ecosystem reaches steady state. Most community-focused models do not assume that the system is at equilibrium at the start of a run since they are interested in the transient dynamics. Community models often start from bare ground or (less often) from some observed or "typical" composition/structure. That said, community models are often run out to some steady state with a lot of emphasis placed on what that steady state is (despite the fact that there's very little information to judge if the steady state is correct). This is in part a reflection of their conception around questions of long-term coexistence. As the spatial scale increases, more and more models use "steady state" as the initial condition for the computer experiments. This is done even when there is widespread recognition that a particular system is not in steady state (and open debate as to whether any ecosystem ever is in steady state). There are two interconnected reasons for this. First, at broad spatial extents datasets do not exist to serve as the initial conditions. There may be partial information from inventories or remote sensing, but many state variables are unconstrained, especially soil properties such as carbon and nitrogen content. The second reason for a steady-state assumption at a broad scale is that models at these scales generally do not explicitly represent successional dynamics and subgrid (landscape, patch) heterogeneity. Current research into ecological data assimilation is in its infancy, one of its goals is to get around the equilibrium assumption at these scales and to acknowledge the impact of this uncertainty on model predictions. Given what we know about the importance and prevalence of disturbance and transient dynamics in forest community and ecosystem dynamics, this is a vital area of research.

CHALLENGES AND CONCLUSIONS

Forest simulators are likely to continue to play a large role in ecological research for the foreseeable future. Many important basic and applied questions about forest models remain unanswered, and important challenges face model developers. This final section highlights issues believed by the authors to be the most important. In a nutshell, the major challenges for forest simulators are that they are very data intensive, hard to initialize correctly, computationally expensive, lack clear analytical solutions, and face a number of scaling issues, particularly when it comes to bridging the community/ecosystem dichotomy. One unifying characteristic of forest models, whether they are ecosystem- or community-oriented, is that because they are generally aimed at predicting real ecosystems they include a lot of processes and require a large number of parameters. Work by Pacala and colleagues in the 1990s on the SORTIE model was a key turning point in the shift from parameterization of models from "the literature" to being much more data driven and connected to experiments designed with model parameterization as an explicit goal. This is still an ongoing change in perspective, though there is a growing recognition of the importance of formalizing data–model fusion and the propagation of uncertainty through models.

Data for Parameterization and Generalization

One important remaining challenge is to better understand to what extent parameters at one site can be applied to another site. In general, gap model parameters are considered site specific, and for larger models the impact of ecotypic variation is largely unknown. Site-to-site variability is not just a "nuance" parameter for models but has large impacts on our conceptual understanding of how forests work and in testing how general our theories of forest dynamics are. Beyond parameterization, forest models are also data intensive when it comes to initialization and drivers. As discussed in the last section, moving away from simple initial conditions that are either "bare ground" or "steady state" to ones that are based on the current state of specific forests requires large amounts of information. Both community and ecosystem models have so many internal state variables that it is virtually impossible to initialize a model precisely for even a single patch, let alone at broader scales, especially once one acknowledges that empirical measurement error is often nontrivial for many ecological processes (especially belowground dynamics). As ecology moves into a "data rich era" thanks to modern observational technologies (e.g., remote sensing, eddy covariance) and research networks (e.g., NEON, FLUXNET, LTER), these challenges will move from the insurmountable toward the routine as ecologists

become more adept at data assimilation and informatics. This is not to say that we won't always be data limited, but that we will be more sophisticated at dealing with the uncertainties. We expect an emerging focus for forest model research will be on determining the quantity, quality, and type of data required to represent and forecast forest dynamics.

Computation

Beyond data, one of the persistent challenges in forest modeling has been computation. While forest simulators have come a long way since the early days of punch cards, the complexity of our models and the scales that we wish to run them on seems likely to continue to outpace Moore's law. In general, forest models are among the most computationally intensive models in ecology. At fine spatial scales, the inclusion of spatially explicit processes can dominate computation (e.g., light and dispersal can be >95% of the computation) and the algorithms involved get disproportionately slower as the spatial scale increases. For broad-scale models, the sheer size of the simulation is usually daunting. For fast time-scale models, such as coupled ecosystem/atmosphere models that include land surface models, the closure of the surface energy budget is computationally expensive and can necessitate complex dynamic numerical integration routines. In all cases, what underlies this computational demand is the fact that forest models lack an analytical solution and thus need to be understood using numerical experiments. The combination of model complexity and lack of a closed-form solution can make forest models difficult to interpret and hampers the ability to reach broad general conclusions. Progress has been made in finding analytical approximations to forest models, and this is an important area of future research and is also closely related to the issues of scaling and crossing the community/ecosystem dichotomy. Partnerships among ecologists, modelers, and mathematicians will be as important as increasing computer power in making these models more useful and interpretable.

Scaling Issues

The frequent dichotomies in the function of forest models (community/ecosystem, annual/diurnal, fine scale/large scale) arise because the processes that affect overall forest dynamics span such a wide range of scales. For computational reasons, it is often impossible to explicitly represent processes important to one class of dynamics (e.g., the emergence of successional dynamics from tree-to-tree competitive interactions) at broader spatial scales. Indeed, individual-based models seem to be limited to a scale of a few km due to the nonlinear scaling of the

computation involved as much as the sheer number of trees that need to be tracked. Given that upscaling individual-based models, or even patch-based models, to regional and global scales will effectively never be computationally possible, an important unresolved question is in what ways do the broad-scale ecosystem models lose representative and predictive power by excluding finer-scale processes. These processes are, especially, (a) neighborhood competition and gap dynamics, (b) the importance and persistence of nonequilibrium dynamics, and (c) the landscape-scale effects of interactions with the abiotic environment. We cannot solve this problem by brute-force computation, so it is essential to understand, by extensive model comparison, analytical insight, and large-scale field campaigns, what is lost in scaling and to devise new scaling approaches. As mentioned above, there are already a small number of models (LPJ-GUESS, Hybrid, and ED) that explicitly attempt to integrate ecosystem and community perspectives and to bring together processes operating across a large range of spatial and temporal scales, but these are just the start and many opportunities for innovation remain.

Species and Functional Types

Another challenge in bridging the community/ecosystem dichotomy is that most community models are parameterized around individual species, whereas most broad-scale ecosystem models are built around plant functional types (PFTs). While the use of PFTs is in part driven by the computational demands of representing diversity, it is more often a reflection of the availability of data to accurately parameterize models. This data limitation is only in part a reflection of what trees have been studied but is also a function of what data are available to modelers. Although there are a number of plant trait database initiatives in progress, these databases need to be made more public and there needs to be a greater incentive for field researchers to archive and document data and to deposit it in such databases. Only with such data can modelers and functional ecologists assess how best to summarize species to the level of functional type and whether important dynamics are lost in doing so. There also needs to be more concerted effort on gap-filling research to constrain the processes that drive model uncertainties, such as belowground dynamics.

Prospects for Forest Simulators

Forests structure the ecological dynamics of many ecosystems, influence regional-scale weather patterns, and dominate carbon fluxes from terrestrial vegetation. They are also economically important globally and locally,

presenting difficult land management challenges such as those arising from logging and fire policy and enforcement. For these reasons, forest simulators will play an increasingly central role both in forecasting global change and in assessing its impacts on existing forests and management practices. Yet current models, despite their increasing sophistication and power, remain highly data dependent and often make predictions without a robust accounting of uncertainty. Because of this, it remains very difficult to do model intercomparisons and to assess model performance confidently. One of most pressing challenges, accordingly, is the availability and integration of data. There is likely to be rapid progress on this front as large new data sources and computational methods become available and widespread. A second set of challenges lies at the intersection of community and ecosystem models: understanding how competitive spatial dynamics and nonequilibrium successional processes influence ecosystem processes and broad diversity patterns, determining how to scale these processes efficiently, and assessing the adequacy of functional types to bridge between species-level dynamics and ecosystem function. Finally, richer information about the belowground components of ecosystem function—including soil microbial ecology and the role of mycorrhizae in flows of energy and nutrients—are fertile areas of investigation, and belowground dynamics are becoming an important frontier of forest modeling. While these are all very active areas of research, there are no clear answers yet, and progress will depend on collaboration among mathematicians, modelers, and field ecologists.

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FREQUENTIST STATISTICS

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Frequentist statistics provide a formal way to evaluate ecological theory using observations. Frequentist inference is based on determining the probability of observing particular values of data given a model that describes how the data arise. This probability provides a basis for discarding models that make predictions inconsistent with observations. The probability of the data conditional on a model also forms the foundation for maximum likelihood estimation, which has been the method of choice for estimating the values of parameters in ecological models.

AIMS AND BACKGROUND
Purpose

Ecological theory seeks general explanations for specific phenomena in populations, communities, and ecosystems. Virtually all scientific theory achieves generality by abstraction, by portraying relationships in nature as mathematical models. Models are abstractions that make predictions. Statistical analysis provides a process for evaluating the predictions of models relative to observations, and in so doing provides a way to test ecological theory. Frequentist statistics, also known as classical statistics, have been the prevailing system for statistical inference in ecology for decades.

Textbooks that introduce frequentist statistics usually emphasize methods—how to estimate a parameter, conduct a test, find confidence limits, estimate power, and so on. Because these texts give only brief treatment of