Simulating Future Changes in Arctic and Subarctic Vegetation

The Arctic is a sensitive system undergoing dramatic changes related to recent warming trends. Vegetation dynamics—increases in the quantity of green vegetation and a northward migration of trees into the arctic tundra—are a component of this change. Although field studies over long time periods can be logistically problematic, simulation modeling provides a means for projecting changes in arctic and subarctic vegetation caused by environmental variations.

It’s increasingly apparent that the Arctic is a sensitive system that has undergone some dramatic changes over the past few decades, including sea-ice and glacier melt, permafrost thaw, increased plant productivity, and northward-moving vegetation.\(^1\)

Observations of vegetation change in the Arctic come in several forms. Remotely sensed data from satellite imagery suggest an increase in vegetation biomass and productivity (indicated by more “greenness”) over the past two to three decades, with green vegetation increasing more than 15 percent in some regions.\(^2\) Repeat oblique aerial photographs in northern Alaska also reveal an increase in the abundance and extent of low shrubs, particularly alders, in the past 50 years.\(^3\) Moreover, experiments that impose warming treatments on arctic tundra vegetation have demonstrated changes in plant growth and community composition in response to temperature increases.\(^4\)

Changes in one component of the arctic system are very likely to affect numerous other system components, so the recent changes in vegetation are expected to have important feedbacks to the overall climate system.\(^5\) It’s therefore important that environmental scientists understand and project changes in vegetation and the subsequent effects of these changes.

Although remotely sensed vegetation data can capture some of the recent past’s coarser-scale changes, only a few sets of long-term, on-the-ground, observational data actually exist.\(^6\) Field experiments give us a glimpse into vegetation dynamics but only for the very near future due to their short duration.\(^7\) Simulation modeling is thus an effective methodology for projecting the response of arctic and subarctic vegetation and plant communities to environmental change.\(^8\)

Modeling Vegetation Change

Researchers can model vegetation dynamics with a variety of different approaches; Woodward and Lomas\(^9\) provide a comprehensive review of vegetation dynamics modeling that discusses these different strategies. *Correlative* models of vegetation, for example, relate vegetation properties or plant processes to environmental factors such as temperature, precipitation, soil characteristics, and topography, to name a few. Simulating vegetation changes via correlative models simply means calculating the new vegetation state under the new en-
Environmental conditions by using spatially constructed functions. These correlative models, however, might not be able to address the interactions among plant species (or types), between plants and soils, and between plants and the atmosphere that dictate the trajectory of vegetation change over time. In other words, the spatial relationships that we find in nature might not persist as environmental controls change over time.10

Mechanistic or process-based models take into account plant functions such as photosynthesis, respiration, transpiration, energy exchange, the biomass allocation among roots, leaves, and stems, and the competition with other plants that ensues. Thus, they have the capacity to simulate vegetation patterns as well as to project ecosystems’ properties over time, potentially across scales from local to global.11 Models can be either static or dynamic, depending on whether they simulate current vegetation distributions or their changes over time.12 We can further characterize dynamic models as either equilibrium or transient models—equilibrium models project a new state of the vegetation at some point in the future, whereas transient models simulate the temporal pathway along which the vegetation moves from one time to another. Researchers have recently built numerous, mechanistically-based dynamic vegetation models13 to address vegetation’s response to a changing climate. The models are dynamic, but they vary in the types of processes incorporated, the degrees to which these processes are detailed, the controlling model variables, and the representation of arctic plant or vegetation types.

Arctic and Subarctic Vegetation Modeling

Several ecosystem models, including the Terrestrial Ecosystem Model (TEM) and the Arctic BIOME BGC (BioGeochemical Cycles) model, simulate changes in key ecosystem-level processes for the Arctic, such as water, carbon and nitrogen cycling, and energy exchange.14,15 However, very few models explicitly examine the dynamics of the arctic and subarctic vegetation and plant communities. Sitch and colleagues16 used the Lund-
BIOME3.20 Driven by GCM output, the BIOME4 model projects a northward migration of the boreal forest at the expense of arctic tundra, as well as the expansion of erect shrubs to displace prostrate shrubs. A more comprehensive analysis using BIOME4 predicts that the boreal forest extent will increase by 55 percent and that the arctic tundra extent will decrease by 42 percent, with a 60 percent loss of prostrate dwarf-shrub tundra.

At the global scale, the BIOME series of models incorporates biogeography and biogeochemistry into a mechanistically-based equilibrium approach that essentially redistributes vegetation types geographically based on a new environment, without explicitly simulating changes throughout time. A more recent version in this series (the BIOME4 model) includes three plant functional types present in arctic tundra (cold shrubs, cold graminoids or forbs, and cushion forbs), adding to the nine plant functional types simulated in BIOME3. Driven by GCM output, the BIOME4 model projects a northward migration of the boreal evergreen forest at the expense of arctic tundra, as well as the expansion of erect shrubs to displace prostrate shrubs. A more comprehensive analysis using BIOME4 predicts that the boreal forest extent will increase by 55 percent and that the arctic tundra extent will decrease by 42 percent, with a 60 percent loss of prostrate dwarf-shrub tundra.

At more regional scales, Lenihan and Neilson used the Canadian climate-vegetation model (CCVM) to simulate Canadian vegetation’s response to a doubling of CO2. CCVM is also an equilibrium model, and it uses several parameters that are strongly applicable to northern systems, such as degree-days, minimum temperatures, and snowpack. Under climate-change scenarios, the CCVM projected reductions in tundra and subarctic woodlands and increases in the extent of boreal and temperate forest, as well as the dry woodlands and prairies. Also at the regional scale, but using a transient (rather than an equilibrium) approach, Rupp and his colleagues simulated vegetation dynamics in Alaska with a spatially explicit model called ALFRESCO (Alaskan Frame-based Ecosystem Code) derived from Starfield and Chapin's point model. Under warming scenarios of +2 and +4 °C, ALFRESCO simulated an increase in forests into arctic tundra, as well as more and larger fires.

To simulate the transient dynamics of arctic tundra vegetation, Howard Epstein and his colleagues developed a point model called ArcVeg that uses a more detailed set of tundra plant types. The original version of ArcVeg contained 20 plant types (including two tree types), but a more recent version enhanced for circumpolar applications uses a reduced set of 12 plant functional types, including mosses, lichens, forbs, and several categories of graminoids and shrubs. ArcVeg is parameterized for five arctic subzones that range from the polar desert at the highest latitudes to the much warmer Low Arctic tundra at the southern extent. Prior simulations using ArcVeg have shown increases in shrub biomass and reductions in moss biomass with summer warming of 3 °C.

Objectives for New Simulations

The signatories to the UN Framework Convention on Climate Change are charged with stabilizing the concentrations of greenhouse gases in the atmosphere at a level that prevents dangerous interference with the climate system. To this end, several nations, organizations, and scientists have suggested that global mean temperatures shouldn’t rise more than 2 °C above pre-industrial levels. Analysis of several different GCMs driven by a range of future greenhouse gas-emission scenarios indicated that a +2 °C global warming over pre-industrial levels would occur between 2026 and 2060 and result in increases in mean and seasonal temperatures in the Arctic that would be substantially greater than the global mean. On average, warming of Arctic land-surface temperatures could reach 3 to 8 °C during the winter months and 1 to 3 °C during summer. To illustrate the varied implications of this warming for Arctic ecosystems, vegetation models driven by climate, soil properties, and CO2 concentrations are used to simulate the Arctic’s changing land cover.

Because most vegetation models were developed to address particular scientific questions, each model represents specific processes in more or less detail. In general, though, vegetation models must make trade-offs among the model’s spatial coverage, spatial and temporal resolution, and the number and types of plants simulated. Computational limitations, the lack of suitable data to parameterize and drive the simulations, and the paucity of specific information about the ecological characteristics of different plant species constrain any one particular vegetation model from being applicable to all situations. One common issue with vegeta-
tion dynamics modeling is the absence of data on species migration patterns and rates (including seedling production, dispersal, emergence, and establishment), hence these processes are rarely included in such models.18

Methods
To provide some context for our International Polar Year research on the “greening” of the Arctic, we conducted a comparison of climate change projections with several arctic vegetation dynamics models. In this study, we used three different vegetation dynamics models to illustrate potential future vegetation change in the Arctic: a global equilibrium model (BIOME4), a regional-scale, subarctic forest dynamics model that includes species migrations (TreeMig), and a nutrient-based model of arctic tundra plant dynamics (ArcVeg).

BIOME4
We used the BIOME4 global vegetation model to simulate equilibrium changes in circumpolar arctic vegetation. The model’s five tundra biomes include low shrub tundra, erect dwarf-shrub tundra, prostrate dwarf-shrub tundra, graminoid and forb tundra, and an extreme-climate cushion forb, lichen, and moss tundra. The model also has a cold parkland biome of forest and shrubs, and two cold forest biomes (evergreen needle leaf and deciduous). The tundra and boreal biome categories used in BIOME4 are specifically intended to be compatible with both present-day observations and those distinguishable in the paleoecological record.21

The model is driven by a single year of monthly mean temperature and surface solar radiation, monthly total precipitation, soil texture, and atmospheric CO2 concentrations. Although BIOME4 doesn’t simulate the horizontal interactions between grid cells that can occur through seed dispersal or the spreading of fire or disease, the model is generally successful at predicting large-scale vegetation patterns and has been widely employed for this purpose.8 Because of the relatively continuous climate and soil data used to run BIOME4, we specified a mosaic biome of cold parkland, which characterizes the spatial transition zone between closed forests and tundra. The cold parkland biome is defined between the absolute limits for tree growth specified by net primary production (> 240 gm−2) and a minimum leaf area index (≤ 1.2 m²m−²). The model would otherwise not simulate this biome, even though it’s observed on the landscape, because of discontinuous permafrost, thin soils and rock outcrops, and other fine-scale spatial heterogeneity that prevents forest development.

For the experiments presented here, we ran BIOME4 with a control environment of late 20th century mean climate conditions in a series of scenarios that illustrate the arctic climate under +2 °C global warming. We compiled the scenarios by synthesizing six GCMs into a probability distribution of temperature changes. The four scenarios are—in order of the magnitude of arctic warming prescribed—10th percentile “cool,” robust mean, mean, and 90th percentile “warm.” In each scenario, we used anomalies in monthly mean temperature and cloudiness and applied total precipitation to the 20th century mean climatology to drive BIOME4. We performed our simulations on a high-resolution 10-km equal-area grid, covering the entire ice-free land area of the Arctic (13.1 × 10⁶ km²). Synthesis of six GCMs demonstrated that a +2 °C global warming would occur some time between 2026 and 2060—that is, approximately 20 to 55 years from today.

Although the equilibrium model is computationally efficient, vegetation doesn’t respond instantaneously to climate change. Changes in vegetation cover lag changes in climate because of the implicit time scales of population and community processes. Seed dispersal and seedling establishment (migration), along with disturbance and succession, are required to change a plant community, so these processes must be included in any model to fully assess the time required for biogeographical changes. By modeling these additional processes, we can assess the large-scale land cover a model such as BIOME4 can simulate in the context of change rates and better estimate the implications of these land-cover changes for feedbacks to the climate system. Thus, to study the potential effects of vegetation migration and succession, and to assess the time lags for arctic vegetation in response to a +2 °C global warming, we needed a second vegetation model with a complete description of plant migration and succession.

TreeMig
The ‘TreeMig model’29 is a dynamic forest stand model that determines forest population dynamics at the species level, including seed production, seed dispersal, seed bank dynamics, germination, growth, competition, and mortality. These processes are functions of light and annual climate data, and incorporate the summation of annual temperatures, minimum winter temperatures, and drought information. TreeMig runs on an equidistant rectangular grid with a typical cell size of 1
km². Finer spatial resolution is possible with TreeMig but is typically unnecessary; coarser resolution presents computational problems that we’ll discuss later. Within-cell heterogeneity is depicted by frequency distributions of tree density and therefore light attenuation.

TreeMig’s computational core is a dispersal function that simulates the intercell interaction of tree species through seed dispersal. The function \( k_s(z) \) represents the probability of one seed landing a distance \( z \) (meters) from its parent tree. The function consists of two negative exponentials that account for frequent short- and rare long-distance dispersal events, respectively:

\[
k_s(z) = \left(1 - \kappa_s\right) \frac{\exp\left(-\frac{z}{\alpha_{s,1}}\right)}{\alpha_{s,1}} + \kappa_s \frac{\exp\left(-\frac{z}{\alpha_{s,2}}\right)}{\alpha_{s,2}}, \kappa_s \in [0, 1].
\]

We estimated mean dispersal distances (\( \alpha \)) for wind-dispersed seeds by species from data on typical sinking velocities and wind-speed distributions. For non-wind-dispersed species, we used our best guesses. To reduce the estimation error involved in calculating the dispersal kernel on a grid with a resolution much greater than \( \alpha \), we calculated the dispersal kernel on a fine-mesh 25 m grid and then summed to the chosen grid cell size.

We ran TreeMig on an idealized transect from 60° to 75° N in central Siberia, at approximately 77° E longitude. Along this transect, the very long, relatively smooth gradient in climate results in the representation of nearly all the subarctic forest and arctic tundra biomes, from the cold evergreen needle-leaf forest to extreme-cold prostrate shrub tundra. The model grid is 2,200 km long by 1 km wide, with half-cyclic boundary conditions—that is, seeds dispersed beyond the grid domain to the opposite boundary; those dispersed to the south or north were lost.

To drive the model, we prepared an interannually variable climate data set of annual temperature sum, minimum winter temperature, and drought stress for the transect by interpolating and summarizing monthly temperature and precipitation observations over the past 30 years from several weather stations between longitude 74° and 80° E. Using these present-day climate data, we ran the model through a spin-up phase of 700 years to reach equilibrium vegetation conditions. To simulate the transient effect of a +2 °C global warming on the model domain, we added anomalies to the climate data set over a period of 100 years (approximately 2000 to 2100) and then continued the model run for an additional 900 years to approximate new equilibrium conditions. We ran the model under a climate-warming scenario that approximates the seasonal asymmetry of arctic climate change under +2 °C global warming observed in analyses of GCM output. This scenario applies anomalies of +2.5 °C from April to September and +7.5 °C from October to March—that is, winter warming is much greater than summer warming, which is consistent with the trends in GCM scenarios used in the BIOME4 simulations.

Finally, we ran the TreeMig model in two modes to assess the relative importance of migration versus succession in controlling the rate of vegetation change. In the succession-only experiments, we simulated a few seeds of every species to be present in every grid cell at every point in time, thus initiating succession if the climatic conditions were appropriate. In the succession-migration experiment, seeds might only reach a grid cell through the dispersal processes described earlier. To compare model results to equilibrium vegetation, we used the vegetation composition of the succession simulation after the entire 1,700 years. From the simulations, we could assess the speed of the advancing treeline (defined as forests > 25 tonnes/hectare).

**ArcVeg**

As mentioned earlier, ArcVeg is a nutrient-based plant community and ecosystem model designed to simulate the transient dynamics of plant biomass and community composition for arctic ecosystems. The current version of the model simulates 12 different arctic plant functional types and is parameterized for five arctic subzones (full details on the arctic subzones appear elsewhere). Because plant-available nitrogen can be a strongly limiting nutrient for tundra plants, the model functions essentially with nitrogen mass balance, moving nitrogen among soil organic matter, soil inorganic nitrogen, and plant pools. The model’s plant parameters are nitrogen uptake efficiencies, the biomass:N ratio, annual proportion of plant material senescing, probability of seedling establishment, and cold tolerance for growth. The model runs on an annual time step, but the growing season is split into five distinct plant-growth periods (the first period follows the onset of growth after the spring thaw, and the last growth period includes the peak of the growing season through senescence), to capture the seasonality across the full arctic climate gradient.
The ArcVeg model’s spatial resolution is a 1 m by 1 m grid cell; the model simulates 100 replicates of these grid cells (essentially a 10 m by 10 m grid). Unlike the TreeMig model (but similar to the BIOME4 model), this version of ArcVeg isn’t spatially explicit, meaning that there are no interactions among the grid cells (a spatially explicit version does exist, however, and incorporates the formation of patterned-ground features). The reason for 100 replicate grid cells is that the model has spatially stochastic elements, such as seedling establishment and frost disturbances, so we need to replicate the grid cells to capture the spatial variability of plant communities across the tundra landscape. Even without a spatial component to the model, plant migration is somewhat constrained by the probability of seedling establishment parameter, which varies as a function of climate.

We simulated a +2 °C warming in mean growing season temperatures over a 50-year period using a model parameterization consistent with previous work. We ran the model for each of the five subzones, which differ in their quantities of soil-organic nitrogen, their rates of nitrogen mineralization, and their temperatures and growing season lengths. We ran model simulations for 500 years to develop an equilibrium vegetation; we then ran the model for an additional 500 years with the present climate. In Year 1,000, we imposed the warming treatment and then ran the model for an additional 500 years (1,500 years total). We grouped plant-type biomass into these categories: mosses, lichens, forbs, graminoids, prostrate shrubs, dwarf-erect shrubs, and tall shrubs.

Results

We found that the equilibrium results compared to transient simulations highlight the importance of understanding the role of migration and succession on large-scale vegetation changes. Migration and succession simulated in the TreeMig and ArcVeg experiments, for example, induced lags in the modeled land-cover change, as compared to the BIOME4 simulations, and would strongly influence the feedback of the land cover to the climate system. For instance, the treeless area remains large over a long time period in the TreeMig model, potentially sustaining high albedo (negative climate feedback) but also potentially increasing permafrost thawing (positive climate feedback). The same situation is seen with the lag in development of the tall shrub canopy in subzone E (most southern tundra) as a result of warming in the ArcVeg model. All model results indicate that biomass increases (negative climate feedback resulting from carbon sequestration) can be seen over a period of up to several centuries. Let’s look more closely at each model’s results.

BIOME4

Model output from BIOME4 illustrates present-day and simulated changes in the equilibrium distribution of vegetation. The arctic vegetation from both satellite-based observations (Figure 1a) and the model (Figure 1b) is characterized by the south-to-north transition from cold forests through a series of tundra biome types, each adapted to increasingly colder growing season temperatures. Qualitative comparison of the model with observations reveals that the model does a reasonably good job of predicting the northern limit of the cold forest biomes and simulating the geographic distinctions among the different tundra types. However, BIOME4 overpredicts the amount of forest observed in the hypermaritime regions of southwest Alaska and seems to underestimate the area of the most extreme tundra types, which could be a limitation of the temperature data used to drive the model. BIOME4 also simulates potential vegetation for areas with exposed bedrock that appear as barren in the observed vegetation map (for example, the northeastern Canadian Arctic). Improved large-scale soil mapping would better match the model with observations in these areas.
In the global +2 °C warming scenarios, BIOME4 predicts forest extent to increase in the Arctic on the order of $3 \times 10^6$ km$^2$ or 55 percent with a corresponding 42 percent reduction in the area of tundra (projected by 2060). In all scenarios, parkland (forest tundra) replaces tundra biomes, and closed forests replace parkland. In the coldest scenario (Figure 2a), increased evapotranspiration leads to a small decrease of forest in areas that are relatively dry today (far eastern Siberia, central Alaska). In contrast, in the warmest scenario (Figure 2d), increases in both temperature and precipitation lead to complete replacement of tundra by closed cold forests, and in the interior regions of the continents, temperate forests encroach on cold forests. Although all the +2 °C warming scenarios contain increases in precipitation over the Arctic, the magnitude of precipitation increase is smallest in the cool scenario. In the warmer scenarios, significant reductions in sea-ice cover lead to higher summertime sea-surface temperatures and greater evaporation, resulting in the greatest positive precipitation anomalies. The more modest warming in the cool scenario results in warmer land surface without significant decreases in arctic sea ice, leading to moisture-deficit conditions over the continents.

Tundra types generally shift north in the model's simulations, with the largest reductions in the extreme cold-tolerant, dwarf-shrub tundra type, in which nearly 60 percent of its habitat is lost. Modeled shifts in the potential northern limit of trees reach up to 400 km from the present treeline, which might be limited by migration rates. Simulated physiological effects of the CO$_2$ increase (to approximately 475 parts per million [ppm]) at high latitudes were small compared with the climate-change effects. Experiments with a dynamic global vegetation model forced by the climate scenarios shown here and resulting in vegetation changes similar to those presented in this article indicate that the increase in subarctic forest area could sequester at least 300 Petagrams (Pg = $10^{15}$ g) of additional carbon, although this effect wouldn't be realized over the next century.

**TreeMig**

Output from the TreeMig model illustrates the biomass of several evergreen and deciduous tree species—as well as grasses and shrubs—along latitudinal gradients. Figure 3 shows the forest latitudinal vegetation change at 0, 100, and 500 years after the onset of climate change. The timberline advances very quickly in succession-only experiments, in which viable seeds of all taxa are present along the transect at all times. In contrast, in the succession-migration experiments, the simulated advance in timberline lags the climate forcing even after 500 years. The front’s migration speed is approximately 235 m/year in the succession-only experiment and 177 m/year in the succession-migration experiment. Averaged over the transect, succession-only leads to a build up of forest biomass for roughly 300 years, followed by a phase of small biomass losses, whereas succession-migration leads to a slower accumulation of biomass over a longer time period.

**ArcVeg**

Output from the ArcVeg model illustrates the temporal dynamics of seven tundra plant types across five arctic bioclimate subzones. These subzones are defined by the presence or absence of certain shrub types as follows: subzone A, cushion forb tundra (absence of shrubs); subzone B, prostrate dwarf-shrub tundra; subzone C, hemi-prostrate...
dwarf-shrub tundra; subzone D, erect dwarf-shrub tundra; and subzone E, low shrub tundra.

Simulated warming in the ArcVeg model led to changes in plant community composition and total plant biomass throughout the tundra. For the Low Arctic tundra in subzone E, warming led to an initial increase in the plant functional types that already dominate these systems—namely, the mosses and dwarf-erect shrubs (Figure 4a). However, we found a more lagged response in the tall shrubs, which begin to increase their biomass after roughly 100 years and become a third dominant plant type after approximately 150 years. The increase in tall shrubs caused a decline in dwarf-erect shrub biomass, following their peak during the warming period. Prostrate shrubs decline in biomass, whereas graminoids exhibit an increase in biomass. Overall, the total biomass of subzone E increases by close to 100 percent (1,500 gm–2) with the appearance of tall shrubs, but this change appears to take up to 200 simulation years (Figure 4b).

For subzone D, the warming increased moss biomass, similar to its increase in subzone E, and also dramatically increased dwarf-erect shrub biomass (Figure 4c). The prostrate-shrub biomass essentially didn’t change, but graminoid biomass increased to some degree. The total biomass of subzone D increased by approximately 60 percent (600 gm–2 in Figure 4d), but this took only 100 years compared to the slower change observed in subzone E. For subzone C, which is the southernmost subzone of the High Arctic, warming led to slight increases in biomass of mosses and prostrate shrubs, the dominant plant functional types in this community (Figure 4e). Biomass of dwarf-erect shrubs and graminoids also increased. Total biomass of the subzone C plant community increased by approximately 33 percent (200 gm–2), with warming over a period of roughly 50 years (Figure 4f).

For subzone B, moss biomass increased substantially with warming, as did prostrate-shrub biomass (Figure 4g). Lichen biomass declined with warming in subzone B, where the total biomass increased 80 to 85 percent (150 gm–2) in fewer than 100 years (Figure 4h). For subzone A, the polar desert, moss and lichen biomass increased rapidly at first (Figure 4i), but this was followed by increases in prostrate shrubs over a 150-year period. This increase in shrub biomass led to declines in both moss and lichen biomass, close to their original levels. Graminoid biomass also showed a slight decline with warming, but total biomass increased approximately 100 percent (80 gm–2; see Figure 4j).

Figure 3. TreeMig model. Compare the changes in forest species composition and cover along the Siberian transect simulated by the TreeMig dynamic vegetation model forced by a +2.5 °C summer warming and a +7.5 °C winter warming applied over 100 years: (a) present-day control situation, (b) simulation after 100 years of the succession-only experiment, (c) simulation after 100 years of the succession-migration experiment, (d) after 500 years in the succession-only experiment, and (e) after 500 years in the succession-migration experiment.
Figure 4. ArcVeg model. A summer warming begins in Year 1000 of the simulation and is linearly ramped to a +2 °C increase in Year 1050. Above ground biomass for different plant types and total biomass (including below ground) for the entire plant community differ in each of the five Arctic bioclimate subzones: (a) plant type biomass for subzone E, (b) total biomass for subzone E, (c) plant type biomass for subzone D, (d) total biomass for subzone D, (e) plant type biomass for subzone C, (f) total biomass for subzone C, (g) plant type biomass for subzone B, (h) total biomass for subzone B, (i) plant type biomass for subzone A, and (j) total biomass for subzone A.
Oftentimes, it’s unrealistic to think that we can project any region’s land-surface properties over a several-hundred-year period, and these simulations shouldn’t be considered definitive forecasts of how vegetation changes will occur over the next century and longer. However, they do illustrate the potential magnitude and time scale of climate-change impacts on the Arctic. The time lags for forest succession and migration observed in the TreeMig simulations mean that the equilibrium vegetation changes simulated by BIOME4 are unlikely to be realized for several centuries, especially if efforts to stabilize the climate system are successful. Many important ecosystem processes are ignored in all three models, including soil development and erosion, permafrost dynamics, and—importantly—the influences of future human land use. The species parameters that control migration in TreeMig and ArcVeg, particularly those related to seed dispersal and establishment, are highly uncertain, and sensitivity analyses have shown that the migration front’s speed is strongly dependent on this parameter. Infrequent strong storms, for example, could lead to the entrainment of wind-dispersed seeds higher into the troposphere, where presumably they would be transported to much greater distances than by typical surface winds.31

These models do however represent a milestone in our ability to model vegetation responses to climate change. Ideally, we would like to combine the different modeling approaches presented here into a unified model to create a more comprehensive assessment of the spatial and temporal extent of future arctic vegetation change. However, such a task is complicated by the different scientific problems for which the models have been designed. Whereas BIOME4 was designed to be applied globally at a coarse resolution and successfully represents current biome spatial distributions, it lacks detail about plant population and community processes at the finer

Figure 4, continued.
scales that govern temporal dynamics. TreeMig and ArcVeg, in contrast, simulate some of the finer-scale processes, yet they face either parameterization or computational problems over large extents.

Although the current distribution of tundra vegetation types and climate-change scenarios can be used to extrapolate the ArcVeg point model to the circumpolar Arctic, the data on soil nitrogen required to run the simulations aren’t available at this time in any reasonable form. TreeMig is already an upscaled and much more efficient formulation than the standard individual-based gap model approach, but the computing time per grid cell and simulated year is still 0.0016 seconds on a typical modern workstation. With more than 1,000 years of simulation required to reach equilibrium conditions, a circumpolar application of a model with the TreeMig succession-migration formulation—over the same domain as the BIOME4 simulations and at the standard grid cell size of 1 km$^2$—would amount to nearly a year of computing time. To reduce model runtime, one choice would be to use supercomputers or parallelization; an alternative would be to increase the grid cell size (say, to the 10-km grid that BIOME4 uses). But this imposes discretization errors because the migration speed is nonlinearly dependent on grid cell size. Thus, the challenge and the next step of our research is to perform sound spatial upscaling of the fine-scale models, taking advantage of state-of-the-art approaches in multiscale modeling, such as adaptive grids, metamodeling, and moment equations or particle methods.

This exercise highlights the potential impact of climate change on arctic ecosystems and presents the strengths and limitations of different modeling approaches. In the coming years, advances in computing technology, development of new large-scale data sets of key parameters and driving data, and combined process representations will all contribute to our ability to model and understand vegetation responses to future climate change. This, in turn, will inform the community and broader public on climate-change impacts for vegetation, animals, and humans and will provide a sound scientific basis for policymaking.

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