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<https://escholarship.org/uc/item/1b67s3rs>

Journal

Proceedings of the National Academy of Sciences of the United States of America,
113(14)

ISSN

0027-8424

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Publication Date

2016-04-05

DOI

10.1073/pnas.1519911113

Peer reviewed

Global change and terrestrial plant community dynamics

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This contribution is part of a special series of Inaugural Articles by members of the National Academy of Sciences elected in 2014.

Contributed by Janet Franklin, February 2, 2016 (sent for review October 8, 2015; reviewed by Gregory P. Asner, Monica G. Turner, and Peter M. Vitousek)

Anthropogenic drivers of global change include rising atmospheric concentrations of carbon dioxide and other greenhouse gasses and resulting changes in the climate, as well as nitrogen deposition, biotic invasions, altered disturbance regimes, and land-use change. Predicting the effects of global change on terrestrial plant communities is crucial because of the ecosystem services vegetation provides, from climate regulation to forest products. In this paper, we present a framework for detecting vegetation changes and attributing them to global change drivers that incorporates multiple lines of evidence from spatially extensive monitoring networks, distributed experiments, remotely sensed data, and historical records. Based on a literature review, we summarize observed changes and then describe modeling tools that can forecast the impacts of multiple drivers on plant communities in an era of rapid change. Observed responses to changes in temperature, water, nutrients, land use, and disturbance show strong sensitivity of ecosystem productivity and plant population dynamics to water balance and long-lasting effects of disturbance on plant community dynamics. Persistent effects of land-use change and human-altered fire regimes on vegetation can overshadow or interact with climate change impacts. Models forecasting plant community responses to global change incorporate shifting ecological niches, population dynamics, species interactions, spatially explicit disturbance, ecosystem processes, and plant functional responses. Monitoring, experiments, and models evaluating multiple change drivers are needed to detect and predict vegetation changes in response to 21st century global change.

climate change | drought | forests | global change | land-use change

Terrestrial plant communities include forests, woodlands, shrublands, and grasslands; they support economic activities including forestry and grazing and provide other ecosystem services (1) such as carbon sequestration and water delivery. Plant communities play a key role in global biogeochemical cycles of carbon, oxygen, water, and nitrogen, with feedbacks to the oceans, atmosphere, and climate. The distribution of animals on land is often influenced by the distribution of vegetation, and therefore, plant community dynamics affect biodiversity. Changes in the Earth's vegetation in response to climate change, and associated faunal changes, may have played a role in the evolution of the human lineage (2, 3). Thus, human populations have a vested interest in understanding rapid global change effects on terrestrial plant communities.

Anthropogenic drivers of global change include rising atmospheric concentrations of CO₂ and other greenhouse gasses and associated changes in the climate, as well as nitrogen deposition, biotic invasions leading to novel species assemblages, altered disturbance regimes, and land-use change (4); terrestrial ecosystems and the services they provide are altered by these drivers and their interactions (5–9). It is therefore imperative that scientists develop robust tools for understanding and anticipating future changes.

How are vegetation responses to rapid 21st century global change forecast? One method uses projections from global climate models to predict how the footprint of climatically suitable habitat for plant species or communities will shift under climate change scenarios (10, 11). These “climate envelope models” describe how

climatic niches are likely to shift spatially but not how species will respond. Models of vegetation dynamics (9), on the other hand, incorporate effects of multiple, interacting global change agents on terrestrial plant community and species range dynamics.

Scenario-driven forecasts of 21st century global change impacts on vegetation cannot be validated without waiting a few decades for changes to happen. These predictions can be informed with a deeper understanding of paleo-vegetation changes (12–14). There is also growing observational evidence that the biosphere is already responding to recent rapid warming with shifting phenology, species distributions, and genetic population structure and that vegetation dynamics are responding to other global change factors as well.

In this review, we present a conceptual framework for interpreting and predicting the effects of global change drivers on terrestrial plant communities, summarize observed changes, and describe modeling tools that can forecast the impacts of multiple drivers on plant communities in an era of rapid change.

Conceptual Framework

Dawson et al. (15) recommended that multiple kinds of evidence should be used to assess climate change impacts on biodiversity, including monitoring, paleoecological records, models of population dynamics and ecophysiological response to the physical environment, and experiments. In our framework, we narrow the focus to terrestrial vegetation and include multiple drivers of global change. We also call for the integration of spatially explicit forecasts with observations of ongoing changes, records of past dynamics, and experiments. There is a pressing need to identify interactions among global change drivers (16) in all biomes (Fig. 1).

Significance

Global terrestrial vegetation plays a critical role in biogeochemical cycles and provides important ecosystem services. Vegetation has been altered by anthropogenic global change drivers including land-use change, altered disturbance regimes, invasive species, and climate change, for decades to centuries, or in some cases millennia. Vegetation responses to land use and disturbance can be more immediate than to climate change and can be long lasting. The effect of global warming on water balance may have a stronger influence than the direct effects of temperature on vegetation. Models deployed at multiple ecological scales, populations, communities, and landscapes will be required to forecast vegetation responses and feedbacks to accelerated global change.

Author contributions: J.F., J.M.S.-D., A.D.S., and H.M.R. designed research; J.F. performed research; J.F., J.M.S.-D., A.D.S., and H.M.R. contributed new reagents/analytic tools; J.F. analyzed data; and J.F., J.M.S.-D., A.D.S., and H.M.R. wrote the paper.

Reviewers: G.P.A., Carnegie Institution for Science; M.G.T., University of Wisconsin-Madison; and P.M.V., Stanford University.

The authors declare no conflict of interest.

Freely available online through the PNAS open access option.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1519911113/-DCSupplemental.

Detecting changes in the climate system and attributing them to anthropogenic greenhouse gases (17, 18) requires that a relationship be found between changing climate and biophysical parameters, that the climate change be attributable to anthropogenic causes (not natural variability), and that the biophysical change be consistent with a process-level understanding of the ecosystem and not consistent with explanations that exclude climate change (19). Detection and attribution is even more challenging when considering multiple, interacting global change drivers (Fig. 1). It is for this reason that we advocate multiple modes and scales of analysis.

Detecting vegetation dynamics in response to global change requires observations and experiments that are spatially extensive and distributed, comparable, and repeated over the long term. A legacy of research sites, vegetation surveys, and field experiments now spans decades to centuries and includes ecological research networks, as well as forest and land surveys that have been “repurposed” to characterize vegetation change. Remotely sensed measurements of Earth’s surface are global in coverage and encompass several decades of rapid global change. Forecasting requires models that can simulate the effects of global change drivers on populations, communities and ecosystems. Key findings from a growing body of literature that support this framework are outlined in the following sections.

Observing Changes in Plant Communities

Meta-analyses, sweeping in their scope, document numerous phenological shifts, range shifts, and other ecosystem changes consistent with temperature tracking by plant and animal species in response to anthropogenic global warming (20–22). Although global syntheses are important, region-specific investigations that consider multiple global change drivers may shed light on interactions among drivers (e.g., land-use change, fire) that are not apparent at the global scale. Synthesis across regions can yield new insights into the causes of vegetation changes.

Ecological Research Networks. Research networks inform understanding of vegetation change by synthesizing long-term data (Table S1). The 25 sites of the US Long-Term Ecological Research (LTER) Network (23), for example, use both monitoring and experiments to understand mechanisms of ecological response to environmental change (24). Existing ecological research networks will need to become more integrated, and multiscale monitoring more extensive, to meet the challenge of understanding the ecological consequences of global change at large spatial scales (25). We review insights gained on patterns and processes of plant community dynamics from data collected from networks. Ecological networks

can shed light on the effects of episodic and chronic disturbance on ecosystems (hurricane or fire vs. nitrogen deposition) (26). Cross-site comparisons showed that, during drought years, all ecosystems exhibited a ratio of net primary productivity (NPP) to rainfall (water use efficiency), similar to arid ecosystems where water stress is the normal condition (24). This understanding can help predict ecosystem response to increasing climate extremes and aridity.

Some research networks have been developed post hoc supported by a culture of scientific collaboration and availability of new technology. For example, FLUXNET comprises more than 200 sites worldwide in various biomes where eddy covariance towers monitor carbon, water, and energy fluxes (27). Global synthesis of FLUXNET data have shown that droughts result in decreased carbon flux and a net decline in the terrestrial carbon sink (28).

Another network initiated by investigators, the Center for Tropical Forest Science–Forest Global Earth Observatory (CTFS–ForestGEO), is a global network of large (most >10 ha) forest plots, where all trees are mapped and measured about every 5 y, starting as early as 1981. These plots were established during a period of increasing CO₂ and global temperatures, deforestation in the tropics, and reforestation in temperate regions. Global warming has affected phenology and growth at high latitude forest plots, but in temperate and tropical sites, these effects are not yet apparent and are confounded by other factors (29). In tropical rain forest throughout the Amazon Basin, whereas gross primary productivity (GPP) is negatively related to seasonal water deficit, NPP is positively influenced by carbon use efficiency and biomass turnover time controlled by tree mortality rates (30). Data synthesis in forest plot networks is leading to improved understanding of global change effects on plant population and ecosystem processes (Table S1).

Observatory networks have emerged in the last decade to monitor phenology: the seasonal timing of life cycle events including various stages of plant development (leaf out, flowering) (31). Advances in spring phenological events are the terrestrial biological responses most strongly attributed to anthropogenic warming (19). Species-level observation networks can complement remote sensing based studies of advancing spring green-up of terrestrial vegetation (32).

These different types of networks are identifying strong effects of climate on carbon flux and primary productivity, with increasing water deficit leading to decreased terrestrial carbon storage. Although temperature has a well-documented effect on phenology, with ramifications for asynchrony between, for example, plants and pollinators (32), warming-induced drought stress is also having a major effect on terrestrial vegetation.

Vegetation Surveys. Forest inventories and land surveys, conducted by government agencies in many countries, provide temporal depth and complement established and developing research networks. During the 19th century, US public land surveys recorded detailed information about individual (witness) trees used as corner markers on a national grid. In the early 20th century, national forest inventories were established to monitor timber resources and forest conditions (33). Forest inventories are geographically extensive, based on probability-designed samples, and repeated. They document broad, decadal-scale responses to global change factors. It was forest inventory data that first implicated historical land-use change, i.e., afforestation following Euro-American land clearing in previous centuries and subsequent agricultural abandonment in the northeastern United States, as a major driver of the large carbon sink in the northern hemisphere extratropics (34, 35). An increasing carbon sink in the world’s vegetation, consistent with forest regrowth in the temperate latitudes (36), and with uptake by intact forests in the tropics owing to CO₂ “fertilization” (37), is a negative feedback on increasing atmospheric CO₂ concentration. Understanding when this ecosystem service may saturate is critical for projecting the climate future.

Using witness tree data in the state of Massachusetts (northeastern United States), Hall et al. (38) found that historical land-use change led to an abundance of early successional trees with long-lasting legacy effects (39) on forest structure. Also in the eastern

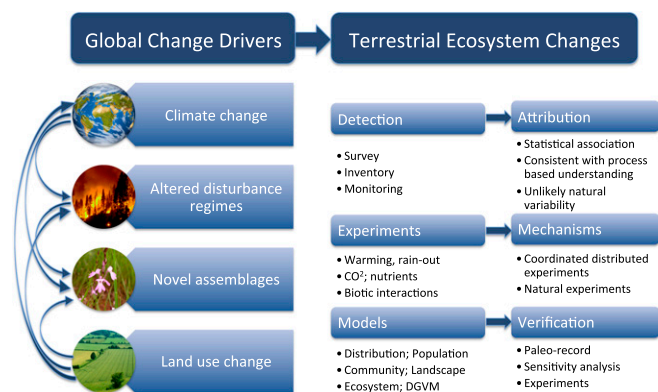


Fig. 1. Framework for understanding effects of global change drivers—climate change, altered disturbance regimes, invasive species leading to novel species assemblages, and land-use change—on terrestrial ecosystems using multiple lines of evidence from observations (detection) for attribution, experiments for elucidating mechanisms, and models deployed at multiple ecological scales for verification.

United States, synthesis of 190 tree census datasets from 50 studies comparing contemporary forests to those established before European settlement suggested that a regional increase in cool-adapted, shade-tolerant, fire-sensitive tree taxa, inconsistent with historic climate warming trends, may have resulted from fire suppression (40). Others argued, however, that high moisture during the same time period could explain the observed patterns (41).

Paleo-ecological records provide even greater time depth for understanding vegetation response to land use, fire, and climate. Comprehensive treatment of how paleo-vegetation studies inform our understanding of ongoing global change (42–44) is, however, beyond the scope of this review.

Comparing the distributions of adults vs. juvenile conspecifics in forest inventories can detect ongoing tree species distribution shifts in response to climate change (Table S1). In the eastern United States, juveniles were found where there was higher temperature and/or greater precipitation than adults for many species, consistent with the hypothesis that higher productivity leads to faster population turnover instead of temperature tracking shifts to higher (cooler) latitudes (45). In California's Mediterranean climate ecosystem, characterized by warm, dry summers and cool, wet winters, there were also more species shifts consistent with turnover than temperature tracking (46). In another study in California, declines in large trees and increased density of small trees with dominance of drought-tolerant oaks correlate with increases in climatic water deficit (47). In the water-limited forests throughout the western United States, lack of seedling regeneration at warmer range margins is more prevalent than expansion along cool margins (48), but forest cover buffers the negative effect of climate warming and drying on recruitment (49).

Spanish national forest inventory data have identified large-scale shifts in forest composition, where several pine species are failing to recruit owing to successional dynamics following prior disturbances (50). Tree species colonization in recent decades was more strongly related to dispersal than climate, and conifer regeneration was negatively related to competition with expanding oaks. Broadleaf species establishment was positively related to precipitation (51), but also to succession (canopy closure) (52). Demographic responses of Iberian trees to global change are highly variable among species and across climate gradients (53). Canopy defoliation and tree mortality during 1987–2006 were related to climate change-induced drought across Europe (54).

A generality emerging from studies based on large-scale forest inventory is that land use and disturbance regimes have large and long-lasting effects on successional dynamics, leading to communities that are not in equilibrium with climate. These legacy effects can have feedbacks to the global carbon cycle (forest growth and carbon sequestration can continue long after deforestation) and can mask direct effects of climate change (increasing temperature) on range shifts (55, 56). Additionally, forest response to climate change will vary depending on whether forests are temperature, light, and/or water limited; forest growth has increased in forests that are temperature limited (57), but so has tree mortality in these energy-limited forests (58). In water-limited forests, increasing temperature leads to greater effective drought (water deficit), even when precipitation does not decline. Climate change-related drought ("hot drought") (59) and increasing water stress have been linked to forest mortality (Fig. 2) (58, 60–62). Forest inventories have also shown that canopy dynamics may play a crucial role in forest dynamics under climate change because of their shading effects.

Remote Sensing of Vegetation Change. Since the 1980s, moderate- and high-resolution satellite remote sensing data have been used to monitor changes in vegetation cover and other properties (biomass, Leaf Area Index, NPP, greenness) in relation to land-use change and other drivers (63, 64). A study using moderate-resolution imaging spectroradiometer (MODIS) data revealed, for example, that there was about 50% more deforestation than reforestation from 2000 to 2010 in Latin America and the Caribbean, with deforestation occurring in tropical moist forest and reforestation concentrated in steeper, drier areas where mechanized agriculture is impractical (65).

Virtually all deforestation in Mexico in the first decade of the 21st century occurred on lands with common-pool tenure, whereas on communal and private lands, forest cover increased (66). Higher-resolution Landsat data detected a "forest transition" (i.e., the shift from net deforestation to reforestation that had occurred in Europe and eastern North America by the early 20th century) in some developing tropical regions in recent decades (67), although not always resulting in an increase in ecosystem services (68). High-resolution (30 m) maps of annual forest change in 2000–2012 have been produced for the entire planet (69), which is a stunning accomplishment. Globally, there was about three times as much forest loss as gain during that period, with the tropics showing a significant loss, the highest rate being in dry forests of South America. High-resolution remotely sensed data also revealed that, in the first decade of the 21st century, forest degradation (selective logging) increased regional carbon emissions in the Peruvian Amazon by 47%, whereas secondary forest growth reduced net emissions by 18% (70).

Remote sensing-based studies, in conjunction with forest inventories and eddy-covariance data, show a global increase in forest productivity in the second half of the 20th century, driven by climate change, in forests where growth was not strongly water limited. In contrast, remote sensing of vegetation greenness has detected tree mortality and changes in canopy conditions associated with hot drought in semiarid ecosystems (62). Ground-based observations of key factors in the global terrestrial carbon cycle—GPP, biomass, and plant traits—are biased toward the northern midlatitudes, with major gaps in the tropics where carbon flux and storage are high, and the boreal/arctic zone where carbon storage is high; new remote sensing observations and methods may be able to fill in these gaps in understanding carbon geography (71), as well as other gaps in understanding and monitoring global vegetation dynamics (72, 73).

Trends and drivers identified using forest inventory data are corroborated by remote sensing studies. Land-use change is an important global forcing (74), with deforestation still outpacing reforestation in carbon- and species-rich tropical forests. Policy-driven spatial patterning of land-use change is detected in the satellite record. Although there are forest transition countries in the tropics, their transition from net deforestation to reforestation has been accomplished by satisfying their demand for forest products with imports, displacing land use abroad (67). Increased forest growth in temperature-limited forests in a warming world contrasts with increased water stress in water-limited forests associated with tree mortality, failure to recruit, fire, and insect outbreaks.



Fig. 2. In the Tehachapi Mountains in southern California, the brown-needled conical crowns on the midslope are *Pinus ponderosa* that are dying as a result of the most severe drought ever recorded in California (Tejon Ranch Conservancy, 9 June 2014).

Experimentally Manipulating Global Change Factors

Experiments have focused on manipulations of temperature, water, and CO₂ in field conditions. Boreal and temperate tree species responded positively to experimental warming near their cold range limit but negatively near their warm range limit; thus, boreal species are expected to be outcompeted by temperate species at their southern range limits under global warming (75). Faster changes in montane meadow plots that were experimentally heated for more than two decades compared with unheated plots could be positively attributed to climate change. Snowmelt date advanced faster in heated plots, limiting water availability, while forb biomass decreased and shrub biomass increased (76). Experimental warming shortened the time to drought-induced mortality in *Pinus edulis* in semiarid woodlands, with carbon starvation implicated as the cause (77). In a planting experiment, drought was the main cause of *Pinus jeffreyi* seedling mortality in a semiarid forest-steppe ecotone (78).

Experimental approaches are more powerful if replicated globally across regions (Table S1). Fraser et al. (79) called for coordinated distributed experiments (CDEs), using common protocols, to address global change questions that cannot be answered by meta-analysis of uncoordinated experiments. The Free Atmosphere Carbon Exchange (FACE) network of large-scale experiments was established in the 1990s and exposed terrestrial ecosystems to elevated levels of carbon dioxide in open-air, natural conditions. A meta-analysis of those experiments found, for example, that carbon fertilization effects were less than expected for C₃ crop plants (80).

Reduced or temporally altered precipitation patterns anticipated under climate change have been experimentally simulated. In temperate grasslands, increasing intervals between rains, or increasing interannual variability, without reducing total rainfall, reduced herbaceous productivity (81) while at the same time increasing shrub productivity (82). Drought-Net is a recently established CDE coordinating water manipulation field experiments across ecosystem types. A synthesis of warming and water manipulations found that warming and increased precipitation independently increased photosynthesis and respiration and generally increased plant biomass and productivity, whereas reduced moisture availability had the opposite effect, reducing plant biomass and photosynthesis (83).

Experimental manipulations of water, temperature, and carbon corroborate other evidence that, although plant performance may increase with temperature at cold range limits, a warming world is effectively drier even if precipitation does not change. Warmer, drier conditions result in lower productivity and biomass and increased mortality. Positive effects of increased CO₂ on growth are greatest for woody plants.

Modeling Vegetation Dynamics Under Global Change

Plant communities respond to disturbance with successional dynamics (84). Historical surveys, paleo-environmental studies, research networks, and experiments reveal how vegetation has previously responded to global change factors, but simulation models are required to forecast. Models address plant community dynamics at multiple scales of ecological organization, from the perspective of range dynamics, population dynamics, species interactions, spatially explicit disturbance, species spatial ecology, ecosystem processes, and plant functional responses. These distribution, population, community, landscape, and ecophysiological models forecast how biodiversity, species composition, productivity, carbon storage, or vegetation structure may respond to global change scenarios. Models vary in their complexity and in the realism with which they simulate different processes, and so as with any forecasting endeavor, the modeling framework must be matched to the research objective, and uncertainty should be addressed.

Species distribution models (85) (SDMs) have been used to forecast the effects of multiple global change factors on species and plant communities, for example, climate and land use (86, 87). This approach assumes that species are in equilibrium with climate, that climate strongly controls distributions via physio-

logical tolerances to temperature and moisture regimes, and that biotic interactions, population dynamics, and disturbance regimes can be ignored when predicting range changes (88). SDMs predict the likelihood of a species occurring where conditions are similar to those where the species has been observed, i.e., habitat suitability. Species niche is defined as conditions where population growth is positive (89). In forecasting the future, will a species persist, and where? This question can be addressed with single and multispecies models that simulate dynamics and range shifts of plant populations and communities (Table 1) (90).

Linking Climate to Species' Vital Rates. A demographic response can be related directly to climate factors that are functionally related to a physiological process, e.g., drought leading to tree mortality via hydraulic failure. Climatic water deficit (CWD) above a threshold correctly predicted stand-level mortality of quaking aspen (*Populus tremuloides*) in the western United States in recent decades (91). Climate has also been linked to tree seedling survival for oaks in California where warming and drying is predicted to reduce recruitment under future climate scenarios (92).

Integral projection models (IPMs) project state variables (size, age) through time by integrating over several vital rates models (93). This regression-based approach can link intraspecific variability in vital rates to population level responses and has been used to make spatially explicit predictions of changes in population growth for a perennial shrub in South Africa under both climate change and altered fire regimes (94). Furthermore, directly estimating vital rates may be preferable to using probability of species occurrence from SDMs as a proxy; for temperate forest trees, high probability of occurrence corresponded to areas of high population density but with slow population growth rates (95).

Accounting for Dispersal Limitations When Predicting Species' Range Shifts. Several models impose seed (propagule) dispersal limitations to predict where a species distribution might shift with shifting climate (96), often using a cellular automaton simulation and a dispersal kernel (97). Some also incorporate demographic factors that can change with changing climate (98). Spatially explicit patch occupancy modeling predicts colonization and extinction of tree species in plots between successive forest inventories accounting for dispersal limitations (99). Using this approach, dispersal and competition were identified as being as important as climate in explaining recent distribution changes of Iberian forest trees (100). Even simple approximations of dispersal limitations improve the realism of predicted range shifts under global change scenarios (101). When dispersal limitations are accounted for, plant ranges are predicted to shift more slowly than climatically suitable habitat.

Single-Species Models: SDMs Linked to Population Dynamics. Population viability analysis (PVA) relies on concepts and models in population ecology and has been widely used in conservation biology to assess extinction risk for individual rare and endangered species (102), to rank potential management actions, and to inform research and data collection. The need to assess the impacts of a broad array of threats on species has resulted in model developments that allow simulation of multiple agents of global change on single species, including invasive species, disease, altered disturbance regimes, land-use change, and climate change. Traditional metapopulation theory typically includes local extinctions in patches that can be recolonized via dispersal. However, in cases where subpopulations are fragmented via habitat loss, or shifted and isolated due to climate change, there may be little to no chance for recolonization of patches following extirpation. In these cases, changing carrying capacities or vital rates within habitat patches through time (103) due to climate change or altered disturbance regimes, captures the effects of changing habitat in conjunction with other threats on population dynamics (104). This approach, using habitat patches defined by SDM under climate and land-use change scenarios, has shown that when demographic rates, metapopulation structure, disturbance,

Table 1. Model frameworks used to forecast effects of global change on plant species and community dynamics

Type of model	Method	Ecological scale	Global change factors	Di	VR	BI	DR	Example key findings
Single focal species								
Species distribution	Statistical	Species (S)	Climate*; land use					Magnitude of predicted shifts in habitat varies widely among species
Cellular automaton; patch occupancy	Simulation	Species (S)	Climate; land use	✓				Plant ranges will shift more slowly than climatically suitable habitat
Metapopulation	Simulation	Population (S)	Climate*; land use; altered disturbance; invasives	✓	✓	(✓)	✓	Extinction risk greater than expected on the basis of available habitat; altered disturbance can be more immediate threat than climate
Integral projection	Statistical	Population (S)	Climate*		✓			Useful when population density is uncorrelated with population growth
Multiple interacting species								
Landscape disturbance and succession	Simulation	Community (M)	Climate(*); land use; altered disturbance; invasives	✓		✓	✓	Legacies of disturbance (logging, fire) will affect forest carbon dynamics and succession under climate change (55); land management interacts with climate change (116)
State and transition	Simulation	Community (M)	Climate; altered disturbance	(✓)			✓	Lag in vegetation response to climate change; sudden vegetation shifts triggered by changing fire regime
Dynamic global vegetation	Simulation	Ecosystem (M)	Climate; altered disturbance; CO ₂ , nitrogen; land use				✓	Increasing tree cover in dry tropics with increased temperature and CO ₂ (130); Xeric vegetation replacing mesic under warming drying conditions, carbon stock stable or declining, mediated by fire suppression and land use

Method of implementation, scale of ecological organization, whether single (S) or multiple interacting species (M) are simulated, and global change factors whose effects can be simulated (multiple factors indicate the model can simulate multiple threats). Ecological processes that are explicitly addressed are indicated with a check: dispersal (Di), population demographic vital rates (VR); biotic interactions (BI), and disturbance regimes (DR).

Climate change effects always, or sometimes (), incorporated via dynamic species distribution models.

and dispersal are explicitly simulated, population declines or extinction risks are often projected to be greater than what would be expected solely on the basis of available habitat (105, 106). Moreover, some populations are projected to decline despite projections of increased habitat due to climate change (107). Especially for plant species sensitive to fire interval, too-frequent fire can pose a more immediate threat to population persistence than future climate-change effects on habitat suitability (Fig. 3) (105, 108). PVA can also be used to evaluate the efficacy of adaptation measures such as fire management, invasive species control, and managed relocation (109, 110).

In another single-species approach, species distributions are primarily controlled by phenology alone or in combination with other biophysical mechanisms (111). Factors such as chilling, length of the growth season, or budburst are explicitly modeled, and key phenological controls explain species distribution for 17 North American trees (112). Recently, these phenology-based models have been linked to population dynamics to show that climate variability at the end of the 21st century could enhance local extirpations at the core of the European beech distribution during a projected migration to higher latitude and altitude (113).

Multispecies Dynamic Vegetation Models. In contrast with single-species approaches, models of vegetation dynamics explicitly consider multispecies interactions, especially resource competition (Fig. 4). Landscape models of disturbance and succession rely on stochastic, spatially explicit simulations to forecast vegetation shifts at extents of 10s to 100s of square kilometers (114). Modeling at this scale allows low-level mechanisms such as photosynthesis and respiration, light availability, and nutrient cycling to be linked to large-scale disturbance regimes (e.g., fire, drought; Fig. 4). They are usually parameterized for tree species, although plant functional types can be used, making landscape models applicable to non-

forest vegetation (115). Although these models have often used predetermined rules to simulate successional dynamics (116), a new generation simulates physiologically based processes of growth, mortality, and regeneration, improving their potential for forecasting climate driven shifts in vegetation (117).

Landscape models have yielded insights about interacting effects of land management and climate change. For example, carbon sequestration in western US forests is projected to continue into the 21st century owing to successional legacies of 19th century logging, but if climate change leads to more high-severity crown fires, this could limit the potential for carbon storage (55). Changes in land use may affect vegetation shifts. Although forests are predicted to expand to higher elevation in the Swiss Alps under climate warming scenarios, intensive pasturing would slow this forest shift and maintain high plant diversity in the landscape (118).

Landscape models can simulate vegetation dynamics for past and future climates to tease apart the effects of climate vs. land use on paleovegetation. Forest composition simulated for the last 7,000 y in northern Italy, using temperature as the climate forcing, showed that moderate climate change during the Holocene could not explain the dramatic decline of *Abies alba* and increase in evergreen oaks detected in the pollen record (119). The observed vegetation changes could only be simulated when increased grazing and frequent fires, associated with Neolithic human settlement, were included in the model.

State and transition modeling (STM) offers a flexible framework for projecting vegetation changes under global change. In STM, vegetation can change from one state to another using either deterministic or probabilistic rules. Simulations of grassland-shrubland-woodland states and their potential feedbacks with climate and fire in Mediterranean-type ecosystems suggested that sudden vegetation shifts may be triggered by small variations in vegetation flammability and fire recurrence (120). Although traditionally nonspatial (121),

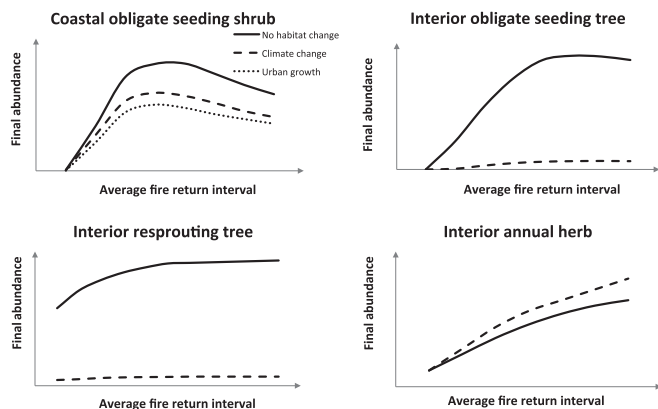


Fig. 3. Relative changes in final population abundance for three plant functional types based on species in southern California, under altered fire regime, climate change, and land-use change (urban growth). The plant functional types span shrubs, trees, and herbs and are long (obligate seeders and resprouter) and short (annual herb) lived. The obligate seeders accrue seed banks. The resprouting tree is the only species with seed dispersal beyond a few meters. All species are adversely affected by frequent fire. The reliance of obligate seeders on optimally timed fires for germination renders frequent fire their most serious threat. Urban growth tends to occur near the coast in this southern Californian scenario and only affects the species with a coastal distribution. The climate change effects differ substantially depending on the functional type and location, strongly affecting the interior resprouting and obligate seeding species; long distance dispersal by the resprouter is insufficient to match the pace of habitat shifts. The coastal obligate seeding species is less affected by climate change than the interior species due to different climatic conditions and projected changes therein. Conversely, population abundance of the interior annual herb increases with climate change as occupied patches of suitable habitat become larger. The only consistent global change effect occurs with very frequent fires which reduce populations in all cases, whereas the effects of urban growth and climate change are context dependent (results based on refs. 106, 109, 110, 141, and 142).

a spatially explicit STM (STSM) (122) has been developed in which a grid cell's transitions are dependent on neighbors' states. Applied to central Oregon, an STSM predicted that, although vegetation would be stable during the first 40 y of climate change, abrupt changes would subsequently occur (123).

The STM framework is well suited to analyze thresholds and abrupt changes in vegetation (124), but also has limitations. For instance, vegetation states and their transitions are defined in terms of existing species assemblages, but patterns of species coexistence and vegetation change may not remain the same under novel climate and biogeochemical conditions in the future (12, 13). Coupling with mechanistic models may, however, circumvent these shortcomings (125).

Dynamic global vegetation models (DGVMs) mechanistically model interactions and feedbacks between the land surface and the atmosphere. DGVMs simulate physiological processes, such as photosynthesis and respiration, and biogeochemical cycles (126), and include the effects of fire, atmospheric CO₂ concentration, and competition between plant life forms for light, water, and nutrients on vegetation dynamics (127, 128). They were designed to predict continental or global patterns of vegetation and feedbacks to climate. Computational and parameter limitations have prevented these models from simulating the many individual species making up plant communities, and, instead, vegetation is grouped into physiognomically defined functional types, such as forest, woodland, grassland, and desert. DGVMs incorporate competition (129) and even land management (130).

Although developed to represent realistic feedbacks between vegetation change (affecting land surface properties) and the climate, DGVMs are now being used to forecast the effects of climate change, land-use change, and fire on vegetation patterns and ecosystem processes. Current vegetation patterns of tropical grassland-savanna-forest in Africa are only reproduced if fire is

included in the DGVM, and future climate scenarios project a growing regional dominance of trees owing to temperature increases and CO₂ fertilization effects (131). Simulations using a newer-generation DGVM (MC2), run for the continental United States under nine future climates, predict that fire and land management may play a substantial role in mediating the extent and composition of major vegetation types, as well as the size of carbon stocks, in the 21st century (132). Although fire suppression led to the expansion of forests and woodlands, offsetting carbon loss due to unmanaged wildfire and other management practices such as forest and crop harvesting substantially reduced carbon sequestration. The importance of fire and land management was also evident in regional-scale simulations using the same DGVM in the Pacific Northwest of the United States (133). Across all simulated climate scenarios, fire frequency was projected to increase with climate change, but fire suppression substantially offset this trend. Although a transition from conifer to mixed forest was projected in some subregions, the overall dominance of conifer forest is expected to continue, albeit with significant loss of subalpine communities. Overall, these multi-species modeling studies highlight the importance of land use and other direct human activities in mediating the effects of climate change on future vegetation dynamics.

Summary and Future Challenges

Forecasts of future vegetation dynamics in the face of rapid global change are informed by a rich legacy of observational and experimental studies, including research networks and remote sensing spanning decades, historical data spanning centuries, and

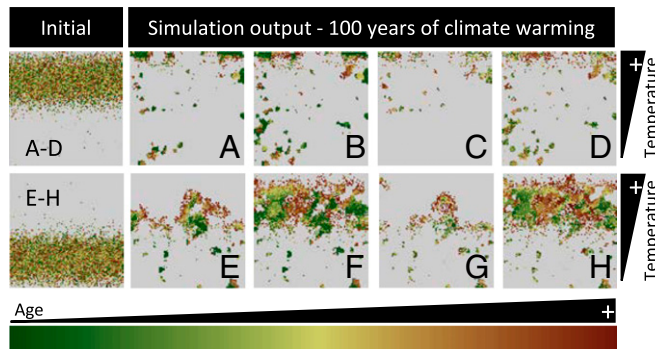
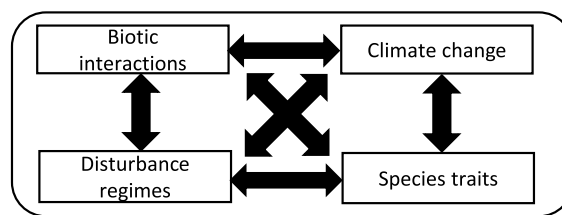


Fig. 4. Multispecies modeling showing vegetation dynamics departing from species climate equilibrium as a result of disturbance, species traits, and competition for light (detailed in ref. 143). Eight species represent a combination of physiological and dispersal traits. A–D are cold adapted species with identical initial distributions in the upper (cold) part of the idealized landscape, and E–H are warm adapted species with identical initial distributions in the lower (warm) part of the landscape. Simulated climate change displaces the climate niche of all species upward. Species interactions, disturbance dynamics, and spatial heterogeneity of climate (refugia) result in patchy distributions after 100 y of climate warming (simulation output). (A and E) Short distance dispersing, shade tolerant with establishment following disturbance. (B and F) Long dispersing, shade tolerant. (C and G) Short dispersing, shade intolerant. (D and H) Long dispersing, shade intolerant. Cold adapted species may be able to persist in warmer areas if enough environmental heterogeneity is present (refugia), especially if they can disperse long distances and/or are shade tolerant (A, B, and D).

paleo-environmental studies spanning millennia or longer. They all point to highly dynamic terrestrial vegetation, responsive to climate and other global change factors, with vegetation changes feeding back to the global climate system and biogeochemical cycles via primary productivity, carbon sequestration, and fire. From a human spatial and temporal scale, it may not be intuitive to think of vegetation as highly dynamic, so these long-term datasets and forecasting models provide broader spatial and temporal perspectives. Continued monitoring going forward, building on legacy experiments and data, will provide deeper understanding of the mechanisms underlying ecosystem response to global change.

What general predictions can be made about changing global vegetation in the 21st century? Land-use change and human-altered fire regimes in recent centuries have had long-lasting effects on vegetation dynamics that can overshadow and interact with climate change impacts. The magnitude and rate of change in both land use and fire regimes has increased dramatically in recent decades, and thus, these may have even stronger long-term legacy effects in the coming centuries, and these effects must be considered in conjunction with any projections of climate change. Long-lived trees and other woody plants are sensitive to land use legacies and are likely to be in disequilibrium with climate, so that as the climate warms, there may be lags in both decline at the trailing edge and establishment at the leading edge of ranges (22). This lagged response may result in vegetation change driven by large-scale forest mortality and lack of reestablishment as a result of extreme climate events (drought) or climate-driven disturbance (fire, pest outbreaks). Even where precipitation does not decline, increasing temperatures negatively affect water availability to plants, and this is a strong driver of forest mortality (134). A challenge is to understand where and under what conditions there may be buffering mechanisms that reduce the vulnerability of vegetation to climate change (Fig. 4).

Forecasting tools that incorporate multiple global change drivers or threats (Table 1) are in an active state of development and include models that focus on a single species and those that incorporate multispecies interactions. Single-species approaches are powerful tools for projecting the future fate of a focal species. Single-species models can also be applied simultaneously to several species, providing a first approximation of community response when species response is relatively insensitive to biotic interactions, or when species interactions may be novel and difficult to predict. Even when detailed demographic parameters are unavailable, models that account just for dispersal ability can determine the degree to which dispersal limits species' ability to track habitat changes caused by global change. Comparison of a growing number of single-species models identifies those best able to provide general predictions of range dynamics under global change, and those tailored to specific predictions for focal species of conservation concern (90).

Landscape disturbance and succession models build on foundational concepts in plant community ecology, incorporating multiple, interacting plant species and disturbances, but are nevertheless data hungry for both species traits and spatially explicit information on initial conditions (species distributions, landscape age structure). Addressing the data gap with aggregated data (135), emerging concepts and tools from functional biogeography (136), and novel remote sensing approaches (72) is an ongoing challenge. Dynamic global vegetation models were originally used to characterize land surface feedbacks to the climate via terrestrial

vegetation's role in biogeochemical cycles. Typically operating at coarser spatial grains than landscape models, they have nonetheless improved in their capacity to simulate at finer scales and to incorporate disturbance and land-use change, projecting the redistribution of plant functional types in response to multiple drivers. The ecological and spatiotemporal scale gaps between landscape models and DGVMs are narrowing (137), but still represent a future challenge; their primary emphases on community vs. ecophysiological processes provide complementary abilities to fully address global change effects on vegetation dynamics. Improved models incorporating the effects of species interaction on population demography and vegetation response to global change are needed (138). Individual-based models of forest dynamics, validated using new remote sensing technology, have been proposed for forecasting climate change effects over large regions at a scale fine enough to capture key ecophysiological processes (73).

What are the future challenges? In addition to expanding and improving the data, experiments, and models we reviewed, there are other challenges for predicting vegetation response in a rapidly changing world. When and where will vegetation dynamics be strongly influenced by novel biotic interactions: both plant-plant interactions in novel assemblages and also with invasive species, pollinators, dispersers, and pathogens? Will novel biogeochemical conditions (CO₂ effect, N deposition) affect interspecific competition, leading to unexpected successional trajectories? To what degree will intraspecific variation in physiological tolerances and other traits allow species to persist in the face of global change threats (139)? Will interactions between climate and disturbance regimes lead to thresholds and rapid shifts between vegetation types? These key questions are still largely unresolved and require models able to integrate plant physiology, demography, and biogeography, as well as social and land-use sciences. A key future challenge is to better account for human decision-making, policy impacts, and feedbacks in models and projections of future vegetation change (140).

Modeling frameworks that can account for the multiple interactive processes are required to predict vegetation change in response to rapid 21st century global change. While advocating for a greater diversity of drivers, we are aware that models are simplifications of reality and limiting model complexity is not only necessary in light of computational constraints but is also required to improve our understanding of socio-ecological systems.

We expect the diversity of models and data being collected to continue to grow, but in the future, models should be seamlessly fused with data streams, so that predictions can be constantly updated with new data. Finally, we encourage joint forecasting using several of the approaches outlined in this review. Inference from complimentary approaches will provide a better global overview of the importance of multiple drivers and short- and long-term responses, but will also provide a more comprehensive picture of what we don't know and a road map to new data collection and synthesis.

ACKNOWLEDGMENTS. I. McCullough kindly provided the photo in Fig. 2. This work was supported by US National Science Foundation's (NSF) Macro-systems Biology Program Grants EF-1065826 (to J.F.) and EF-1065753 (to H.M.R.), NSF's Division of Environmental Biology Grant 0824708, US Department of Energy Grant DE-FC02-06ER64159, and California Landscape Conservation Cooperative Grant 5288768.

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