Current Climate Change Reports
https://doi.org/10.1007/s40641-020-00168-6

ADVANCES AND FUTURE DIRECTIONS IN EARTH SYSTEM MODELLING (I SIMPSON, SECTION EDITOR)

Trait-Based Modeling of Terrestrial Ecosystems: Advances and Challenges Under Global Change

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Accepted: 24 November 2020

Abstract

Purpose of Review We summarize the general structure of modern terrestrial ecosystem models and investigate how advances in trait-based modeling approaches help to better constrain predictions for ecosystem sensitivity to global change.

Recent Findings In ecosystem models, empirical parameters are increasingly being replaced with plant physiological trait-based parameters, which can be directly measured in the field. The needs to predict long-term terrestrial ecosystem dynamics under climate change have spurred novel model developments including the representation of (i) vegetation processes across the critical zone, (ii) wood and belowground ecophysiology, and (iii) the effects of physiological trait acclimation.

Summary Trait-based modeling of terrestrial ecosystems allows for the direct integration of measured plant ecophysiology with model processes, increasing the potential to constrain uncertainty and improve predictions under novel climate regimes. However, such increased model complexity requires careful model design, standardized intercomparisons, and benchmarking for model responses to both climate extremes and long-term trends.

Keywords Terrestrial ecosystem model · Climate change · Plant functional trait · Trait acclimation · Optimality theory

Introduction

Terrestrial ecosystems host enormous biological diversity and provide vital ecosystem services to human and natural systems [1]. From a biogeochemical perspective, terrestrial ecosystems sequester approximately a quarter of anthropogenic CO_2 emission annually [2], contribute disproportionately to inter-annual variability in the global carbon cycle [3], and exert diverse and complex climate feedbacks [4]. Therefore, terrestrial ecosystem dynamics are a central component of Earth system models (ESMs), which are a primary tool for understanding the dynamic responses of the Earth system to a rapidly changing climate and increased anthropogenic disturbance [5]. Despite the known importance of terrestrial processes in Earth system feedbacks, internal model uncertainty associated with terrestrial ecosystem processes exceeds the uncertainty associated with different climate scenarios in the current generation of ESMs, even at the decadal and longer time scale [5], implying the paramount need to improve terrestrial ecosystem models.

Vegetation is the foundation of all terrestrial ecosystems and regulates the carbon-water-energy nexus as well as other biogeochemical cycles from local to global scales. Because of its foundational role as primary producer, vegetation is the focus, and in many cases the only life form incorporated in the ecosystem component of ESMs. Historically, ecosystem model development was motivated to represent biological and Earth system processes at two contrasting scales. At the global scale, the need to explain biogeographic patterns, biogeochemical cycles, and their interactions with climate spurred development of the very first generation of dynamic global vegetation models (DGVMs) [6]. DGVMs prognostically simulate the distribution of vegetation plant functional types (PFTs) instead of merely prescribing vegetation types from land cover maps. In these early DGVMs, vegetation was

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This article is part of the Topical Collection on *Advances and Future Directions in Earth System Modelling*

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simplified as multiple “green blankets” (usually referred to as big leaf models) with no explicit representation of ecosystem structures within a model grid cell (usually > 1° in spatial resolution). In contrast, at the stand scale, individual-based models (IBMs or stochastic gap models) aim to predict forest dynamics by explicitly simulating the fate of individual trees with consideration of stochasticity within a finite population [7, 8]. In recent decades, cohort-based models, such as the ecosystem demography (ED) model, integrate the global scope of big leaf models with a more detailed representation of vegetation demography drawn from IBMs into vegetation classes or “cohorts” within terrestrial biosphere models [8, 9•]. Such refinement of ecosystem structure in models benefits from a more mechanistic representation of ecophysiological processes, such as competition for light within a canopy. As a result, model parameters that used to be highly empirical and require calibration and/or tuning can now be directly connected with field observations of plant physiological traits.

The development of ecosystem models toward trait-based approaches over empirical functions has several advantages. First, trait-based models have the potential to be more accurate when predicting ecosystem responses to unprecedented novel climate regimes because they better reflect the ecophysiological processes underlying ecosystem responses to climate variations [10•]. Thus, trait-based models can reduce model predictive error associated with physiological processes [11], as well as the need for empirical model parameters or constraints [12]. Second, trait-based models can better account for plant functional diversity compared with the traditional physiognomy-based PFTs (e.g., evergreen broad-leaf forest). Third, trait-based models allow for assimilation of the wealth of global functional trait data to reduce model predictive error associated with parameter uncertainty [11, 13•]. Lastly, trait-based approaches empower ecosystem models to become the platform for numerical experiments that can help to generate and evaluate hypotheses in an iterative feedback loop between modelers and eco-physiologists.

Recent reviews on ecosystem modeling span vegetation demographics [[illegible]•], the evolution of gap models [8], hydrodynamics [14], and agricultural ecosystem modeling [15]. However, despite the rapid evolution and model development in trait-based modeling, a review on advances and challenges of trait-based approaches in mechanistic terrestrial ecosystem modeling is lacking. Here, we aim to summarize (1) the key ecophysiological processes in modern trait-based ecosystem models, drawing on developments from approximately the last decade up to 2020, (2) the incorporation of new model processes, physiological traits, and the associated predictive benefits, particularly in the context of model predictions during a time of rapid global change, and (3) the trade-offs associated with more mechanistic, but also more complex ecosystem models. Finally, we make recommendations as to the usage, interpretation, and future development of trait-based ecosystem models targeted at a wide-ranging audience from field-based ecophysiologists to Earth system scientists and ecosystem modelers.

Key Process-Based Modules That Comprise Modern Terrestrial Ecosystem Models

Modern terrestrial ecosystem models consist of interacting modules (here defined as relatively self-contained submodels) that reflect distinct ecophysiological processes and their integral to capturing ecosystem dynamics at [illegible] scales ranging from minutes to decades. Inevitably, these ecophysiological processes are tightly coupled with land surface processes such as carbon, water, nutrient, and energy balances, forming an integrated terrestrial biosphere model (TBM) that simulates terrestrial ecosystem dynamics and the associated physical, chemical, and biological processes at regional to global scales for coupling with ESMs. Here, we focus only on the plant physiological processes that occur at the individual scale and the ecological interactions that occur between individuals. These ecosystem processes are nested within other land surface processes in the Earth system. In this section, we summarize the general module structure shared by most mainstream ecosystem models (Fig. 1), as well as common implementations of these modules. Subsequently, we discuss novel developments and future research needs for trait-based modeling.

Individual-Level Modules

Resource acquisition is the foundational process in terrestrial ecosystems. The representation of resource acquisition in terrestrial ecosystem models begins at the leaf-level with the photosynthesis-stomata module. The purpose of the photosynthesis module is to predict leaf-level carbon assimilation from measurable biochemical parameters (or physiological traits) and abiotic environment (such as intercellular CO_2 concentration, light, and temperature). The stomatal module bridges the leaf intercellular space with canopy air spaces and biophysically constrains carbon and water fluxes from the aspect of gas diffusion. The most commonly used framework in ecosystem models is the Faqhuar, von Caemmerer, and Berry system [29]. Collectively, the photosynthesis-stomata modules form the foundation for mechanistic ecosystem predictions under climate change. In addition to leaf-level photosynthesis, the rhythmic seasonal changes, or phenology, of plant leaf area are also important for characterizing vegetation carbon gain [30]. Generally, ecosystem models simulate seasonal dynamics of leaf area using abiotic cues such as light, temperature, and water for deciduous trees while assuming a constant leaf area for evergreen trees [31]. In contrast to the aboveground, ecosystem model representation of

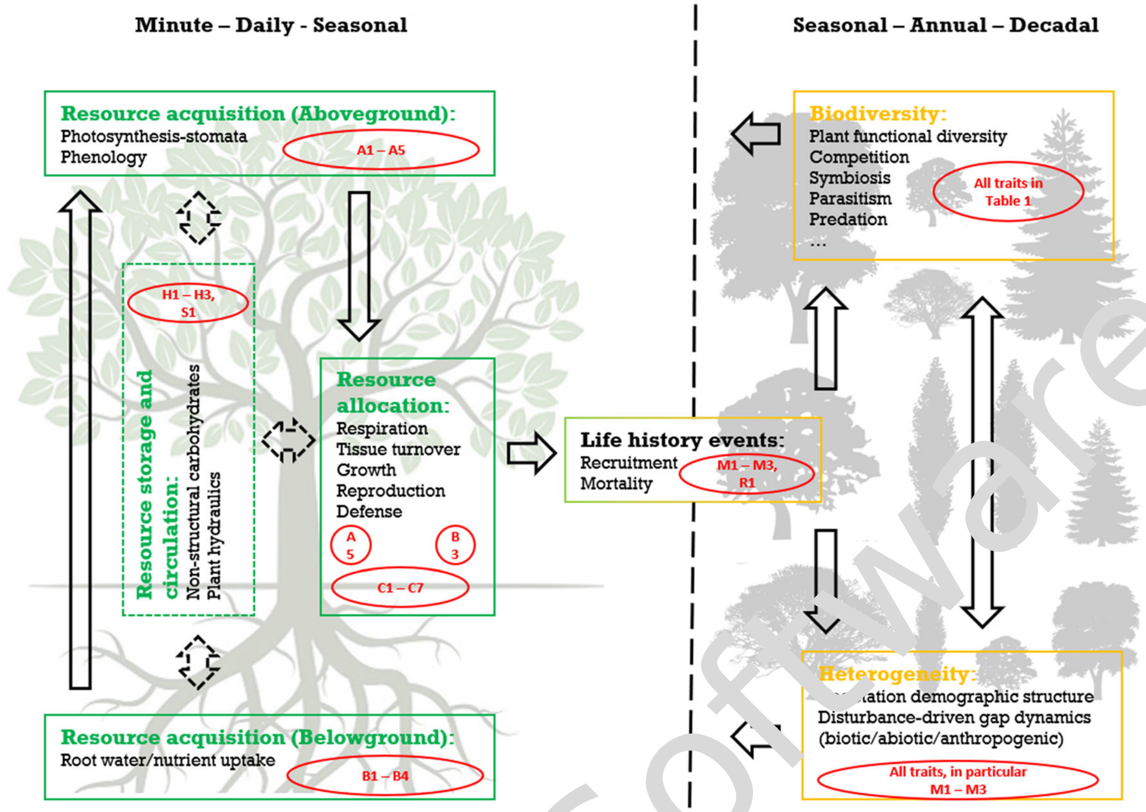

Fig. 1 Key process-based modules (rectangles) within modern ecosystem models, separated into individual-level physiological processes (green) that operate from minute to seasonal scales and community to ecosystem-level ecological processes (orange) that operate beyond seasonal times scales. Life history events bridge the two scales and are thus colored by both green and orange. Arrows denote the dominant direction of interactions between modules. In most ecosystem models, belowground resource acquisition will directly exert limitation on aboveground resource acquisition using semi-empirical parameters. Novel model developments of resource storage and circulation (dashed green rectangle) can represent resource flows within plants in a more mechanistic way and interfaces with both resource acquisition and allocation. Select trait-based parameters in each module as summarized in Table 1 are shown in red circles and ellipses

belowground resource usage is relatively simple due to limited data availability and mechanistic knowledge on belowground processes. Key belowground processes, including water and nutrient acquisition (if applicable), are usually represented using empirical functions dictated by belowground plant root biomass [32].

Resource allocation is coupled to resource acquisition and describes how plants distribute resources, particularly carbon derived from photosynthesis, among different tissues, including leaves, stems, roots, and nonstructural carbohydrate reserves (NSC). In ecosystem models, the carbon gained by an individual through photosynthesis, or the gross primary production (GPP), is allocated based on a distinct hierarchy of priorities for different physiological processes. First, carbon is used to satisfy processes which maintain plant activity including autotrophic respiratory costs of different organs (leaves, stems, and roots), and necessary tissue turnover from phenological processes or disturbance. Extra carbon is then allocated to structural and reproductive growth following allometric relationships [10•]. At the cutting edge of ecosystem model development, some models have begun to incorporate plant defense investment, including bark growth [33] and VOC emissions [34].

Resource acquisition and allocation ultimately determine key plant life history events such as recruitment and mortality, bridging individual- and ecosystem-scale processes (Fig. 1) and enabling the prediction of long-term ecosystem dynamics [35]. In traditional big leaf ecosystem models without vegetation demographics, seedling recruitment is absent, and new plant individuals are added to a common biomass pool of a given PFT within a given grid cell. Thus, recruitment is analogous to growth in that both increase the PFT biomass pool. The introduction of vegetation demographics into modern ecosystem models [9•] requires explicit consideration of vegetation recruitment and its sensitivity to different environmental factors because the states of the seemingly insignificant understory seedlings have the potential to determine ecosystem structure and composition decades in the future [36].

Mortality, and especially mortality of large individuals, can strongly affect vegetation carbon storage in the Earth system [37]. However, the mortality module in ecosystem models has been recognized as one of the most mechanistically uncertain processes, the impacts of which are especially apparent for predictions over long (decades to centuries) time scales [38•]. Most ecosystem models include a background mortality rate, which is insensitive to environmental stressors and stand density and is usually constrained by observed maximum tree size or age (in models with vegetation demography) [38•, 39]. Stress-driven mortality is usually limited to mortality driven by carbon starvation based on a variety of metrics ranging from net primary productivity, growth rates, or plant carbon balance [38•]. In practice, carbon starvation mortality in ecosystem models has mostly been optimized for systems where the stress of light competition dominates, rather than other stressors such as water or nutrient stress [40]. Ecosystem model mortality modules may also represent mortality from other biotic stresses such as low temperature, hydraulic failure, and insect attack [41], which can be more dominant processes during extreme events [42].

Ecosystem-Level Modules

Ecosystem-level processes can be organized into two interconnected ecological themes: biodiversity and heterogeneity (Fig. 1). Biodiversity across multiple scales strongly shapes ecosystem function and sensitivity to environment [43]. In fact, ecosystem diversity is both a key motivation and a grand challenge for improving ecosystem dynamics within Earth system models [5]. The most common method for representing biodiversity in ecosystem models is through multiple co-occurring PFTs, a conceptual group of species that perform similar functions in the ecosystem. The level of ecosystem complexity can range from relatively simplistic, such as a tree PFT shading a grass PFT, to more sophisticated, such as competition between trees of different size of the same PFT and between different PFTs in demography-enabled models. Depending on the model, competition for resources may include light, water, nutrients, or multiple co-limiting resources. PFTs are often defined by life forms and physiognomy (e.g., deciduous broadleaf trees and evergreen needleleaf trees) with biome boundaries constrained by empirical climate envelopes [12]. This approach has the advantage of easy parameterization and is readily able to be integrated with landscape-scale observations. However, the lack of (i) mechanistic representations of biome shifts [12] and (ii) functional diversity within each biome makes it impossible to robustly simulate ecosystems under novel climate regimes and thus difficult to predict ecosystem resilience to global change [44]. Therefore, recent modeling studies tend to define multiple competing PFTs following key plant functional and demographic trait trade-offs, especially in hyper-diverse tropical forests [45–47]. In addition to competition among plants, there are other ecological interactions among diverse life forms such as symbiosis, predation, and parasitism. Due to limited observations and mechanistic understanding of complex ecological interactions across life forms, few ecosystem models mechanistically include these interactions (but see [48] for representing parasitic lianas in the ED2 model).

Heterogeneity due to variations in ecosystem structure represents another layer of complexity that affects ecosystem dynamics in conjunction with biodiversity. Variations in abiotic and biotic conditions like tree size distribution, soil type, and topography regulate the micro-environment for individuals [49, 50]. It is thus critical to represent within-ecosystem heterogeneity because some ecological and ecophysiological processes, like photosynthesis and plant hydraulics scale nonlinearly within the canopy or among individuals [9•, 51]. Failing to capture these heterogeneous effects on ecosystem dynamics in an ecosystem model can result in cascading effects and diverging predictions for ecosystem structure and function over decadal scales [52, 53].

To account for sub-grid scale heterogeneity, modern ecosystem models are increasingly incorporating vegetation demography (i.e., explicit representation of tree size distributions and the associated competition for resources, see [9•]), enabling for the prediction of nonlinear dynamics associated with light competition within a forest canopy and the physiological constraints of vegetation hydraulics that scale with tree size (to name a few processes). Vegetation demography, which is controlled by the self-organized individual-level resource competition [54], is also strongly shaped by natural and anthropogenic disturbances. We subsequently review three major disturbance types included in ecosystem models, including fire, biotic disturbance, and anthropogenic disturbance.

Among disturbance types, fire is the most commonly represented in ecosystem models [41, 55–57] due to its large impact on not only vegetation but also other Earth system processes (e.g., carbon, water, and energy fluxes). The level of detail and complexity varies widely across fire models, but some models have even included the impact of functional traits such as bark thickness on plant survival with fire [33, 58]. In fact, the importance and complexity of fire dynamics have led to the development of a number of stand-alone fire models [57]. Though the inclusion of fire modules within ecosystem models is by no means a new development, it is still an active area of research and validation. For example, none of the ecosystem models used in climate change predictions were able to capture the extent of the severe fire season in Australia in 2019 [59], and a fire model intercomparison has not yet been included in the Coupled Model Intercomparison Project (CMIP) as of Phase 6 [60].

Other natural disturbance types, such as tree windthrow, are usually modeled as prescribed events or constant disturbance rates (e.g., [41]) with increasing efforts toward more mechanistic representations (e.g., wind [61] and lightning [62]). Meanwhile, few modeling studies explicitly include biotic disturbances from herbivores and insect attacks other than by treating them as prescribed events that modify ecosystem states empirically [63, 64]. Finally, anthropogenic disturbances such as logging and land use changes are usually introduced as external forcing to ecosystem models and are based on historical land use data sets and stand-alone land cover and land use models [65].

A common trend of model development is to replace empirical parameters and functions with mechanistic trait-driven approaches (see Table 1). Though this trait-based approach has the potential to improve ecosystem model predictions, in practice, biological systems are extremely complex and biological traits are more variable and dynamic than their physical parameter counterparts used in ecosystem models. In the next two sections, we summarize the progress and challenges toward representing biological complexity, and specifically hone in on temporal variations of trait-based parameters, to attain realistic predictions at decadal or longer time scales.

Beyond the Canopy: Integrating Plant Function Across the Critical Zone

Vegetation function connects natural processes across the critical zone (Earth's permeable near-surface layer) from tens of meters above the ground at the top of forests' canopies, all the way to the deep groundwater tapped by tree roots. Historical ecosystem model development focused mainly on canopy processes [6, 31, 66–68] for several reasons. First, canopy leaves exert the first-order control on plant resource acquisition and ecosystem carbon and water dynamics. Second, canopy states and dynamics such as leaf area index (LAI), leaf carbon assimilation rates, and evapotranspiration are relatively easier to measure across scales with the increasing prevalence of high resolution environmental remote sensing products [69, 70] compared to belowground processes.

Recent advances in canopy ecophysiology have led to more mechanistic and trait-based canopy models, although many of them are still experimental and have not been integrated into ecosystem models as standard components. Some examples of these experimental new developments include the representation of triose phosphate use (TPU) limitation to photosynthesis [29], optimality-based stomatal conductance models [71], and optimality-based ecohydrological equilibrium models [72]. Another avenue of active research pertains scientists' physiological understanding of leaf function (such as maximum photosynthetic rate), and how leaf function varies with phenological stage due to ontogenetic changes [73], especially in tropical evergreen forests with mild climatic seasonality [74]. Modeling experiments suggest that these phenological processes can substantially change ecosystem carbon budgets [75–78].

The canopy-centric view in ecosystem models has increasingly been recognized as myopic, given that canopy function is tightly coupled to stem and belowground processes. Moving forward, it is widely acknowledged that a better representation of the integrated critical zone, and in particular belowground processes, should be one priority in model development [32, 79, 80].

Wood biology has also been long under-represented in ecosystem models [79]. Woody stems regulate the transport of water, sugar, and nutrients through formation and maintenance of xylem and phloem, thus comprising a fundamental part of organismal metabolism. In contrast, in ecosystem models, stems are generally represented as a passive biomass pool dictated by empirical allometric equations [81]. However, an increasing realistic representation of wood biology is becoming a more standard module in ecosystem models (Fig. 1). For example, xylem vessels in the stem transport water from roots to canopy and thus link resource acquisition from both the above- and belowground. Water transport in the xylem can become the major bottleneck for plant water use, carbon assimilation, and survival even with adequate soil water supply [82]. While plant water stress functions and parameters are highly uncertain among ecosystem models [40, 83], incorporating hydrodynamics along the soil-plant-atmosphere continuum allows for a more mechanistic simulation of plant water stress for both acquisition, resource allocation, and plant life history (see [14, 84] for excellent reviews). Recently, the incorporation of plant hydraulics has received significant attention in the ecosystem modeling community [46, 85–87], fueled by the increasing availability for key hydraulic traits such as xylem hydraulic conductivity and vulnerability [88]. In hydraulically enabled ecosystem models, the downregulation or catastrophic failure of plant physiological activities under water stressed conditions where plant water potentials (a diagnostic of plant water status) become critically negative (see Table 1) is explicitly represented. Importantly, the physiological traits governing plant responses to water stress can be directly measured and mapped spatially with increasing capacity [85, 88–90].

Wood biology also affects tree carbon sink capacity (respiration costs and growth activity, in contrast carbon source capacity, which is regulated by photosynthetic carbon supply). As described in the last section, resource allocation in ecosystem models is tightly coupled to GPP (carbon source capacity), and thus variability in growth and other investments always tracks variability in GPP at all time scales. However, this modeling framework contradicts field observations on the seasonal and inter-annual variability in woody growth rates [91, 92]. Therefore, ecophysiologists have begun experimenting with sink-driven frameworks by representing growth needs as a function of environmental factors [93]. A sink-centric representation may change the sensitivity of ecosystem carbon drawdown and storage to climate change. To better integrate the process of sink-driving growth, ecosystem models need to

Table 1 Summary of select trait-based parameters for ecophysiological processes in ecosystem models

Trait-based parameter groups	Label in Fig. 1	Parameter uncertainty*	Abiotic drivers of trait acclimation**	Notes
Photosynthetic capacity	A1	Low	Temperature Light [16, 17]	e.g., Vcmax, Jmax, TPUmax Can vary due to leaf aging and leaf position in the canopy
Temperature sensitivity of photosynthetic capacity	A2	Medium	Temperature [18]	e.g., Q10 or activation energy for Vcmax and Jmax
Stomatal sensitivity	A3	Medium	CO_2 [19]	e.g., stomatal slope in traditional stomatal models and marginal water use efficiency in stomatal optimality models
Thresholds for leaf flushing and shedding	A4	Medium	Unknown	e.g., thresholds for growing degree days, photoperiod, and soil moisture
Leaf structural traits	A5	Medium	Light [17, 20]	e.g., leaf mass per area, leaf size
Root biomass spatial distribution	B1	Medium-high	Soil moisture and nutrient supply [21]	e.g., maximum depth, lateral and vertical distribution
Root uptake potential for nutrients	B2	High	Unknown	Mainly for nitrogen and phosphorus
Root structural traits	B3	High	Unknown	e.g., root specific length/area
Root mycorrhizae association	B4	Medium	Unknown	e.g., arbuscular mycorrhizae, ecto-mycorrhizae, and nitrogen fixation
Root/shoot ratio	C1	Medium-high	Moisture [22]	
Stoichiometry	C2	Medium-high	Unknown	e.g., C:N, C:P ratios
Biomass allometry	C3	Medium-high	Light [23] Moisture [24]	Aboveground allometry is relatively well characterized but belowground allometry has high uncertainty
Wood density	C4	Low-medium	Unknown	Determines carbon density of a given stem volume
Respiration rates and temperature sensitivity	C5	Low-medium	Temperature [25]	Uncertainty of leaf respiration is relatively low while wood and root respiration have limited data
Tissue turnover rates (or maintenance cost)	C6	Medium-high	Unknown	Leaf turnover rates can be constrained by leaf longevity while branch turnover is highly uncertain
Carbon partitioning between reproductive and structural growth	C7	High	Unknown	Can be size dependent
Hydraulic conductance	H1	Medium	CO_2 [26]	Including conductivity and sapwood area
Hydraulic vulnerability	H2	Medium	Water [27]	e.g., Turgor loss point and P50 (water potential with 50% loss of conductivity)
Hydraulic Capacitance	H3	Medium	Unknown	Include saturated water content and other parameters from pressure-volume curves
Allocation and turnover rates of non-structural carbohydrates	S[illegible]	High	Unknown	
Seed germination, dispersal, and seedling survival	[illegible]1	High	Unknown	
Background mortality rates	M1	Medium	Unknown	Independent from plant density
Density-dependent mortality rates	M2	Medium	Unknown	Mortality due to carbon stress
Mortality sensitivity to biotic stress and natural disturbance	M3	High	Unknown	e.g., mortality threshold for hydraulic failure, flooding, fire, and wind

*Check [28] for a more quantitative analysis of parameter uncertainty

**Note that trait acclimation is often not incorporated in ecosystem models

To improve readability, we group closely related parameters and relate them to the relevant modules in Fig. 1. We qualitatively assess the uncertainty of each parameter group using a three-tier classification: (i) traits with little or well-characterized variability across scales are labeled as *low* parameter uncertainty; (ii) traits with a qualitative understanding of variability but that are less well constrained than (i) are labeled as *medium* parameter uncertainty; (iii) traits with very limited understanding of variability are labeled as *high* parameter uncertainty. Finally, we identify the key abiotic factors that have been found to be important in trait acclimation from the literature simulate non-structural carbohydrates and other more labile and flexible resource storage pools [94] so that the source and sink capacities are partially decoupled.

Finally, woody respiration is generally overlooked or highly empirical in ecosystem models (e.g., implicitly included by a growth efficiency parameter [56]). In contrast, physiologists and ecologists have found that wood respiration can comprise one-third of canopy leaf respiration [95]. Thus, partitioning wood respiration into maintenance and growth-driven components with explicit linkages with plant size [96] would be helpful to constrain ecosystem carbon budgets in future ecosystem model developments.

Similar to woody stem processes, plant roots and the rhizosphere have long been represented in a simplistic manner or are totally absent in many ecosystem models, largely due to serious data limitations for the belowground [32]. However, there is strong interest across fields including plant ecologists, microbiologists, biogeochemists, and modelers to improve understanding and modeling of the belowground [32, 97]. For example, in a recent experimental ecosystem model development, the coupling of vegetation dynamics and rhizosphere root-microbe nutrient competition enabled a more realistic representation of soil nutrient limitation on biomass storage when compared to observed ecosystem responses [98]. Further, ecosystem models that include a representation of major plant-microbe symbiosis (e.g., facultative N-fixation, mycorrhizal association) predict higher vegetation carbon storage compared to models where these processes are absent [99, 100•]. These two model examples demonstrate the potential importance of the belowground on terrestrial carbon cycling and serve as a platform for future research.

In addition to nutrients, water uptake is also highly dependent on root structure and traits, especially in arid and semi-arid ecosystems. Important physiological attributes include rooting depth, root spatial distribution, and their inter-specific variations [101]. Understanding both within- and between-species variations has been recognized as increasingly valuable given the introduction of vegetation demography into ecosystem models because water stress responses can be size-dependent [102]. While most models assume an exponential distribution of root biomass with soil depth following ecosystem-level observations [103] and ecohydrological theory [104], the root distribution and its absolute rooting depth can be extremely variable depending on local hydrological conditions and species composition [102, 105]. Thus root morphology and root water access can contribute to the predicted uncertainty in plant water stress across space and time. Experimental model developments using a dynamic root hydraulic framework where water availability dictates plant root investment have recently been tested in some water-limited ecosystems [21]; however, this is still an area of active research. Finally, structural roots can also act as a large biomass storage, accounting for 10–20% total biomass in moist forests and up to 50–90% in dry and grassy ecosystems [103]. Overlooking structural root carbon pools or assuming a constant root/shoot ratio can lead to biases in carbon storage estimation in ecosystem models.

In sum, the expansion of trait-based processes beyond the canopy is shown to improve model performance [46, 85, 102] and significantly change long-term model predictions [98, 100•] while comprehensively evaluating the effects of incorporating these processes remain challenging at regional to global scale because of the increased model complexity and parametric uncertainty (Table 1). Moving forward, understanding how trait-based parameters across plant organs are related remains a critical area of research. Indeed, some studies have shown strong trait correlations driven by either coordination or trade-offs to form resource usage niches within a given plant organ ([106–108]; but see [88] for a lack of trade-off for hydraulic traits). However, within-species, among-species, and cross-site patterns can differ significantly [109], and in some cases coordination along the economic spectra is weak or absent [110]. Since trait assemblages represent a unique resource-use strategy that may underlie distinctive responses to climate change, either overstating or understating such trait correlations can lead to potentially large biases for future ecosystem predictions. This biological complexity can result in uncertainty in ecosystem model predictions and subsequent compensating errors when validating model predictions against present-day observations. Although the uncertainty associated with unknowns in the physiology can be partly mitigated through new techniques such as integrating trait and ecosystem dynamics observations into ecosystem models using Bayesian frameworks [13•], overcoming the biological complexity challenge ultimately requires novel data collection [69], open and effective data sharing [111], and careful data interpretation drawing on ecological and evolutionary theory.

Acclimation and Adaptation: Trait Plasticity to Environmental Changes

Plant traits are normally assimilated into ecosystem models as fixed parameters for each PFT. However, plant traits can vary widely in space and time, even within the same species [109, 112–114]. In fact, many key ecosystem model parameters respond to abiotic environmental changes (Table 1) such as temperature, moisture, light, nutrients, and CO_2 through acclimation (within a life cycle) and adaptation (across many generations) of plant physiological traits. Representing such trait evolution is another priority for trait-based ecosystem models [115] because trait acclimation and adaptation may greatly modify biosphere-climate feedback [116]. In this section, we review the recent progress and challenges in modeling key trait plasticity responses to environmental changes.

The most widely studied trait plasticity response is thermal acclimation of plant photosynthetic traits, such as the maximum rate of carboxylation (a photosynthetic trait) and leaf dark respiration under warming [114, 116, 117]. In ecosystem models, the temperature sensitivity of photosynthetic parameters is typically represented through literature-constrained Q10 relationships representing enzymatic sensitivity to temperature. However, these Q10 relationships in ecosystem models include no acclimation or adaptation to changes in temperature with routine exposure. In contrast, meta-analyses of spatial variations in plant traits provide evidence for significant temperature acclimation in the sensitivity of photosynthetic [18] and respiratory [118] parameters. In addition, warming experiments [114, 119] and optimality theory [16, 120] further support meta-analysis diagnosed acclimation trends. Recent physiological evidence indicates that such trait-temperature acclimation can happen as quickly as 2 weeks [114] and counters enzymatic sensitivity such that photosynthesis and respiration rates are relatively stable across a gradient of growth temperatures, in contrast to the strong temperature sensitivity currently represented in ecosystem models [16, 120]. As a result, if thermal acclimation processes are included in ecosystem models, projections for terrestrial carbon sequestration and storage may increase [117], depending on the relative change in sensitivity of photosynthesis versus respiration.

Another well-documented plasticity for plant biochemical, structural, and allometric traits is driven by light availability [17, 20, 113]. However, the extent to which these plasticities are represented is generally confined to photosynthetic acclimation in sunlit versus shade leaves [67], and the full implications of the light-driven plasticity (e.g., changes in leaf mass per area, leaf longevity, and allometry as presented in [17]) under global change are not well constrained. Aside from temperature and light, increasing CO_2 and changing moisture conditions can also influence the slope parameters in stomatal conductance modules [19] and plant hydraulic traits [26, 27].

In contrast to acclimation that can happen in a relatively short period of time, genetic adaptation takes multiple generations and thus is harder to measure and model with few attempts to account for mutation and adaptation in ecosystem models [115]. The physiology of adaptation of these processes has not yet been constrained to the point where it is feasible to include a representation in ecosystem models.

Given our limited understanding of the physiology of acclimation and adaptation, an alternate approach is to use optimality theory to estimate the best set of traits from an eco-evolutionary perspective [121•]. Coupled with evolutionary stable strategy analyses, optimality theory can help to generate the equilibrium sets of traits for an ecosystem [122], which in turn can constrain a best-case scenario prediction (where plants are super plastic and adaptive) for ecosystem dynamics under global change. Another enticing feature of optimality-based models is the compression of trait-based parameters into several key factors controlling coordination and trade-offs [121•]. However, understanding the time scale of reaching optimal equilibrium is a crucial consideration when aspiring to attain realistic future predictions, especially considering the changing disturbance regimes and increasing frequency of climate extremes. As an example, the novel P-model built on the optimality rules was able to capture average spatiotemporal ecosystem carbon fluxes but showed substantial biases during climate anomalies without additional constraints [123]. Overall, using optimality theory to constrain spatiotemporal variability in trait-based parameters holds significant potential for both improving the next-generation ecosystem models and enhancing our understanding as ecologists and physiologists as to the variations and limits of trait acclimation and adaptation. However, such optimality approaches can only be successful with careful model benchmarks for both long-term trends and responses to climate extremes [124, 125].

Conclusion

Ecosystem models serve as our main tool for predicting the future fates of our terrestrial ecosystems, and for informing effective mitigation plans to prevent catastrophic turning points in ecosystem structure and function under the ongoing rapid climate change [5, 115, 126–128]. While near-term variability in ecosystem dynamics can be successfully forecasted with minimalistic empirical models, such as data-driven models based on empirical relationships and remote sensing products [129], projecting long-term evolution of terrestrial ecosystems under novel climate regimes requires ecosystem models that consider ecophysiological and evolutionary processes. Our review summarizes the recent progress in ecosystem models toward a more explicit representation of physiological processes using plant functional traits and lays out major challenges for future trait-based model development (summarized below).

1. Development of trait-based models often increases the complexity of model structures by increasing the number of physiological and ecological processes (Fig. 1). While such complexity may help to make more rigorous model predictions of ecosystem functions (such as productivity, evapotranspiration, and biomass), it can hinder effective interpretation of model intercomparisons, especially when the comparisons only focus on high-level model outputs. As a community, we must carefully consider how we can gain knowledge about ecosystem sensitivity to global change from a range of complex models with different

assumptions of ecosystem dynamical processes that are often not apparent to the user of model products.

2. Compared with the traditional physiognomy-based PFT configuration, trait-based models require a more detailed representation of trait diversity for canopy leaves and increasingly stems and roots (Table 1). As a community, we must effectively incorporate plant functional diversity in trait-based models while maintaining model parsimony and identify priority datasets of traits and observations on vegetation dynamics for model parameterization and benchmarking.
3. In the context of climate change, the role of trait acclimation and adaptation in determining ecosystem sensitivity to various environmental factors has been identified as important, but more data is needed to parameterize ecosystem models. As a community, to advance this difficult problem, we need to identify what the key trait plasticities are to long-term climate regime shifts, at which point we can move towards determining how to incorporate these plasticities, while still capturing ecosystem dynamics to short-term environmental perturbations.

Comprehensively addressing these three challenges requires close collaboration between modelers, ecosystem ecologists, ecophysiologists, evolutionary biologists, and climate scientists. Here, we make the following recommendations for the usage, future development, and applications of trait-based ecosystem models.

1. Conducting standardized intercomparison studies for sub-modules (e.g., [29]) with homogenized inputs in addition to ecosystem models as a whole is critical to understanding the distinctive behaviors in sub-modules and diagnosing idiosyncratic model behaviors. Such module intercomparisons will require a more modular design of the models within the generalized overarching modeling framework for ecosystem processes. One possible method of systematic organization could require organizing processes according to key resource stocks and flows, as well as the dominant timescales of the associated dynamics (as outlined in Fig. 1) so that each sub-module has a set of well-defined and [illegible]able inputs and outputs. However, restructuring existing code can require careful planning, software engineering, and monetary resources.
2. Understanding coordination and trade-offs among physiological traits that affect plant carbon-, water-, and nutrient-use strategies is critical to constraining the trait-based parameter spaces. We recommend approaching this problem both through further measurements of trait coordination in conjunction with optimality theory and other organizing principles revealed for ecosystem dynamics [122]. In particular, belowground traits and dynamics are still the most uncertain processes followed by wood biology. These types of measurements need to be priorities for future data collections.
3. Constraining model sensitivity to trait-based parameters under different scenarios (e.g., long-term climate change and extreme events) is critical when prioritizing data needs for model parameterization. Such analyses are possible using Bayesian data assimilation system such as the Predictive Ecosystem Analyzer (PEcAN, [11, 13•]) and would benefit significantly from coordination and integration with ecosystem experiments [124, 125].

Acknowledgments X.X. acknowledges funding from Cornell CALS. A.T.T acknowledges funding from the USDA National Institute of Food and Agriculture, Agricultural and Food Research Initiative Competitive Programme Grant No. 20[illegible]-67[illegible]-3149[illegible], the University of California Laboratory Fees Research Program Award No. LFR-20-652467, and the NSF Grant 2003[illegible]05. We also thank two anonymous reviewers for providing insightful suggestions to improve the manuscript.

Compliance with Ethical Standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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