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Advancing Our Understanding of Tropical Forests and Improving the Predictive Capability of Vegetation Models with Data–Model Integration at Barro Colorado Island

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ABSTRACT. Tropical forests cycle large amounts of water, carbon, and energy between the land and atmosphere and are therefore essential components of the Earth system that must be adequately represented in models that predict the Earth's future climate. Representing the structural and functional complexity of tropical forests requires the ability to make detailed observations to inform model algorithms and parameters. In this chapter, we show how decades of data collection at Barro Colorado Island (BCI) have contributed to the development and testing of large-scale vegetation models and highlight the ways that these models in turn have improved our understanding of dynamics at BCI and across tropical forests. By sharing, assembling, adapting, and filling gaps in these data, integrated teams of modelers and empiricists have developed BCI into a high-value vegetation model testbed. We conclude with a discussion of future opportunities for data–model integration and call for a continued and strengthened collaboration between empiricists and modelers.

Keywords: demography; functional traits; hydrology; hydrodynamics; data–model integration; model testbed; vegetation demographic models

INTRODUCTION

Tropical forests cycle more carbon, water, and energy than any other biome but generally are underrepresented in observations and field experiments, making it difficult to use simple scaling or interpolation approaches to infer ecosystem sensitivity to change. Tropical forests are also structurally and functionally complex, and they exhibit dynamics that are still poorly understood. Yet their accurate representation within vegetation and Earth system models (ESMs; global coupled climate–biogeochemical models) is critical to better understanding these systems and to projecting global forest responses and feedbacks to ongoing environmental change. Addressing this challenge requires synthesizing and expanding a process-based understanding of tropical forest functioning and implementing this understanding within vegetation models.

In this chapter, we showcase the role that decades of intensive field observations at Barro Colorado Island (BCI) have played in the development and application of the newest ESM-integrated vegetation models and discuss how these models have advanced our understanding of the forest dynamics at BCI. We begin by introducing

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dynamic global vegetation models and describing the datasets and knowledge that make BCI an excellent vegetation model testbed. We then review ESM-enabled research on BCI forest structure and dynamics and on forest hydrodynamics. We close with a discussion of directions for future research. By highlighting advances from data–model integration at BCI, we invite greater collaborative effort between empiricists and modelers across biomes to advance the predictive ability of vegetation and ESMs.

NEXT-GENERATION GLOBAL VEGETATION MODELS

Dynamic global vegetation models, components of ESMs, are essential tools to understand, scale, and project vegetation dynamics and their feedbacks to the Earth's carbon, water, and energy cycles under global change. Most current ESM-coupled vegetation models have a "big-leaf" approach to biomes, meaning they represent vegetation with a single canopy layer and lack vegetation competition for light. In these models, global plant diversity is typically represented by a dozen or so plant functional types (PFTs), which are distinguished by their functional traits. Recently, a number of groups have developed cohort-based vegetation demographic models (VDMs) that represent structural and functional diversity at regional to global scales (Fisher et al., 2018). These next-generation vegetation models explicitly represent recruitment, growth and mortality, and height-based competition for light between a small number of PFTs within individual forest patches. PFT differences in growth, mortality, and response to climate and disturbance result in vegetation structure and distribution that varies across environments. By encoding first principles of community and physiological ecology based on trait-environment interactions, these models have more ecologically realistic predictive power. Because of the increased realism of VDMs, hypotheses can more easily be informed by, as well as tested against, field data. Once rigorously validated, the added complexity enables prediction of transient, multidecadal change in ecosystem structure and function under novel environmental conditions as well as terrestrial feedbacks to carbon dioxide (CO_2) and climate change.

Given the complexity of VDMs, a core focus of model development has been to enable reduced complexity configurations of models. This modular approach facilitates testing alternative process representation and degrees of complexity in different dimensions (Fisher and Koven, 2020). For example, in the Functionally Assembled Terrestrial Ecosystem Simulator (FATES), which is fully embedded in the land components of the Energy Exascale Earth System Model (ELM; Lu et al., 2018; Ricciuto et al., 2018) and the Community Earth System Model (CLM; Lawrence et al., 2019), it is now possible simulate demography and disturbance, using assumptions about photosynthesis and net primary productivity (NPP; Needham et al., 2020), or simulate physiology using assumptions about static stand structure (Chitra-Tarak et al., 2021). Given the large number of physiological and ecological processes that VDMs simulate, it is essential to constrain VDMs with empirical data.

BCI AS A VEGETATION MODEL TESTBED

To establish process-level confidence in model performance and to test new model capabilities, researchers have developed BCI as a vegetation demographic model testbed. We define a software testbed as the combination of datasets, model software, analytical, and visualization scripts (e.g., as narrative Jupyter Notebooks; http://jupyter.org) that can be used to test and improve a model at a site of interest. Specifically, the testbed consists of high-quality data that define initial conditions, boundary conditions, parameterizations, and model benchmarks for simulations at the site (Fig. 1).

One hundred years of research at BCI have resulted in a uniquely extensive collection of tropical forest data with which to drive, develop, and benchmark VDMs. Continuous subdaily meteorological data are required to run VDMs, and such long-term observations of BCI temperature, precipitation, humidity, radiation, and wind speed have been gap-filled and published as data products for reuse in models (Powell et al., 2017; Knox et al., 2019; Faybishenko and Paton, 2021). Forest census data from the 50-ha plot (Condit et al., 2019; https://forestgeo.si.edu/explore-data) have also been parsed for use in initializing VDMs so that the model starts with current stand structure, and for benchmarking VDMs by comparing model predictions of stand structure against observations. Measurements of ecosystem states and processes such as flux tower observations of gross primary productivity (GPP) and evapotranspiration (Detto, 2022), aboveground biomass (AGB), and soil moisture also serve as valuable benchmarks for model simulations (Chitra-Tarak et al., 2020, 2021; Fang et al., 2021).

Because VDMs do not represent individual species, modelers have assigned species to the PFTs used in their simulations based on functional traits and demographic trade-offs (Wright et al., 2010; Powell et al., 2018). Measurements of plant traits, such as those defining the leaf economic spectrum and hydraulic traits, may map directly to parameters that control photosynthesis, transpiration, autotrophic respiration, and tissue turnover. Other traits can help constrain parameter estimates. For example, measurements of tree height, crown area, and diameter near BCI informed estimates of allometry parameters (Martínez Cano et al., 2019). Variation within and correlation among plant traits have been used directly to examine alternate parameterization of PFTs and the range of ecosystem predictions that result (Koven et al., 2020).

Individual model development and application efforts may require additional specialized datasets that target gaps in observations (Fig. 1), such as hydraulic traits (Wolfe et al., 2021). Permanent repositories for data synthesized into model-ready data products or filling observational gaps for model

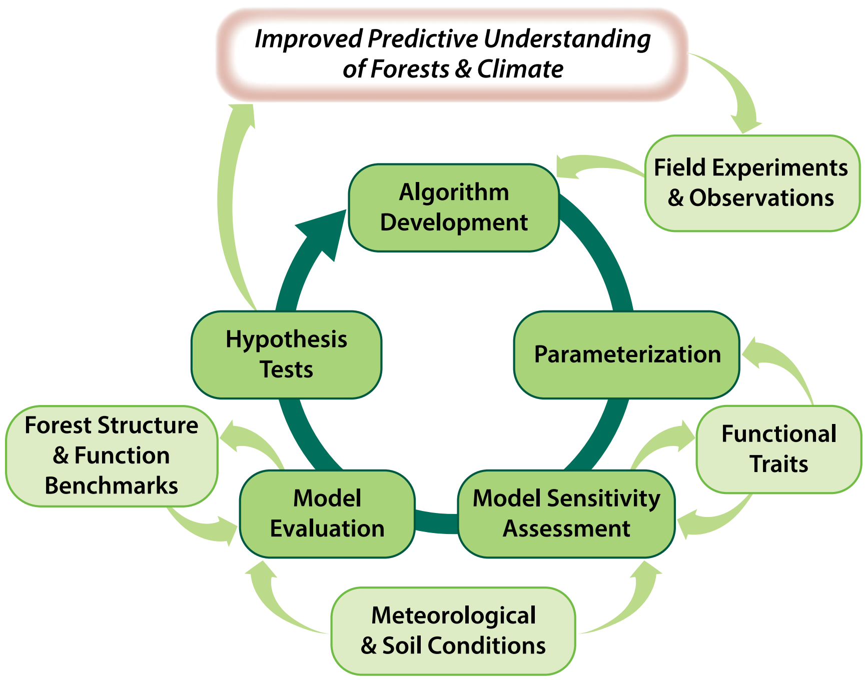

FIGURE 1. Illustration of how a collaborative model testbed, such as for Barro Colorado Island, can function. The diagram depicts an iterative set of vegetation demographic model activities (dark green boxes) and observational datasets and activities (light green boxes), which contribute to and can be influenced by each modeling effort. Existing knowledge, datasets, or data synthesis efforts contribute to model algorithm development, parameterization, sensitivity assessment, and evaluation, while many of these model activities reveal gaps in available data (and understanding), motivating new empirical work (arrows).

parameterization and evaluation (e.g., Table S1 for BCI) can more rapidly advance predictive science. By making core datasets publicly accessible, BCI has enabled its rapid development as a testbed for VDMs.

MODELING FOREST DEMOGRAPHY AND STRUCTURE AT BCI

Predicting demographic rates and forest structure are central goals of VDMs. Tree size distributions emerge from the combination of growth, survival, and recruitment of different species. Reproducing tree size distributions is thus a way to test ecological theories (chapter 33, Falster, 2024) and to ensure that important processes are properly represented in VDMs. Multiple VDM studies have used the BCI testbed to address questions related to forest demography and structure or to develop new model capabilities (Powell et al., 2018; Koven et al., 2020; Martínez Cano et al., 2020; Hanbury-Brown et al., 2022a).

VDMs in turn shed new light on forest dynamics at BCI and more generally. This is due to the capacity of models to forecast or hindcast over periods ranging from seasons to decades, to simulate forest dynamics with alternative hypotheses that can be informed by data, and to fill knowledge gaps by estimating hard-to-measure or unmeasured components of the ecosystem. For example, to estimate long-term dynamics, Needham et al. (2020) added alternative hypotheses of size- and age-dependent mortality to FATES and found that any increases in aboveground woody biomass under elevated CO_2 could be reduced by nearly half if large trees suffer increased mortality.

VDMs have made important progress in simulating dynamics at BCI. Trait and census data from BCI have been used in several new features of the land model LM3PPA-TV, including a novel growth allocation scheme and a tropical shade-tolerant PFT (Martínez Cano et al., 2020). Simulations with these novel features were able to reproduce mean canopy and understory growth rates, tree size distributions, and stand-level biomass. The model also reproduced annual GPP estimated from eddy-covariance data, along with annual NPP, estimated from both satellite and plot-based data. Furthermore, even though it was parameterized and tuned only for BCI, LM3PPA-TV was able to reproduce considerable variation in AGB and tree size distributions among other tropical sites.

Koven et al. (2020) tested the sensitivity of FATES to PFT parameters, using trait data collected mostly at BCI. The range of GPP simulated by different parameter combinations was large but spanned the observations, and the best parameter combinations were also able to reproduce biomass and tree size distributions. However, many observationally constrained parameter combinations led to overestimated biomass because of the persistence of too many large diameter trees. To address the large-tree bias and improve the representation of canopy disturbance, a new crown damage module was added to FATES (Needham et al., 2022). The crown damage module in FATES has been extensively benchmarked using annual damage and mortality surveys within the BCI 50-ha plot (Zuleta et al., 2022), in combination with dendrometer band data and drone imagery at BCI (Araujo et al., 2021). The crown damage module leads to decreases in biomass and a shift toward smaller canopy trees.

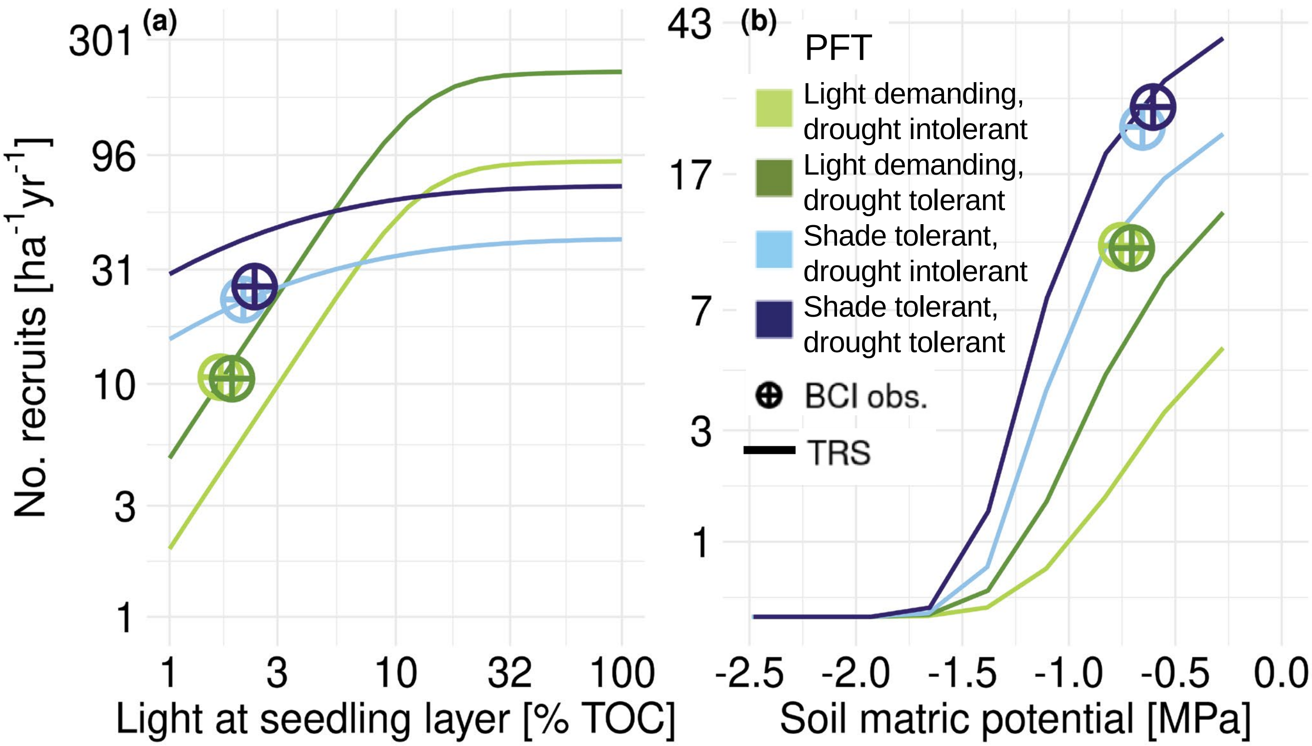

FIGURE 2. Predictions of tree recruitment (at 1-cm dbh) across a range of idealized (**a**) patch-level light and (**b**) soil moisture conditions with locally observed meteorology (2008–2014) at Barro Colorado Island (BCI) using the Tree Recruitment Scheme (TRS). Observed plant functional type (PFT)-specific mean annual recruitment rates ("BCI obs.") are shown for reference and were calculated from 2005–2010 and 2010–2015 census intervals. Observed means are plotted at light levels equal to the mean understory light level across all patches in the (a) Forest Dynamics Plot (Rüger et al., 2009) and (b) soil moisture equal to the mean measured at the BCI Lutz catchment between 2008 and 2014 (Paton, 2020). TOC = top of canopy. From Hanbury-Brown et al. (2022a).

Empirical data from BCI have also been used to develop, parameterize, and benchmark new regeneration algorithms in the Tree Recruitment Scheme (TRS; Hanbury-Brown et al., 2022a). Census observations from the BCI Forest Dynamics Plot were used to quantify mortality-adjusted (Kohyama et al., 2018) recruitment rates (Hanbury-Brown et al., 2022b) and indicated that current recruitment algorithms in the Ecosystem Demography Model v.2 (ED2) and FATES overpredict recruitment rates at BCI (Hanbury-Brown et al., 2022a). Observations of sapling mortality rates (1- to 5-cm diameter at breast height [dbh] size class) suggested that hyperactive recruitment in ED2 leads to compensating model errors in sapling mortality (Powell et al., 2018; Hanbury-Brown et al., 2022a). By predicting recruitment as a function of size-dependent reproductive allocation (Wright et al., 2015; Visser et al., 2016), and light and moisture sensitive regeneration processes at the forest floor (Engelbrecht and Kusar, 2003; Engelbrecht et al., 2007), the TRS better represents the PFT rank order of recruitment rates compared with ED2 (Fig. 2a; Hanbury-Brown et al., 2022a). PFT-specific recruitment observations from a wider spectrum of light and soil moisture conditions, such as canopy gaps and other microsites (only the site-level mean is shown in Fig. 2), are needed to further test the connection between regeneration and functional composition and would provide improved recruitment benchmarks.

MODELING FOREST HYDRODYNAMICS AT BCI

Several studies have used the BCI testbed to improve understanding of forest drought responses and to inform the underlying hydrodynamic mechanisms in VDMs, including water transport along the soil–plant–atmosphere continuum (Powell et al., 2018; Chitra-Tarak et al., 2021; Fang et al., 2021; Detto and Pacala, 2022).

Powell et al. (2018) used the hydrodynamic version of ED2 to explore the sensitivity of forest functional composition to alternate environmental forcings at BCI. ED2 was benchmarked against AGB and mortality of four PFTs varying along

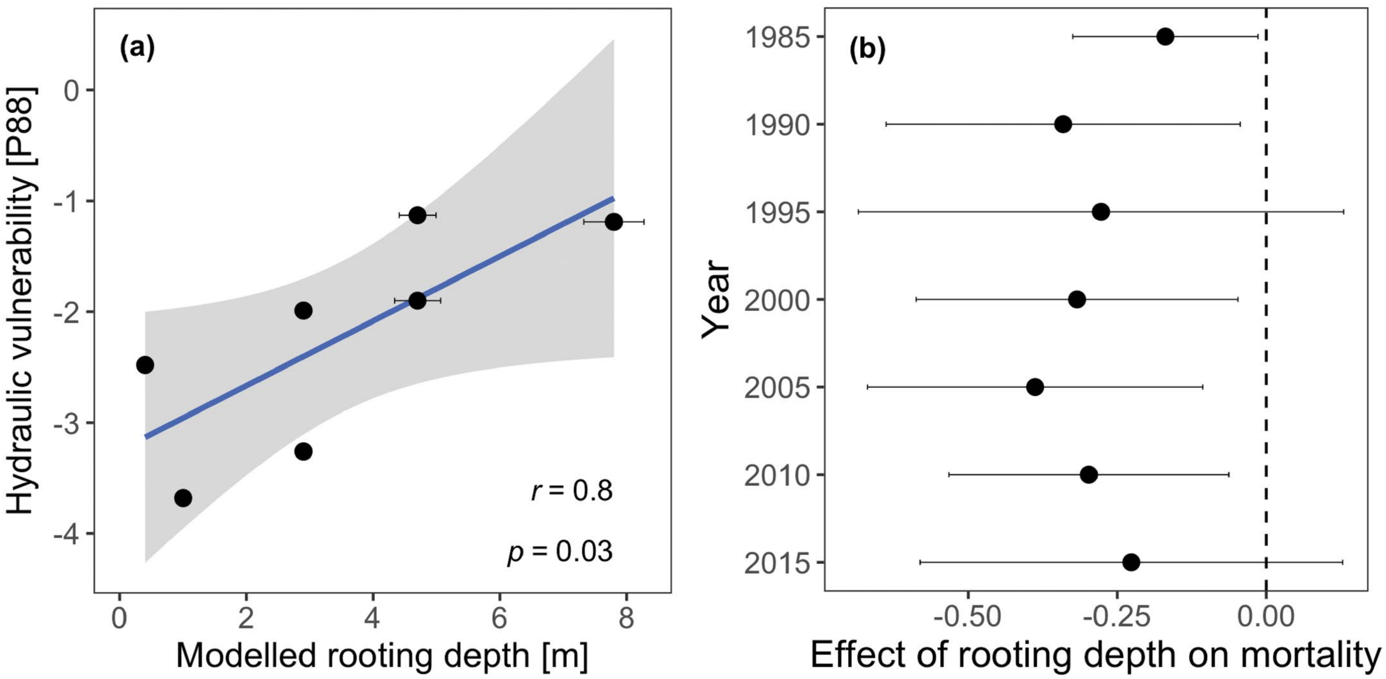

FIGURE 3. (**a**) Measured hydraulic vulnerability was positively related to estimated rooting depth among Barro Colorado Island (BCI) tree species, (**b**) yet deeper-rooted species had lower mortality rates than shallow-rooted species in five out of seven censuses conducted over 35 years, during which BCI witnessed droughts of a variety of intensities and duration. In (a), P88 is water potential (MPa) at 88% loss of stem conductivity, with less negative values corresponding to greater hydraulic vulnerability (lower embolism resistance). Spearman's *r* and significance level are given, along with linear model fit in blue and 95% confidence band in gray. In (b), temporal variability in slope coefficients (circles with 95% confidence intervals) for regressions of mortality rates on estimated rooting depth for 12 evergreen, canopy species. From Chitra-Tarak et al. (2021), licensed under CC BY 4.0.

light- and water-use axes (the latter defined by aboveground hydraulic traits). ED2 predicted that a shift to a chronically drier hydroclimate will sustain AGB but reduce functional diversity, by increasing mortality of drought-intolerant species and shifting composition to drought-tolerant species. In the chronic drier dry-season scenario, however, such functional compensation was more limited.

Chitra-Tarak et al. (2021) subsequently found a trade-off at BCI whereby deeper-rooted species were more vulnerable to hydraulic failure than shallow-rooted species. Yet, because of reduced drought exposure, deeper-rooted species had higher survival rates through a variety of hydrological droughts compared with shallow-rooted species (Fig. 3). This finding suggests that if VDMs ignore rooting depths, they may overestimate mortality of hydraulically vulnerable species under drought scenarios, yet prolonged or intense drought exposure may threaten the survival of deep-rooted species (Chitra-Tarak et al., 2019). For this study, FATES was parameterized and benchmarked with multiple hydrological states and fluxes to characterize hydrological droughts, and the rooting depth model was calibrated against isotopically derived estimates and leveraged leaf hydraulic conductivity and leaf phenology data. In general, competition for water in VDMs remains poorly resolved (Fisher et al., 2018) and rooting or water-sourcing depth is a critical hydraulic trait for which more measurements are needed.

Finally, Fang et al. (2021) used the BCI testbed to disentangle whether atmospheric vapor pressure deficit or soil drought limited canopy conductance with a hydrodynamic version of FATES, and they found greater support for the latter. Data–model comparison pointed to the need for reducing model structural and parameter uncertainty, particularly for stomatal conductance and soil evaporation.

OPPORTUNITIES FOR FUTURE DATA–MODEL INTEGRATION AT BCI

Several datasets and model developments are required to improve VDM predictions of tropical forest drought responses. Soil water is generally predicted for a one-dimensional soil column for computational efficiency, but to realistically estimate plant available water at large spatial scales (0.5–2°), models need to represent lateral flow from hills to valleys. In addition, data resolving landscape-scale water availability (e.g., water tables, stream discharge, evaporation, transpiration, and spatial heterogeneity in soil moisture) are urgently required, as are parameters for soil depth, texture, conductivity, and water retention curves by depth; drought avoidance and tolerance traits (e.g., stem, root and leaf vulnerability curves, soil-to-root conductance, capacitance, leaf phenology, temporal dynamics of water sourcing depths, stomatal regulation); their covariation with other functional traits; and demographic rates under varying water availability (Chitra-Tarak and Warren, 2023).

To improve representation of nutrient dynamics, VDMs should make use of datasets from BCI on soil nutrient dynamics, including nitrogen fixation (chapter 57, Batterman and Wurzburger, 2024) and other microbial and symbiont activity. Field measurements of plant tissue stoichiometry (leaves, fine-roots, sapwood, heartwood/deadwood, reproductive), nutrient storage, and translocation of nutrients during tissue turnover will enable improvements to the representation and parameterization of nutrient biogeochemistry, especially nitrogen and phosphorus cycling.

Despite the wealth of information from BCI, the difficulty of accessing the canopy has limited the opportunities to gain insight into the physiological processes that drive photosynthesis and transpiration, which are core ESM processes. Recently, leaf reflectance data have been collected from foliage sampled using line launchers and pole saws as part of an effort to link leaf optical properties to key physiological processes. These statistical models can enable us to estimate the variation in physiological parameters across species and growth environments that is needed to represent photosynthesis (Burnett et al., 2021; Lamour et al., 2021). These could be used to estimate functional trait diversity and physiological process rates in the canopy using airborne or drone-based observations (also see Park et al., 2019).

Many processes in VDMs can be informed by manipulative field experiments that test the sensitivity of physiological or demographic processes to changing temperature, precipitation patterns, CO_2, and nutrient availability (Winter and Lovelock, 1999; Wright et al., 2011; Nasto et al., 2019; Wright, 2019; Slot et al., 2021a; Slot et al., 2021b). Many of these experiments have been performed at BCI and are described in the section "Experimental Ecosystem Studies" of this volume (chapter 60-68). For example, Slot (2024) describes how experiments and observations of temperature effects on trees are improving our understanding of potential limits to productivity in a hotter, drier world. To date, few model experiments or VDM development efforts have leveraged these experimental data.

VDMs provide capabilities needed to predict how interacting stressors will affect forest dynamics and community shifts. Chapter 50 (Cushman, 2024) describes how lidar and photogrammetry across BCI provide insight into variation in forest structure and canopy disturbance relative to soil and topography. These insights are essential for including the influence of landscape heterogeneity in VDMs when running simulations at broad spatial scales. Globally, wildfires and land use change are dominant drivers of forest dynamics. To simulate forests at regional and global scales, VDMs will benefit from testbed sites that experience or experiment with a range of disturbance types, beyond what is observed at BCI.

There are discrepancies between the current generation of ESMs and observations from forest plots regarding the size of the pantropical net carbon sink and how it is changing through time (Koch et al., 2021). To improve the performance of global simulations, modeling groups should ensure good model performance at testbed sites such as BCI (Koven et al., 2020; Martínez Cano et al., 2020). This requires iterative simulations that use trait data to constrain model parameters, environmental and meteorological data to run the model, and ecosystem state and flux data to evaluate predictions under a range of conditions (Fig. 1). The rich legacy and wide availability of BCI's ecological and environmental datasets has created a foundation for model development and calibration that should be replicated across biomes and successional stages to advance Earth system predictions.

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ONLINE SUPPLEMENTARY MATERIAL

Table S1. List of NGEE-Tropics Datasets, Barro Colorado Island, Panama. https://doi.org/10.25573/data.22775651

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