Improving collaborations between empiricists and modelers to advance grassland community dynamics in ecosystem models

By: Kevin R. Wilcox, Kimberly J. Komatsu, Meghan L. Avolio, C2E Consortium⚡

⚡C2E Consortium: William D. Bowman, Ethan Butler, Scott L. Collins, Jeffrey S. Dukes, Rosie Fisher, Trevor F. Keenan, Nancy Y. Kiang, Alan K. Knapp, Sally E. Koerner, Lara Kueppers, Nathan P. Lemoine, Guopeng Liang, Michael E. Loik, Yiqi Luo, Ben Poulter, Peter B. Reich, Katherine Renwick, Melinda Smith, Andrew Tredennick, Anthony P. Walker, Ensheng Weng

Abstract:

Climate change, increasing atmospheric CO2, and land use change have altered biogeochemical and hydrologic cycles world-wide, with grassland systems being particularly vulnerable to resulting vegetation shifts (Komatsu et al., 2019). Therefore, incorporating plant community dynamics into ecosystem models is critical for accurate forecasting of ecosystem responses to global change (Levine, 2016). Process-based ecosystem models, which simulate the biogeochemical transfers of mass and energy among biota, the subsurface, and atmosphere, require representation of dynamic composition of organisms within ecosystems. For example, these models simulate leaf and plant-level characteristics, such as electron transport rate and allometry of carbon (C) allocation, to predict how net primary productivity and other ecosystem processes respond to abiotic drivers. These models are particularly useful in scaling from organismal to ecosystem levels but are still underdeveloped in their ability to capture community change, especially in grassland ecosystems. To represent compositional changes, these models

must simulate competition, mortality, establishment, and reproduction of plant populations within communities. Yet, current ecosystem modeling approaches to forecast plant community change have derived from studies of forested systems and are either too coarse to capture fine-scale community dynamics (e.g. dynamic global vegetation models (DGVMs)) or too complex to be used at large spatial scales (e.g. forest gap models).

Article:

Introduction

Climate change, increasing atmospheric CO2, and land use change have altered biogeochemical and hydrologic cycles world-wide, with grassland systems being particularly vulnerable to resulting vegetation shifts (Komatsu et al., 2019). Therefore, incorporating plant community dynamics into ecosystem models is critical for accurate forecasting of ecosystem responses to global change (Levine, 2016). Process-based ecosystem models, which simulate the biogeochemical transfers of mass and energy among biota, the subsurface, and atmosphere, require representation of dynamic composition of organisms within ecosystems. For example, these models simulate leaf and plant-level characteristics, such as electron transport rate and allometry of carbon (C) allocation, to predict how net primary productivity and other ecosystem processes respond to abiotic drivers. These models are particularly useful in scaling from organismal to ecosystem levels but are still underdeveloped in their ability to capture community change, especially in grassland ecosystems. To represent compositional changes, these models must simulate competition, mortality, establishment, and reproduction of plant populations within communities. Yet, current ecosystem modeling approaches to forecast plant community change have derived from studies of forested systems and are either too coarse to capture fine-scale community dynamics (e.g. dynamic global vegetation models (DGVMs)) or too complex to be used at large spatial scales (e.g. forest gap models).

Community ecology often relies on statistical models describing population dynamics or the abundance/frequency of individual species to identify linkages between community dynamics and ecosystem processes. For example, there is a vast literature linking species richness to ecosystem function using statistical models (Hooper et al., 2005; Cardinale et al., 2006). Yet, statistical models are rarely able to scale leaf and plant-level characteristics to ecosystem levels owing to data constraints and the fact that they do not incorporate process knowledge. Process-based ecosystem models are thus needed to predict whole ecosystem function, especially under novel environmental conditions. Yet, as already mentioned, these models often struggle to link plant characteristics to local-scale community dynamics.

To better represent community dynamics in ecosystem models, scientists must identify: (1) how physiological and morphological traits of plant species or functional types, and their diversity, can drive changes in community structure (Fig. 1, arrow 1); and (2) how community dynamics alter the distribution of traits across the entire community (Fig. 1, arrow 2); leading to (3) improved ability to simulate shifts in community structure and their concurrent effects on ecosystem functioning (Fig. 1, arrows 6 and 7). Additionally, ecosystem processes, as forced by abiotic drivers, should alter the competitive balance in community dynamics that are sensitive to the coupling between their physiological/morphological traits and the abiotic drivers (Fig. 1, grey arrow). Integration across organismal, community, and ecosystem ecology, as well as between empirical and process-based modeling approaches, is necessary to address this issue. Toward this end, we (K. Komatsu, M. Avolio, K. Wilcox) led a working group funded by the Long-Term Ecological Research Network from 2017 to 2019, where we gathered scientists from diverse fields (C2E Consortium) to identify challenges and formulate directions for better integration of community dynamics in land surface models (LSMs).
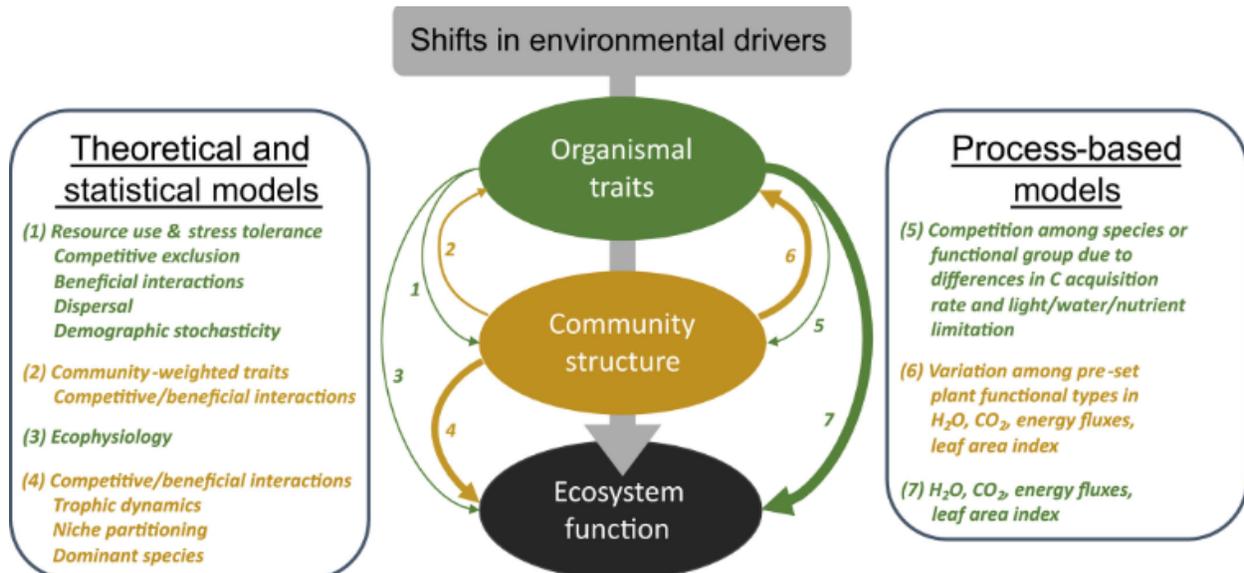

Figure 1. Conceptual figure showing how ecologists bridge hierarchical scales (ovals) using both statistical and process-based models to predict how ecosystem function will respond to shifts in environmental drivers, with arrow thickness representing our interpretation of the general level of understanding and/or frequency of scaling attempts in the field. These scaling attempts focus on various processes and biotic characteristics (examples in italics). Traditionally, statistical models have been used to assess how variation in environmental drivers results in variation in ecosystem function (large gray arrow), as well as how differences in community structure (biodiversity, species composition) result in differences in ecosystem function. Process-based models use information about plant characteristics (i.e. traits) within ecosystems to determine water, energy, and biogeochemical fluxes (arrow 7), sometimes incorporating direct impacts of shifts in abundance of plant functional types or cohorts (arrow 6). More recently, capacity for species-level responses to environmental drivers has been built into process-based models (arrow

5), yet our understanding of how species-level physiological responses translates to changes in community structure (arrow 1), and how these changes alter the physiological/morphological traits of the ecosystem (arrow 2), is still lacking. We propose that future research strives to increase our mechanistic understanding of how organismal responses lead to shifts in community structure so that these mechanisms can be incorporated into process-based models.

Modelers and empiricists have similar goals

Whether simulating ecosystem processes or conducting field studies, our goal in ecology is often the same: to provide predictions of ecological states and processes under a variety of environmental conditions. Many studies of community dynamics do not collect the data necessary to parameterize process-based models, and models do not represent many of the processes that empiricists consider fundamental. This is often due to limited communication between process-based modelers (hereafter 'modelers') and 'empiricists' who collect biotic and abiotic data, where both modelers and empiricists lack familiarity with the needs of the other's approaches. Though there are existing channels of communication, there is room for more discussion between modelers and empiricists focusing on population, community, and ecosystem dynamics. During our meetings, participant modelers and empiricists agreed on three existing knowledge gaps that should be prioritized by the scientific community to better represent critical processes controlling ecosystem dynamics: (1) resource competition; (2) community and population dynamics; and (3) grassland plant processes. To fill these knowledge gaps, empiricists should seek input from modelers when designing experiments, and modelers should consult empiricists when altering or developing models. In other words, let's all talk more.

Resource dynamics in dynamic global vegetation models

Whether simulating ecosystem processes or conducting field studies, our goal in ecology is often the same: to provide predictions of ecological states and processes under a variety of environmental conditions. Many studies of community dynamics do not collect the data necessary to parameterize process-based models, and models do not represent many of the processes that empiricists consider fundamental. This is often due to limited communication between process-based modelers (hereafter 'modelers') and 'empiricists' who collect biotic and abiotic data, where both modelers and empiricists lack familiarity with the needs of the other's approaches. Though there are existing channels of communication, there is room for more discussion between modelers and empiricists focusing on population, community, and ecosystem dynamics. During our meetings, participant modelers and empiricists agreed on three existing knowledge gaps that should be prioritized by the scientific community to better represent critical processes controlling ecosystem dynamics: (1) resource competition; (2) community and population dynamics; and (3) grassland plant processes. To fill these knowledge gaps, empiricists

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Community dynamics in models

Plant community dynamics can have strong impacts on ecosystem function, which has been demonstrated both theoretically (Smith et al., 2009; Langley & Hungate, 2014; Polley et al., 2014) and empirically (Isbell et al., 2013; Reich & Hobbie, 2013; Avolio et al., 2014; Smith et al., 2015; Xu et al., 2015; Fig. 1, arrow 4). Ecosystem function can be altered when community dynamics result in a system having a different collection of plant physiological and morphological traits. Thus, incorporation of community dynamics related to species identities and their traits into process-based models is critical for accurately forecasting ecosystem processes.

The need to incorporate community dynamics into process-based models has been recognized by the scientific community, and increasing efforts are being made to achieve this goal for LSM-coupled DGVMs (Moorcroft, 2006; Evans, 2012; Scheiter et al., 2013; Levine, 2016). Ecosystem models represent community change in a few different ways: DGVMs define suites of traits associated with broad functional groups; gap models assign traits to individual organisms to allow species and cohorts to compete for resources; and trait-based models allow traits to vary plastically with environmental conditions without explicit representation of species (Fisher et al., 2018). Each of these methods provides unique strengths and challenges. For example, community shifts within functional groups (e.g. shift in dominance from one C4 grass to another C4 grass) can have large impacts on ecosystem function (Wilcox et al., 2016), which would not be captured by DGVMs; gap-based models do well to represent cohort competition for light after disturbance, yet they struggle to represent competition for resources such as water and nutrients (Powell et al., 2013); and global or regional-scale trait–environment relationships used within trait-based approaches often make assumptions about space-for-time substitutions, which can be problematic (Burke et al., 1997). Thus, better understanding and representation of mechanisms behind intra-functional group dynamics within ecosystem models is important to improve accuracy of temporal projections under chronically altered environmental scenarios. This requires expanding the number of species or functional groups represented within ecosystem models and a better parameterization of these species/groups.

Grasslands are not well represented in land surface models

Grasslands, in addition to driving the evolution and rise of hominids (Bobe, 2004; Uno et al., 2016), cover c. 40% of the Earth's ice-free terrestrial surface (White et al., 2000) and provide vital ecosystem services, such as forage production, C sequestration, and agriculture (Sala & Paruelo, 1997). Yet, many ecosystem models were initially designed based on forest dynamics and so have difficulty representing important dynamics in grasslands, including C3 vs C4

competition, the distribution of mixed grass–tree systems, and intra-functional group competition. Some reasons for these difficulties are variable grassland phenology and grass allometry, and inadequate representation of key drivers of grassland dynamics, such as fire and grazing.

Through our discussions, we identified some important considerations for overcoming current limitations of representing grasslands in ecosystem models. First, grasses and trees have fundamentally different growth forms, and models need to move beyond current approaches that incorporate grasses as either miniature trees or as a green carpet. Instead, ecosystem models should represent the unique attributes of grasses, including strong water limitation, fast tissue turnover rates, multiple aboveground stems from one belowground organ system, and a high prevalence of vegetative reproduction. These are major distinctions important for the C balance and total biomass of grasses. Additionally, moving beyond a 'green carpet' approach may be important for accurate representation of surface roughness in grasslands. Going forward, vegetation demographic models (Moorcroft et al., 2001) are emerging as an approach to solve the potential pitfalls of scaling from individuals to the ecosystem level, as well as from ecosystem patches to the global scale. This approach could be particularly applicable to grasslands, where the number of individuals per square meter makes modeling interactions among individuals computationally unreasonable. Second, the way that fire – a key driver of grassland form and function (Bond & Keeley, 2005) – is currently modeled in LSMs has also been built with forested ecosystems in mind, leading to poor representation of this driver for grassland ecosystems. For example, although fire can result in mortality in forest systems, thus 'resetting' the ecosystem, fire in grasslands often does not kill individuals, and many dominant grassland species are promoted by frequent fire (Hulbert, 1988).

Leveraging existing coordinated experiments

One exciting opportunity to realize better understanding and forecasts of community-to-ecosystem linkages is to leverage existing coordinated experiments. Coordinated experiments implement the same experimental design at many sites around the globe, typically involving teams of investigators at each site. Coordination with these existing teams could allow for the measurement of necessary environmental and species physiological/morphological trait data around the globe, which may then be incorporated into models. Examples of such coordinated networks include the Nutrient Network (NutNet; Borer et al., 2014), Drought Network (DroughtNet), and Forest Geological Observatory (ForestGEO; Anderson-Teixeira et al., 2015). For these networks to be leveraged, prioritization of measurements is needed to prevent overloading of network investigators, as these experiments have been designed to limit time investment by any one investigator. Alternatively, the network can be leveraged without relying on many individual investigators if outside funding is available for a small team to make many measurements across many sites. By highlighting the common goals of empiricists and modelers for investigators within coordinated networks, and developing protocols for field

measurements of key model parameters, the goal of improved understanding of how community dynamics drive ecosystem processes can be made more achievable.

Conclusions

Working together, empiricists and modelers can overcome some of the limitations of isolated empirical studies (relatively short timescale, small spatial extent, costs of measuring everything required to mechanistically explain responses) and modeling efforts (unreasonable/simplistic assumptions, limited representation of environmental heterogeneity and ecological complexity). This may be done using data collected from empirical studies for model initialization and parameterization, using updated models to quantitatively test and develop mechanistic ecological hypotheses, and to help explain the processes causing observed community dynamics. We have identified three core areas where both empiricists and modelers could work together to improve understanding of community and ecosystem processes: first, trait diversity in resource use and trade-offs; second, better representation of mechanisms controlling community dynamics; and third, more accurate representation of key grassland processes. Achieving these core goals will require an iterative process where empiricists and modelers work together to develop hypotheses about community dynamics and ecosystem processes, design experiments to generate data to test these hypotheses, and incorporate these data into ecosystem models for evaluation, which can lead to development of new hypotheses. These types of collaborative research cycles will allow scientists to greatly increase understanding and forecasting capabilities of ecological patterns and processes at broad scales.

Author contributions

KRW, KJK and MLA conceived of and organized the meeting. All co-authors attended the meetings. KRW, KJK and MLA wrote the manuscript, with editorial contributions from all other co-authors.

ORCID

Meghan L. Avolio https://orcid.org/0000-0002-2649-9159
Kimberly J. Komatsu https://orcid.org/0000-0001-7056-4547
Kevin R. Wilcox https://orcid.org/0000-0001-6829-1148

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