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RESEARCH ARTICLE

Attributing interannual variability of net ecosystem exchange to modeled ecological processes in forested wetlands of contrasting stand age

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Abstract The drivers of interannual variability (IAV) of net ecosystem exchange (NEE) in forested wetlands are poorly understood, making it difficult to predict changes in atmospheric fluxes in response to land use and climate change. Similarly, these ecosystems demonstrate dynamic physiological and phenological responses to climate over time yet are typically modeled using static parameters that represent unchanging ecological conditions. Though static first-order ecosystem models are informative, they fundamentally lack the ability to represent dynamic annual changes in ecological processes that may drive IAV of NEE through time. We aimed to improve understanding of how forested wetlands dynamically respond to climate and which key ecological processes may contribute to IAV of NEE. Simultaneously, we aimed to develop tools to evaluate dynamically parameterized process based first-order ecosystem models. To achieve these objectives, long-term ecological data were fused with the Total Ecosystem (TECO) model in three loblolly

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pine plantations and a bottomland hardwood forest of contrasting stand age in wetland areas of the lower coastal plain of North Carolina. Variance decomposition was used to assess changes in large-scale ecosystem drivers. To investigate individual processes, both static and dynamic data-assimilation were conducted to simulate time–invariant and time–varying ecological response. Anomalies in dynamic ecosystem process response were correlated with NEE anomalies to attribute IAV of NEE to underlying process-based mechanisms that may drive annual changes in NEE across stand age and sites. Assessment of large-scale drivers of IAV of NEE across sites demonstrated that maximum carbon uptake (MCU) dominated IAV of NEE in the mature pine plantation. These large-scale NEE signals were further parsed into ecological processes in the TECO model, where process anomaly correlation showed that slight variations in root maintenance respiration and woody biomass turnover rates may be underlying drivers of IAV of MCU and subsequently NEE. However, in the young pine plantations and bottomland hardwood forest IAV of NEE was not dominated by MCU. In contrast, IAV of NEE in young plantations was influenced most by annual changes in maximum carbon release (MCR) and carbon uptake period (CUP), while IAV of NEE in the bottomland hardwood forest was dominated by CUP. These results demonstrate that dynamic data assimilation (DA), variance decomposition, and process anomaly correlation are investigative and diagnostic tools for process-based models, though maximum GPP was systematically underestimated by models across sites. Despite problems with peak GPP representation, anomaly correlation between ecological processes and IAV of NEE allowed investigation of the specific ecological drivers of annual variability in ecosystem-level carbon exchange. As ecosystems show dynamic physiological and phenological properties through time, it may be important to allow models to have dynamic/time–varying ecological responses, especially if the root causes of IAV of NEE are to be attributed to ecological processes in process-based models.

Keywords Data assimilation · Ecological modeling · Forested wetlands · Interannual variability · Managed forests · Net ecosystem exchange

Introduction

At the global scale, interannual variability (IAV) in the enrichment of atmospheric carbon dioxide (CO_2) has been attributed primarily to IAV of net ecosystem exchange (NEE) in the terrestrial carbon (C) cycle, and thus to changes in the size of the terrestrial C sink (Le Quéré et al. 2018). Small annual imbalances in ecosystem-scale gross primary productivity (GPP) and total ecosystem respiration (RE) create annual variability in the size and direction of NEE, and subsequently determine land C sink or source capacity. Though several climate factors have been reported to have dominant control of IAV of NEE, including solar radiation (Ichii et al. 2005), precipitation (Jung et al. 2017; Poulter et al. 2014), and temperature (Wang et al. 2014), the ecological mechanisms affecting IAV of NEE are poorly understood. Overall, despite a lack of attribution to individual ecological processes, IAV of NEE is expected to be predominantly controlled by ecological factors compared to direct climate effects (Shao et al. 2015).

Many large-scale ecological factors have been investigated as important controls of IAV of NEE. For example, 90% of IAV of GPP can be explained in temperate and boreal ecosystems by the product of maximum daily GPP (GPP_{max}) and growing season length (Xia et al. 2015; Zhou et al. 2016), while GPP_{max} dominated IAV of GPP over mid and high latitudes of North America at the ecosystem and regional scales (Zhou et al. 2017). Similarly, extensions of the net carbon uptake period annually may lead to larger net land C sink capacity (Churkina et al. 2005; Dragoni et al. 2011), with effects potentially greater in water-limited systems experiencing increased precipitation (Poulter et al. 2014; Ahlström et al. 2015;). Further, increases in maximum net C uptake tend to increase the land C sink while increases in maximum net C release tend to reduce the land C sink (Zscheischler et al. 2016; Fu et al. 2017). However, these large-scale factors represent grouped effects of many phenological and physiological processes operating at the ecosystem-scale, and

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to our knowledge no analysis has parsed IAV of NEE to specific ecological processes within process-based models.

In wetlands specifically, ecological processes that drive IAV of NEE are uncertain, though it has been established that stand age influences C dynamics (King et al. 1999; Pregitzer and Euskirchen 2004 Magnani et al. 2007) with NEE differences between forests often proportional to differences in stand age (Noormets et al. 2007; Schwalm et al. 2007; Mkhabela et al. 2009;). As a large component of the terrestrial C cycle, wetland ecosystems perform unique biogeochemical functions (Chmura et al. 2003), are among the most economically valued and productive ecosystems globally (Moreno-Mateos et al. 2012), and face multiple anthropogenic pressures (Day et al. 2008; White and Kaplan 2017). Wetlands are also important C stores under threat of extreme weather events, sea level rise and climate change (Miao et al. 2017), thus identifying drivers of IAV of NEE that can be targeted by forest management or ecological restoration activities may be important to mitigate net C release in these ecosystems. To assess ecosystem trajectories in these regions and parse the effects of changing climate, land use and stand development, eddy covariance research towers were previously established in three managed loblolly pine plantations and a natural mixed hardwood forest in the lower coastal plain of North Carolina (Aguilos et al. 2020, 2021; Domec et al. 2015; Noormets et al. 2010). These tower-based studies allow the investigation of several key aspects of landscape ecology, including landscape history and legacy effects in the transition from bog hardwood forests to managed loblolly pine plantations, as well as investigation of mechanisms and ecological impacts of land use change.

To explore attribution of IAV of NEE to potential ecological drivers in these forested wetland ecosystems, especially to individual ecological processes, we investigated two data assimilation techniques across four forested wetland sites of contrasting stand age and community composition. Using the Total Ecosystem (TECO) model (Weng and Luo 2008), we conducted data-model fusion by static and dynamic data assimilation (DA) to create model simulations that exhibit time–invariant and time–varying ecological responses, respectively. Model simulations of NEE from both static and dynamic model parameterizations were decomposed following Fu et al. (2019), to parse large-scale ecosystem effects that may be driving differences in IAV of NEE across stand age. We further correlate annual anomalies of modeled ecological processes to annual NEE anomalies at each site to delve deeper into specific ecosystem processes that may drive IAV of NEE. As ecosystem properties are expected to change dynamically through time (Luo and Schuur 2020), we hypothesized that time–varying model parameterization would improve data-model agreement. We also expect that by creating models that allow ecological properties to vary inter-annually that we could correlate the divergence of ecological properties and NEE from their respective long-term means to attribute IAV of NEE to individual ecological processes. In terms of landscape ecology, these approaches represent innovative methods in landscape analysis and modeling, with the aim of developing better tools to assess accuracy and uncertainty of tower-based landscape studies alongside attribution of ecological processes to ecosystem change.

Methods

Study area and data collection

Eddy-covariance towers were established at four long-term experimental sites to study both managed and unmanaged forested wetlands in the southern U.S. lowlands of the North Carolina coast, from 2005 to present (Aguilos et al. 2020, 2021; Miao et al. 2017; Noormets et al. 2012). In this study, we modeled two young loblolly pine plantations ($YP_{2\text{-}7}$, $YP_{2\text{-}8}$), one mature plantation (MP), and one bottom-land hardwood forest (BHF) using long-term eddy-covariance and ground-based measurements from previous work (Fig. 1). As ecosystems experience climate change, we expect changes in ecosystem structure and function which may change carbon sink/source dynamics - especially the IAV of carbon exchanged with the atmosphere. To investigate IAV of NEE in these ecosystems, observed NEE fluxes were parsed into ecologically relevant ecosystem fluxes of GPP and RE using a webtool developed by the Max Planck Institute for Biogeochemistry named REddyProc (Wutzler et al. 2018). Though technically data products, GPP and RE were considered here as observations that were fused with the TECO model

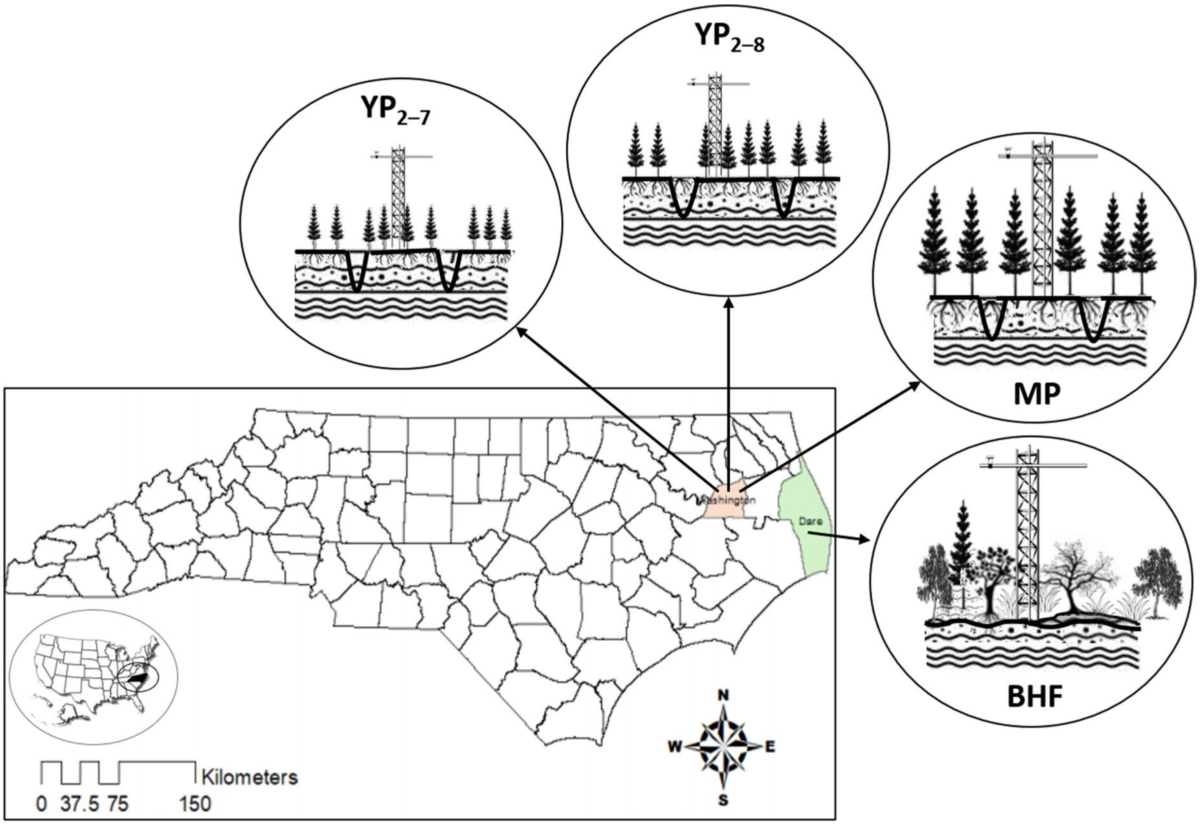


Fig. 1 Locations of young plantations (YP_{2-7},YP_{2-8}), mature plantation (MP), and bottomland hardwood forest (BHF) sites that were modeled in this study [after Aguilos et al. (2021)]

through data assimilation. Other data, including aboveground biomass, root biomass, coarse woody debris, and litterfall are described elsewhere (Aguilos et al. 2020, 2021) and were used during model setup and parameterization.

Ecological model

The process-based terrestrial ecosystem (TECO) model, described by Weng and Luo (2008), was used to investigate IAV of NEE across forested ecosystems of contrasting stand age and community composition. Briefly, TECO has four major components that include canopy photosynthesis, soil water dynamics, plant growth (allocation and phenology) and soil carbon transfers. Canopy photosynthesis is simulated using a multi-layer process-based model, evolved from Wang and Leuning (1998), that simulates transmission of radiation through the canopy using Beer's law and divides foliage into sunlit and shaded leaves. Leaf photosynthesis is simulated using the Farquhar photosynthesis model (Farquhar et al. 1980) and the Ball-Berry model of stomatal conductance (Ball et al. 1987). To capture diurnal and seasonal ecosystem dynamics, the canopy photosynthesis and soil water dynamic submodules are calculated on an hourly time step, while the plant growth and soil carbon submodules are calculated on a daily time step. More detailed description of the TECO model can be found in Weng and Luo (2008).

Though model structure is important, the focus of this work was to investigate ecological processes that may influence changes in annual NEE. Thus, the methods conducted here can be applied to any process-based model. To force the TECO model, specifically, seven observed meteorological variables were collected at each site, including air temperature, soil temperature, relative humidity, vapor pressure deficit, air pressure, wind speed and shortwave incoming radiation. Meteorological observations, measured by eddy-covariance towers at each site, were more than 80% complete and were averaged to an hourly timestep. Any remaining gaps in climate forcing were filled by adjacent tower measurements or by simple averaging of adjacent years in the rare case multiple towers were not functioning at any given time. In contrast, C flux measurements were averaged to daily values and fully gap-filled as described by Aguilos et al. (2020) for use in data assimilation.

Data assimilation

Data assimilation was accomplished using the TECO model and a Model Independent Data Assimilation (MIDA) framework (Huang et al. 2021). The MIDA framework allows abstraction of the carbon-cycle model from the Markov Chain Monte Carlo (MCMC) procedure, which uses Bayesian inference to estimate model parameters that maximize data-model agreement. In this work GPP and RE were used as observational data for data-model fusion with initial carbon pool sizes estimated from C pool measurements at each site from Aguilos et al. (2020). Data-model fusion of GPP and RE into the TECO model was also conducted at each site in two ways—by both static and dynamic DA. Static DA fused model outputs and data across all site-years, creating a single parameter set that exhibited static ecological properties through time. Dynamic DA fused model outputs and data annually, creating annual parameter sets that allowed the model to display dynamic changes in ecological properties on an annual basis. For both approaches the same parameters and initial values were used (Supplementary Table S1). This approach was used to investigate how ecological responses may change each year and how changes in ecological response may relate to IAV of NEE.

Variance decomposition

Interannual variability of NEE was decomposed into phenological and physiological indicators following Fu et al. (2019). The five indicators that affect IAV of NEE in this method include the uptake coefficient (alpha), release coefficient (beta), maximum carbon uptake (MCU), maximum carbon release (MCR) and carbon uptake period (CUP). Briefly, the alpha and beta coefficient describe the ratio of actual C uptake or release compared to theoretical maximum C sink or C source capacity, respectively. MCU and MCR describe the maximum positive and negative C flux, respectively, while CUP defines the number of days where net C uptake occurred. Mathematically, the annual NEE flux curve can be expressed as a function of these five indicators, the differentials of which can be estimated by anomalies of each indicator variable from their long-term mean. The relative contribution of each indicator to IAV of NEE is then calculated as the consistency of each indicator's differential with respect to annual NEE anomaly over the period of interest. A more detailed description can be found in Fu et al. (2019). Applying this variance decomposition to both the NEE observations and simulated NEE responses from the TECO model allowed diagnostics of both the comparative influence of indicators on IAV of NEE across forests of varying stand age and how well our simulations captured these large-scale effects.

Anomaly correlation

To further investigate individual ecological processes that may drive IAV of NEE, we correlated annual NEE anomalies to annual ecological process anomalies in the TECO model when parameterized using dynamic DA. Dynamic DA allows ecological processes to change annually in process-based models, like the TECO model, with annual changes in ecological processes assessed in the same way as NEE anomalies—in comparison to their long-term mean. For example, root maintenance respiration is a parameter optimized in the TECO model during dynamic DA that represents an ecological process. By fusing data and models year-by-year, we can assess the long-term mean of root maintenance respiration expected by the TECO model, and how root maintenance respiration may change annually. The correlation between ecological process anomalies and simulated NEE anomalies then indicate what processes are changing with IAV of NEE as potential drivers in the TECO model. Positive correlation between ecological processes and NEE anomalies indicated ecological processes that increased with increased net ecosystem C loss, while negative correlations indicated ecological processes that increased with increased net ecosystem C storage.

Results

Static vs. dynamic data assimilation

Compared to static parameterization, dynamic DA of the TECO model led to better agreement between simulated and observed ecosystem carbon fluxes at all sites for all carbon fluxes (Figs. 2 and 3). Static DA produced simulated NEE, GPP, and RE that showed 0.13, 0.58, and 0.67 R^2 agreement to observations when averaged across sites, respectively (Fig. 3). In contrast, simulated NEE, GPP, and RE from dynamic DA showed an average R^2 agreement to observations of 0.27, 0.68, and 0.81 R^2 across sites, respectively. The average increase in R^2 by dynamic DA over static DA was 13.5%, 9.2%, and 14.3% for NEE, GPP and RE, respectively. Allowing annual changes in ecological response was the most effective at improving

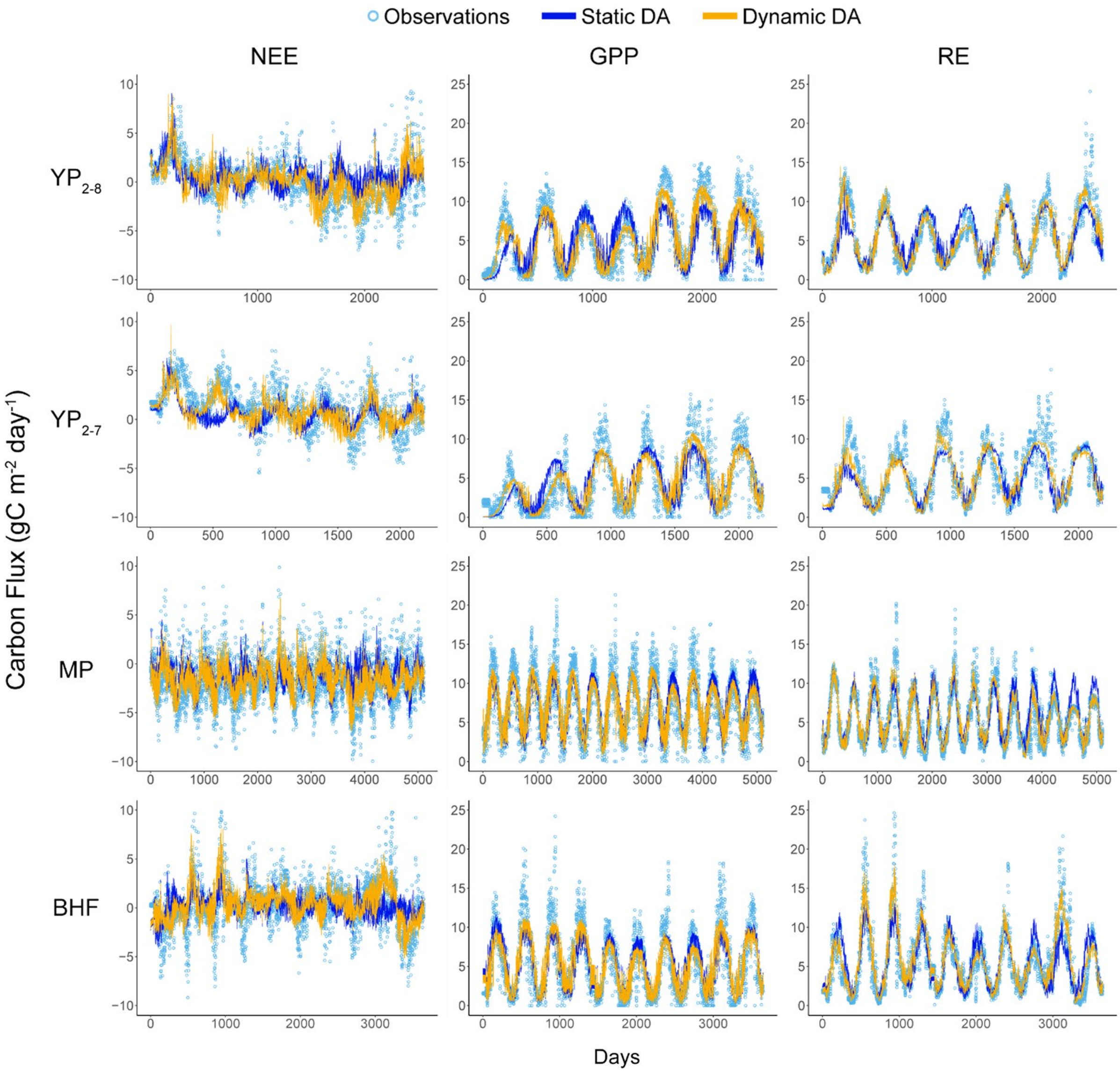


Fig. 2 Data-model fusion of eddy-covariance carbon flux data and the TECO ecosystem model. Simulations were constrained statically using multi-year data (dark blue lines) and dynamically by year (orange lines) compared to daily mean observations (light blue circles) at four sites (YP_{2-8}, YP_{2-7}, MP, BHF)

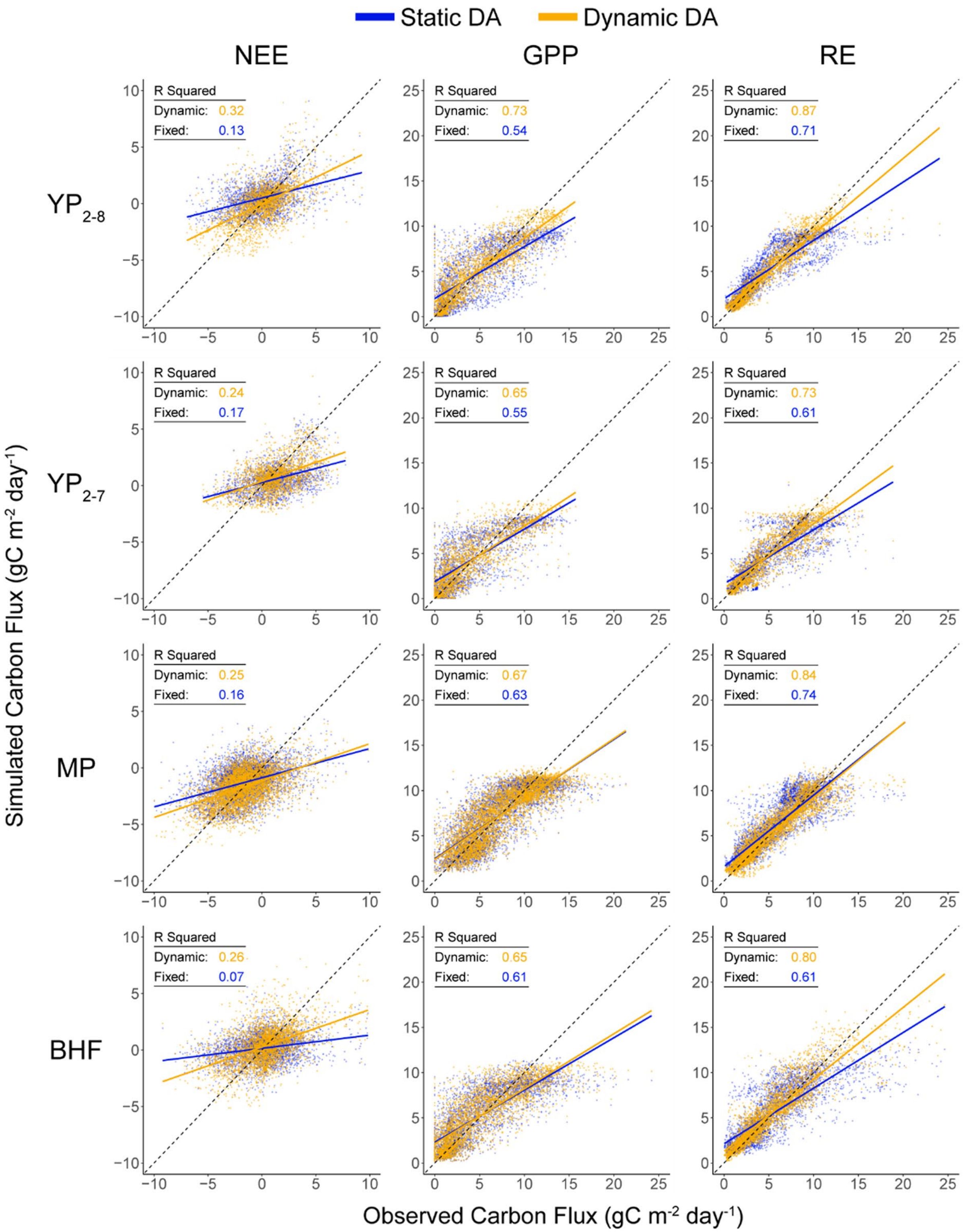


Fig. 3 Correlation between simulated and observed ecosystem carbon fluxes at four sites (YP_{2-8}, YP_{2-7}, MP, BHF). In all cases dynamic data-assimilation (orange) improved agreement between simulated and observed carbon fluxes compared to static data-assimilation (dark blue), while RE was always better represented than GPP by the TECO model

simulated RE response across these forested wetland sites. This can be visualized by both the closer agreement between the daily flux simulations from dynamic DA and the rotation of the dynamic DA fit line towards the 1:1 line compared to static DA.

Across all sites, the TECO model was generally worse at simulating GPP compared to RE, largely due to the mismatch between observed and simulated peak GPP fluxes during the growing season. When comparing the highest observed daily flux compared to highest simulated daily flux, peak GPP was always underestimated by the simulations. On average, simulations missed observed annual peak GPP by 32% and 31% across all site-years for models parameterized by static and dynamic DA, respectively. Simulated peak RE was more accurate, and was both over and underestimated, missing annual peak RE observations across all site-years by an average of 19% and 23% after static and dynamic DA, respectively. Underestimation of peak C fluxes contributed to lower data-model agreement for NEE for simulations from both static and dynamic DA using the TECO model. Throughout the year, the combined effect of both GPP and RE data-model mismatch also showed overall suppression of simulated NEE maxima, resulting in general underestimation of maximum net ecosystem uptake and loss. Despite systemic challenges in representing peak C fluxes, dynamic DA improved data-model agreement, most notably in the representation of RE and allowed investigation of inter-annual changes in ecological processes.

Variance decomposition

Partitioning variance of NEE following Fu et al. (2019) for both the observed data (Fig. 4a) and the comparative contributions to IAV of NEE when simulated using static DA (Fig. 4b) and dynamic DA (Fig. 4c) showed large-scale drivers of ecosystem-level carbon fluxes and how well models captured these trends. Contribution of alpha, beta, MCU, MCR, and CUP show contrasting contributions to IAV of NEE across stand age and forest composition. The young loblolly plantations (Fig. 4a; YP_{2-7}, YP_{2-8}), which represent managed forest regrowth after disturbance (harvest and replanting with 1 year seedlings), showed mixed contributions to IAV of NEE, generally dominated by MCR and CUP. In contrast, MP showed IAV of NEE dominated by MCU, explaining 67% of IAV of NEE. The BHF, as the natural late-successional community in the region, showed 62% IAV of NEE influenced by CUP. Models showed mixed results in replicating these ecosystem-level drivers based on static vs. dynamic DA. Static DA, representing time–invariant ecological responses to climate drivers, showed better agreement to large-scale influences of IAV of NEE at the MP and BHF sites that had more consistent NEE through time (Fig. 4b). Dynamic DA, which represents time–varying ecological response, showed better agreement to observed drivers of IAV of NEE at the YP sites, where annual carbon fluxes were more variable (Fig. 4c).

Process anomaly correlation

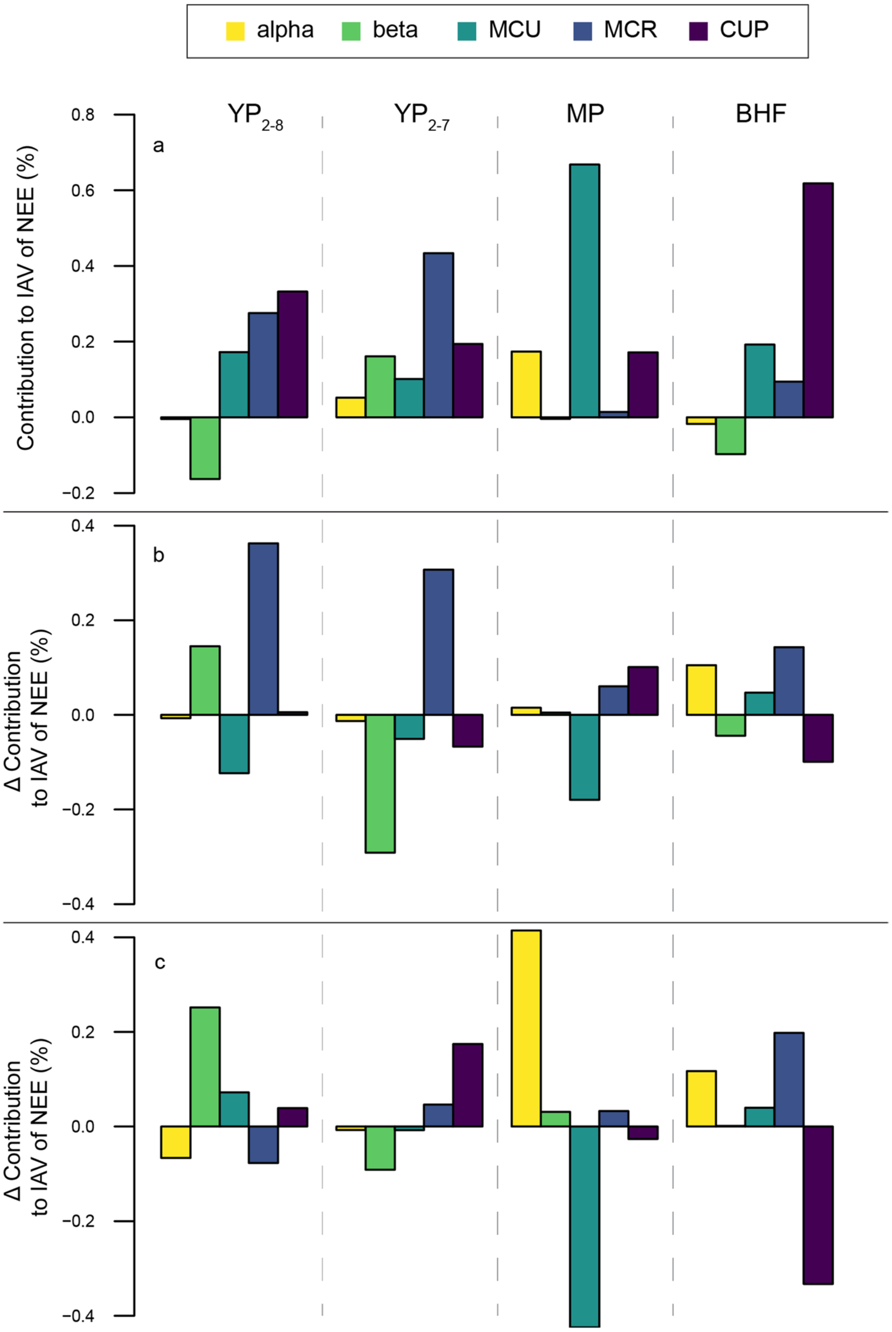
Root maintenance respiration was the strongest positive correlate between modeled ecosystem processes and NEE departures from the mean across all sites (i.e., increased root maintenance costs aligned with annual increases in net ecosystem C loss at all sites). In general, positive correlations were strongest between NEE anomalies and plant processes controlling respiration and productivity, while negative correlations were strongest between NEE anomalies and soil/litter processes (Fig. 5). Increases in dead C pool turnover times, and the rate at which C entered slower moving pools, generally aligned with years where net C storage was greater than the mean. At the MP site, where NEE is dominated by high GPP and shows consistent net C uptake, models generated by dynamic DA showed that small annual variability in both the rate of woody biomass turnover and root maintenance respiration were the strongest potential drivers of IAV of NEE. At the YP and BHF sites, both of which experienced widespread disturbance (i.e., harvest at YP sites and hydrologic stress and increased tree mortality at BHF), processes strongly correlated to NEE anomalies were more numerous, suggesting that a confluence of factors may affect IAV of NEE at these sites.

Discussion

Dynamic data assimilation

The inability to perfectly simulate GPP and RE C fluxes is an ongoing difficulty for ecological and Earth System models. As NEE is the difference between

Fig. 4 Variance decomposition of NEE at four sites (YP_{2-8}, YP_{2-7}, MP, BHF) using the observed NEE (**a**) and the difference of observed variance decomposition compared to variance decomposition of simulated NEE from static (**b**) and dynamic (**c**) data assimilation. Following Fu et al. (2019), NEE variance was decomposed into a carbon uptake coefficient (alpha), carbon release coefficient (beta), maximum carbon uptake rate (MCU), maximum carbon release rate (MCR) and carbon uptake period (CUP)



GPP and RE, inaccuracies created while simulating either GPP or RE may lead to pronounced NEE data-model mismatch. This can be attributed, in part, to uncertainties in observational data and model parameterization, simplifications in model representations and unknowns in terms of important or missing processes within contrasting ecosystems. It has also been demonstrated that ecological processes may have a greater effect on C dynamics than direct climate impacts (Shao et al. 2015), though whether this is due to important missing climate drivers or a lack of understanding with regard to indirect climate effects, is not established. Here we show that annual ecological changes can increase data-model agreement,

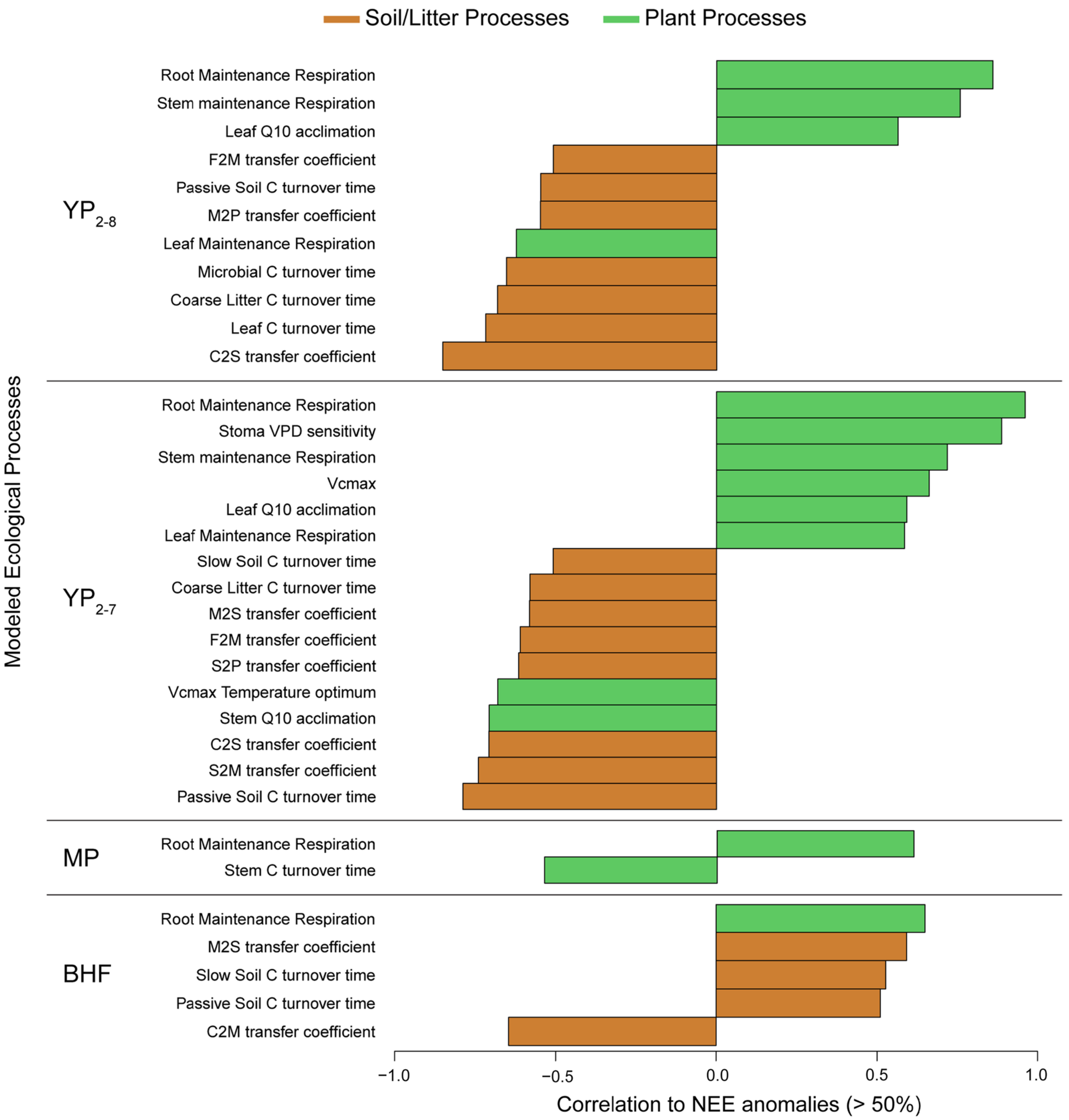


Fig. 5 Correlation between annual NEE flux anomalies and ecosystem processes anomalies across stand age and sites. Only correlations above 50%, as an arbitrary cut off, are shown. Negative correlations relate to process response that increased with ecosystem C storage, while positive correlations relate to process response that increased with net ecosystem C loss to the atmosphere

allowing models to act more like the ecosystems they are simulating, without changing observational data, model structure, or any process-based model assumptions. Importantly, typical first-order ecological or earth system models do not allow for annual changes in parameterization, and thus ecological properties, thereby creating systems where IAV is driven exclusively by climate variation. First-order kinetic models thus have difficulties recreating IAV of NEE, largely we expect due to static model parameterization (Luo and Schuur 2020), which was the impetus behind investigating dynamic DA in these forested wetlands.

Despite increases in data-model agreement at all sites, and for all C fluxes from dynamic DA, consistent underestimation of peak GPP shows that simulating annual change in ecological processes is not a panacea. Changing processes within the GPP module to better represent peak GPP may be an important next step to improve fidelity of secondary analyses, though a separate research question. Here, our focus was to demonstrate the usefulness of variance decomposition of observed and simulated NEE signals and further correlate modeled ecological processes to IAV of NEE. Comparing multiple models across regional to global scales would be another way to investigate systematic model errors and ecological processes that influence IAV of NEE in different ecoregions. Future work to integrate matrix model representations would also provide further model diagnostics to look deeper into model uncertainty and processes driving IAV of NEE.

Variance decomposition of large-scale ecological factors

Assessing the observed NEE signal in terms of large-scale drivers of IAV of NEE across wetland forests of varying stand age, we found that, similar to the study from Fu et al. (2019), that MCU dominated IAV of NEE at the MP site. However, in contrast, we also found that IAV of NEE at the YP and BHF sites was typically influenced most by CUP and MCR. This suggests that fluctuating soil carbon losses and changes in favorable growth days during the year, where GPP can outpace RE, contributed most to IAV of NEE during forest recovery after harvest and replanting at the YP sites. Taken together, variance decomposition of observed NEE suggests that mature pine plantations are insensitive to variability in climate, disturbance, or ecosystem responses throughout the year, but are influenced by variability during peak growing season that affects peak GPP. Whereas, both during regrowth from disturbance (YP) and at late-successional community in the region (BHF), daily variability in climate and ecosystem responses influence IAV of NEE by changing the CUP, while MCR from soils after harvest were dominate in YP sites.

Patterns in observed NEE signals were not perfectly recreated in simulated NEE. Though both DA approaches simulated NEE sufficiently well to generally recreate ecosystem-level influences of IAV of NEE at certain sites, they also both tended to under and overestimate key influences. For example, both DA approaches created simulations that underestimated the contribution of MCU to IAV of NEE at the MP site compared to the observed NEE signal (Fig. 4). Models created using dynamic DA further overestimated the influence of alpha at the MP site, indicating that changes in the ratio between actual vs. hypothetical maximum uptake was the largest contributor to IAV of NEE, which does not align with observations. Despite challenges in replicating observed annual C flux patterns, our results demonstrate how variance decomposition can be used as a benchmark for ecosystem models and their ability to reproduce ecosystem-level influences on IAV of NEE.

Process anomaly correlation

At the MP site, small increases in C loss through root maintenance respiration and small decreases in C loss from woody biomass turnover were indicated as the strongest correlates to IAV of NEE by process anomaly correlation, aligning with the large-scale assessment of the observed NEE signal by variance decomposition. We cannot say with certainty that root maintenance respiration and the turnover rate of woody biomass are the only individual ecological processes controlling IAV of NEE at the MP site, as repeating the procedure with other models, process-based assumptions and parameterization could show contrasting outcomes (Luo and Schuur 2020). However, it is encouraging that the assessment of specific processes showed reduced root respiration and slower woody biomass turnover correlate with reduced NEE, while large-scale NEE assessment showed similarly that general carbon uptake dominated IAV of NEE. The correlations are bidirectional so that increased root respiration at the YP sites correlates with increased NEE and aligns with carbon release dominating IAV of NEE at these sites. By fusing data and models and allowing models to demonstrate dynamic ecology, we were able to take a first look into what individual ecological processes in process-based models align with IAV of NEE. Though model identifiability issues remain, this approach allowed us to investigate what individual ecological processes may be driving IAV of NEE based on current process-based understandings and if these modeled outcomes align with ecosystem observations and expectations.

Conclusions

This and other works have shown that capturing peak growing season GPP is an ongoing issue that contributes to uncertainty in simulating NEE. We further showed that allowing ecological responses to vary year-by-year, through dynamic annual parameterization, did not generally improve the simulation of peak GPP. Despite underestimation of peak GPP response, allowing time–varying ecosystem properties did improve data-model agreement at all sites for all carbon-flux responses. As ecosystems show dynamic physiological and phenological properties through time, and across space, it may be important to allow models to do the same, especially if the root causes of IAV of NEE are to be attributed to ecological processes in process-based models. Here, we demonstrated that covariance allocation and process anomaly correlation can be used as tools to investigate agreement between the shape of simulated vs. observed NEE responses, and the ecological processes that may be driving IAV of NEE in process-based models. In terms of landscape ecology and application, continuing to improve modeling capabilities and assessment will play an important role in improving our understanding of the key ecological processes driving ecosystem change in a changing climate. Future work is still necessary to further constrain models with time–varying ecological responses and confirm if the identified ecological processes affecting IAV of NEE are realistic at these sites.

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Author contributions JW: Conceptualization, Methodology, Software, Validation, Formal analysis, Writing—Original draft, visualization MMA: Conceptualization, methodology, data curation, Writing—Review & Editing XH: Conceptualization, Methodology, Software, Writing—Review & Editing. YG: Conceptualization, Methodology, Software, Writing—Review & Editing EH: Conceptualization, Methodology, Software, Writing—Review & Editing WH: Conceptualization, Methodology, Writing—Review & Editing CL: Conceptualization, Methodology, Writing—Review & Editing LL: Conceptualization, Methodology, Writing—Review & Editing RZ: Conceptualization, Methodology, Writing—Review & Editing. HQ: Conceptualization, Methodology, Writing—Review & Editing KA: Conceptualization, Methodology, Writing—Review & Editing JSK: Conceptualization, Resources, Funding Acquisition, Writing—Review & Editing AN: Conceptualization, Resources, Funding Acquisition, Writing—Review & Editing LJ: Conceptualization, Methodology, Resources, Supervision, Project administration, Funding Acquisition, Writing—Review & Editing YL: Conceptualization, Methodology, Resources, Supervision, Project administration, Funding Acquisition, Writing—Review & Editing.

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Declarations

Competing interests The authors declare no competing interests.

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