Climate–trait interactions dominate vegetation light use efficiency distributions across China

Dear Editor and reviewers,

Thanks for handling our manuscript and offering us this valuable opportunity to revise our manuscript. We would like to express our sincere gratitude for your valuable time and the insightful comments provided by you and the reviewers. We have carefully addressed all the comments, and we believe the revised manuscript is now significantly improved in both clarity and scientific rigor.

We are pleased to upload the revised manuscript for your further consideration. Three major changes compared to the earlier version are listed below:

- First, we have added the comparisons between the estimated LUE and SIF yield to strengthen the robustness of our results. Figure 8 is added in the revised manuscript to illustrate the consistency between LUE and SIF yield.
- Second, we have added some descriptions to clarify the analyses and results of this study. Specifically, we have clarified the model training and validation processes, and stated the reasons for selecting the climate factors and functional traits clearly in this study.
- Third, we have added several discussions to better clarify the limitations of this study, including limitations from flux site distributions, factor selections (without consideration of CO_2). We also provide in-depth discussions about regional LUE patterns.

All changes are clearly tracked in the revised manuscript, and a detailed, point-by-point response is provided below to address each reviewer's comment. We are truly grateful for the constructive feedback we received, which has played a crucial role in improving the quality of our work. We hope that the revised manuscript now meets the standards for publication in your journal and look forward to your positive response.

Yours sincerely,

Mingzhu He (on behalf of the author team)

Reviewer 1

LUE quantifies the fraction of absorbed light used in photochemistry to produce chemical energy during photosynthesis and is essential for understanding ecosystem productivity and the global carbon cycle. Previous study have identified the key role of plant trait driving LUE variations, this study further advanced this topic by considering the climate-trait interactions. The manusript is well-written. The spatial resolution and time span is good. The logic and algorithm is clear and robust. After reviewing the manuscript, I have several issues that need to be addressed.

Response: We thank reviewer 1 (R1) for the positive comments regarding the manuscript. Please find below the responses to R1 comments.

1.Representation of Cropland or agricultural ecosystem in the flux tower upscaling. As we konw, Cropland usually showed large LUE. Currenly, this study overlooked the role of cropland sites. The spatial map also failed show the distribution over agricultural areas. I know, this might due the flux tower availability. At least, Sensitivity test should be incorpated. I doubt, whether the overall temporal trend is related to the cropland ecosystem.

Response: Thanks for this important comment. We agree that croplands generally have large LUE, and exclusion of cropland in this study may show data gaps to indicate the regional LUE variations. However, the gridded trait datasets used in this study have limited spatial coverage of plant functional traits over croplands across the entire study domain, particularly leaf nitrogen content (N) and specific leaf area (SLA), which are key predictors to map regional LUE variations (Line 132-133). Including croplands without consistent and enough trait information could introduce large uncertainties into model training and regional upscaling results. Additionally, exclusion of cropland into our analyses could also reduce the human management-related impacts (i.e. irrigation, fertilization) on vegetation LUE spatiotemporal variations in China, supporting straightforward linkages of LUE with environmental factors and plant functional traits. Nevertheless, we acknowledge that the exclusion of cropland in our study limits the representation of agricultural ecosystems in our regional estimates. We clarify this limitation and highlight the need for future studies incorporating enough cropland flux tower observations and spatially consistent trait data in the revised manuscript (Lines 379-384), which is also listed below.

"In addition, the trait datasets show limited spatial coverage of leaf nitrogen content (N) and specific leaf area (SLA) data over croplands, causing the exclusion of cropland LUE in the analyses of this study.

Such exclusion could induce limitations in the resulted regional LUE estimates as they do not fully represent LUE characteristics for agricultural ecosystems across China, and the extent to which croplands contribute to regional LUE variability and long-term trends remains uncertain. Future studies incorporating enough cropland flux tower observations and spatially consistent trait datasets are highly encouraged."

2. LUE product comparison. I know LUE could not directly derived, usually calculated by GPP and fapar. Maybe, checking the spatial consistency between normalized LUE and normalied SIF yield could partly address this issue.

Response: Thank you for this helpful suggestion. Following the reviewer's suggestion, we calculate the SIF yield as the ratio of SIF to APAR, with SIF obtained from the CSIF dataset. The data sources and the calculation method have been added to the Methods section (Lines 137–141). The comparison reveals the strong and significant positive spatial correlations between LUE and SIF yield over 2003–2020 (Pearson's r = 0.563, P < 0.001; Figure 8). Such complementary evidence of spatial consistency between LUE and Sif yield suggests that the LUE estimated in this study is robust. These results and their interpretation have been added to Section 3.3 (Lines 350-357).

Line 137-141: "Solar-induced fluorescence (SIF) data are obtained from the global spatially contiguous SIF (CSIF) dataset (Zhang et al., 2018), which covers the period 2000–2022. SIF yield is calculated as the ratio of SIF to absorbed photosynthetically active radiation (APAR), with APAR is estimated as the product of photosynthetically active radiation (PAR) and the fraction of absorbed photosynthetically active radiation (FPAR). FPAR is obtained from the MODIS MOD15A2H.061 product(Myneni et al., 2021), and PAR is obtained from the MODIS MCD18C2.062 product(Wang, 2025)."

Line 350-357: "To further address the robustness of the estimated LUE, we compare its multi-year mean spatial consistencies with SIF yield over 2003–2020. Since LUE and SIF yield have different units, the normalized values (Z-score) of these two variables are used for comparisons. The strong and significant positive spatial correlations are shown here (r = 0.563, P < 0.001; Fig.8), indicating broadly consistent spatial distributions between these two datasets, and implying the reliability of the estimated LUE in this study."

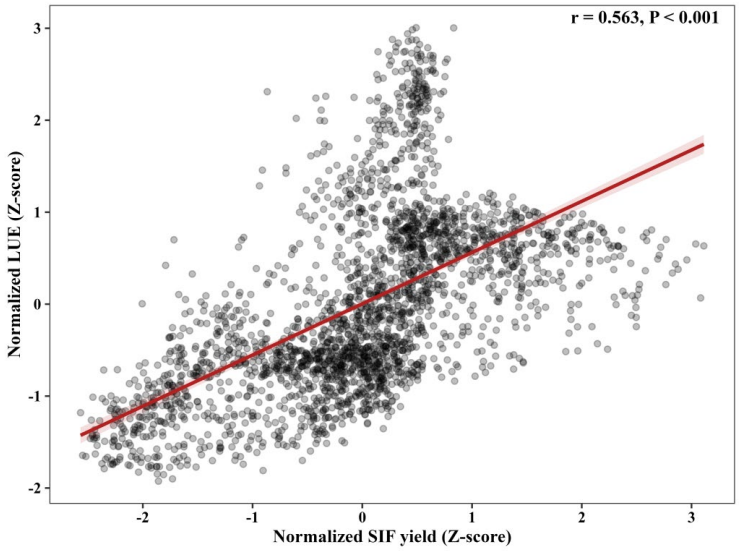

Figure 8: Spatial relationship between multi-year mean normalized LUE and SIF yield across China during 2003–2020. The red line represents the ordinary least squares (OLS) linear regression fit, and the shaded area indicates the 95% confidence interval.

3.Discussion. Large area of significantly decrease LUE are found in South China (Figure7). If this is robust, how to explain those decrease?

Response: Thank you for this valuable comment. To address this concern, we further examine the VPD conditions in areas exhibiting significant LUE declines across China and their relationships with the RF–SHAP results. Our analysis shows that these areas exhibit relatively low VPD, with a mean of 0.442 kPa and a 10th–90th percentile range of 0.177–0.614 kPa. These values largely fall within the range associated with negative VPD SHAP contributions (below approximately 1.2 kPa; Fig. 5d), suggesting that low-VPD conditions may be associated with lower model-predicted LUE. Previous studies also highlight the role of VPD in regulating photosynthetic processes and ecosystem LUE (Fei et al., 2019; Grossiord et al., 2020). In addition, widespread warming and spatially heterogeneous changes in soil water content (SWC) may further influence LUE through temperature and water limitations (Duffy et al., 2021; Zhou et al., 2015). We have revised the Discussion to incorporate these findings and clarify the potential roles of VPD, temperature, and SWC in the observed LUE declines (Lines 330-341), as detailed below.

"The significant LUE declines in parts of southern China may be associated with the nonlinear responses of LUE to atmospheric moisture conditions. Our additional analysis shows that areas exhibiting

significant LUE declines across China are characterized by relatively low VPD, with a mean of 0.442 kPa and a 10th–90th percentile range of 0.177–0.614 kPa. These values largely fall within the range associated with negative VPD SHAP contributions in our RF model (below approximately 1.2 kPa; Fig. 5d), suggesting that low-VPD conditions are associated with lower model-predicted LUE. Previous studies highlight the important role of VPD in regulating ecosystem LUE and photosynthetic processes (Fei et al., 2019; Grossiord et al., 2020). In addition, widespread warming occurs across southeastern China during 2003–2024, while SWC exhibits spatially heterogeneous changes, including decreases in some areas. Photosynthetic carbon uptake can be constrained when temperatures exceed ecosystem-specific optima (Duffy et al., 2021), whereas reduced soil water availability can limit photosynthesis through stomatal and non-stomatal processes (Zhou et al., 2015). Together, these findings suggest that the LUE declines may reflect the combined influence of atmospheric moisture conditions, temperature, and soil water availability, although the relative contributions of individual factors remain uncertain."

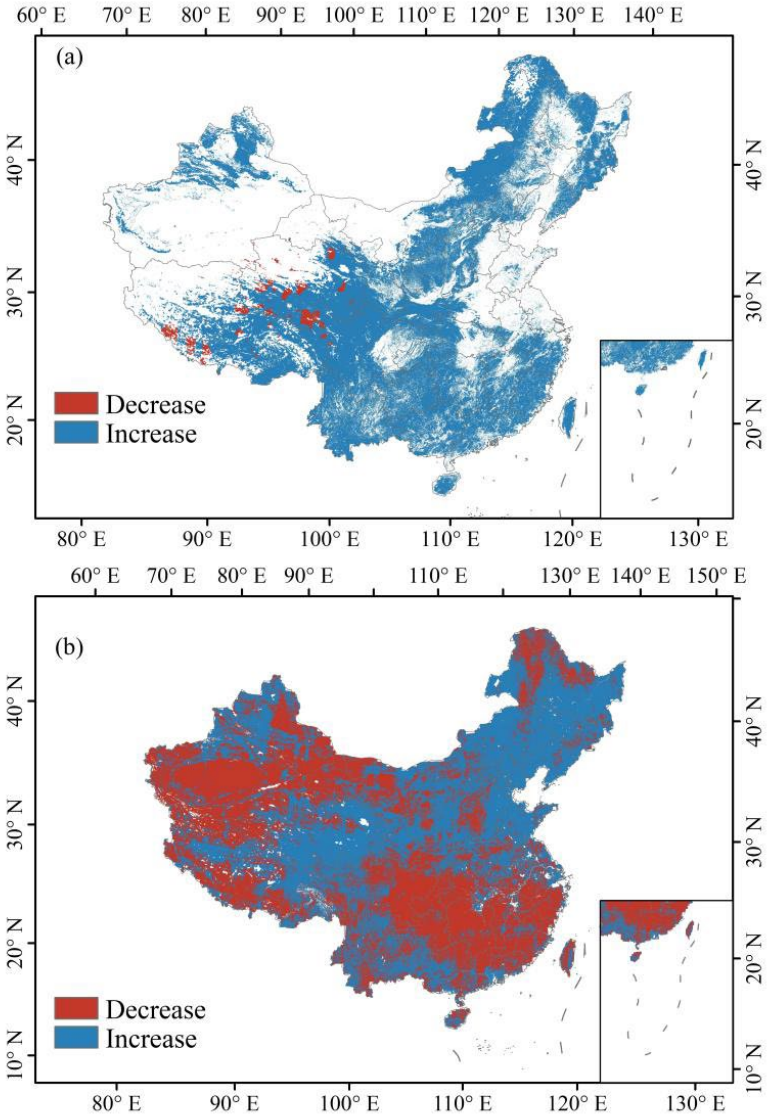

Figure R1. Spatial patterns of changes in air temperature (TA) and soil water content (SWC) across China during 2003–2024. (a) Spatial distribution of TA trends; (b) spatial distribution of SWC trends.

Reviewer 2

This manuscript investigates the drivers of LUE through the usage of flux tower observations, together with climatic and traits data. They mainly find that the interaction between climate factors and functional traits were the main drivers of LUE variations. They then upscaled this relationship to the national level and mapped LUE across China. The topic is novel and interesting, and the manuscript is generally well written. I have some minor suggestions, which may be helpful for revising the manuscript.

Response: We thank reviewer 2 (R2) for the positive comments regarding the manuscript. Please find below the point-by-point responses to each comment.

1.Although the 29 flux towers have provided a lot of observational datasets, it is still rarely observations for some specific regions and land cover types. This will lead to some uncertainties for the upscaling map. It is suggested to add some discussions on this issue.

Response: Thank you for this important comment. We totally agree with the reviewer that, although the 29 flux tower sites provide valuable observations across major ecosystem types in China, their spatial distribution and representation of different vegetation types are uneven and may induce some uncertainties for regional LUE mapping. Accordingly, we expand the discussion in Section 3.4 to clarify the potential limits of the uneven spatial and ecosystem-level distribution of flux tower observations on the regional LUE estimates, and highlight the need for more flux tower observations in the future (Lines 398-403), which is also shown below.

"The spatial distribution of the 29 flux tower sites is uneven across China, with varying number of sites over different PFTs. The limited number of sites for some PFTs may not fully capture the characteristics of LUE within those ecosystem types. Similarly, the uneven spatial distributions of flux tower observations may limit the performance of resulted regional-scale LUE representations. Further study with more even distributed flux tower observations with relatively longer time period are needed to improve our understanding of regional LUE variations."

2. The authors used the RF model to identify the drivers of LUE and for the generation of China's LUE map. However, the validation of the RF model are not comprehensively provided, for example, the performance for the training datasets and testing datasets. Do the authors used the k-fold cross validation? It will be helpful to provide some details of the model performance.

Response: Thank you for this valuable comment. In the revised manuscript, we clarify that we do not use the k-fold cross-validation, but instead employ a repeated site-based random partitioning approach. In each iteration, approximately two-thirds of the flux tower sites are selected for model training, and all available sites are used for model testing. This procedure is repeated 50 times, and R^2 and RMSE are calculated separately for each iteration, with the results reported as mean ± standard deviation. The full model achieves an R^2 of 0.924 ± 0.011 and an RMSE of 0.165 ± 0.017 g C MJ^{-1} for the training processes, and 0.583 ± 0.123 and 0.393 ± 0.060 g C MJ^{-1} over all of the sites, respectively. We have clarified this information in the revised version in Line 218-226.

Line 172-176:"The RF model is trained using a repeated site-based random partitioning approach. In each iteration, approximately two-thirds of the flux tower sites are randomly selected for model training, while data from all the available flux tower sites are used for model testing. Model performance is hence assessed using the coefficient of determination (R^2) and root mean square error (RMSE). This procedure is repeated 50 times, and the results are shown as mean ± standard deviation."

Line 218-226:"Across the 50 repeated iterations, the full model achieves a mean R^2 of 0.924 ± 0.011 and an RMSE of 0.165 ± 0.017 g C MJ^{-1} from the training processes. When the trained model is applied to all available flux tower sites, the mean R^2 and RMSE are 0.583 ± 0.123 and 0.393 ± 0.060 g C MJ^{-1}, respectively (Fig. 3). The climate-only model shows relatively lower performance, with a mean R^2 of 0.842 ± 0.025 and an RMSE of 0.237 ± 0.028 g C MJ^{-1} from the training processes, and 0.454 ± 0.176 and 0.449 ± 0.070 g C MJ^{-1} across all available sites, respectively. Notably, the full model outperforms the climate-only model with a higher R^2 by 0.129 and lower RMSE by approximately 12.5% based on the results from all the available sites. These results indicate that incorporating plant functional traits improves the overall representation of LUE variability across the available flux tower sites, highlighting the importance of plant functional traits in LUE simulations and vegetation photosynthesis modeling."

3.They author selected some climate factors and functional traits, such as temperature, VPD, N, SLA etc. It will be helpful to add some discussions of why select these factors for explaining LUE.

Response: Thank you for this helpful suggestion. Specifically, these selected predictors represent complementary ecological and physiological controls on LUE. Air temperature characterizes thermal constraints on photosynthesis, while VPD and SWC represent atmospheric water demand and soil water

supply, respectively, indicating the water status/stress experienced by vegetation. Leaf nitrogen content and SLA reflect the photosynthetic biochemical capacity and leaf resource-acquisition strategies, whereas rooting depth and isohydricity characterize plant water acquisition and stomatal regulation strategies. PFT is further included to account for broad differences in vegetation structure, phenology, and ecosystem functioning. The data availability is another reason for selecting variables, as these climate factors and functional traits are easily accessible and have regional products for analyses. We have added relevant literature to support these explanations and clarified that the selected variables represent key complementary controls on LUE. These revisions are provided in Section 2.2 (Lines 134-149).

"These predictors are selected according to their complementary physiological roles in regulating ecosystem LUE and the availability of spatially continuous datasets for nationwide analysis. Air temperature (TA) represents thermal constraints on photosynthetic processes, as photosynthetic activity exhibits nonlinear responses to temperature, with declines occurring beyond optimal thermal conditions (Duffy et al., 2021). Vapor pressure deficit (VPD) represents atmospheric water demand, which can induce stomatal closure and restrict photosynthetic carbon uptake under strong atmospheric dryness (Grossiord et al., 2020; Novick et al., 2024). Soil water content (SWC) represents soil water supply and complements VPD by distinguishing soil water limitations from atmospheric water demand. SWC can directly constrain photosynthesis and interact with atmospheric dryness to regulate ecosystem carbon uptake (Humphrey et al., 2021). At the leaf level, nitrogen content (N) is closely associated with photosynthetic biochemical capacity, whereas specific leaf area (SLA) reflects leaf construction and resource-acquisition strategies along the leaf economics spectrum (Evans, 1989; Walker et al., 2014). At the whole-plant level, rooting depth reflects the potential capacity to access water in deeper soil layers (Fan et al., 2017), while isohydricity characterizes variation in stomatal regulation strategies under changing water availability (Konings and Gentine, 2017; Tardieu and Simonneau, 1998). In addition, PFT is included to represent broad differences in vegetation structure, phenology, and ecosystem functioning that are not fully captured by individual plant traits (Díaz et al., 2016). Collectively, these predictors represent complementary climatic, physiological, and vegetation-level controls on LUE, and are selected for analyses in this study."

4. For fig. 6, I wondering why the Northern east generally had a higher LUE values? Could you provide some discussions on this?

Response: Thank you for this helpful comment. We dig into the results in the Northern east through examining all the variables used in this study. Our analysis indicates that leaf N content (Figure R2) is generally higher in northeastern China than the rest of China. Such high leaf N content may help explain the relatively high LUE in this region, given the important role of leaf N content in photosynthetic processes. Specifically, leaf nitrogen is an essential component of photosynthetic enzymes and proteins and is closely associated with photosynthetic capacity (Evans, 1989; Walker et al., 2014). Therefore, the relatively high leaf N content in northeastern China may partly contribute to its higher LUE. We include this discussion in the revised manuscript to provide a potential physiological explanation for the regional LUE pattern (Section 3.3, Lines 341-345).

"The relatively high LUE in northeastern China may be partly associated with regional differences in leaf N content. Our analysis indicates that leaf N content is generally higher in northeastern China than the rest of China. Leaf nitrogen plays an important role in photosynthesis, as it is an essential component of photosynthetic enzymes and proteins and is closely associated with photosynthetic biochemical capacity (Evans, 1989; Walker et al., 2014). Thus, higher leaf N content may support greater photosynthetic capacity and potentially contribute to the relatively high LUE observed in northeastern China."

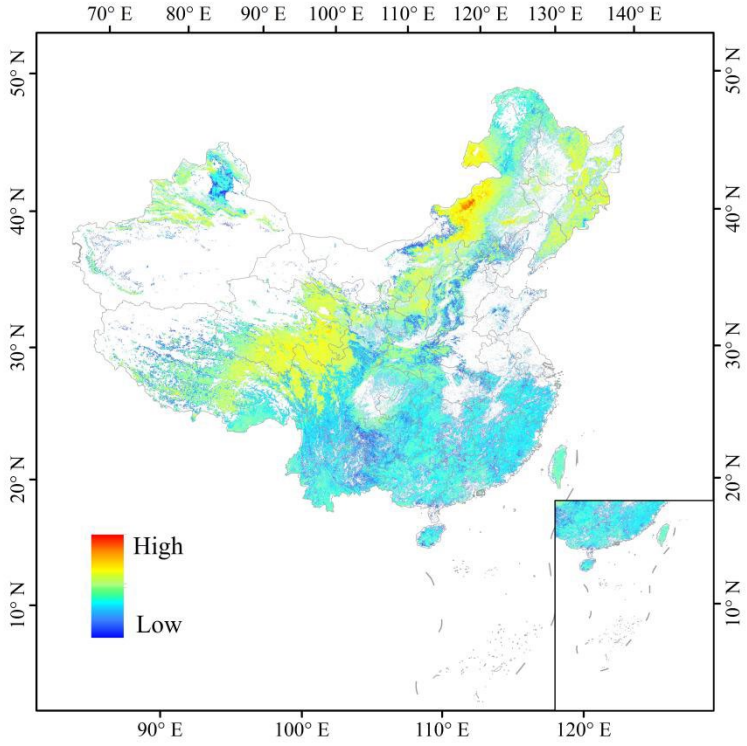

Figure R2 Spatial distributions of leaf nitrogen content over China

5. For the upscaling to global long-term trend in LUE, please be noted that there are some other factors may affect LUE, such as CO2. When modelling LUE using the spatial model, you did not consider CO2. So when you extend this model to the time-scale, this model may fail to capture the long-term variations of LUE. That means, the long-term trend of LUE you modelled by this RF model may have some biases. I suggest at least to add some discussions on this.

Response: Thank you for this important comment. Yes, rising CO_2 fertilize terrestrial vegetation, which may also affect LUE. However, we do not consider the effects of CO_2 on LUE variations, which may introduce uncertainties in future predictions. One reason that we do not incorporate CO_2 into analyses is that this study conducts LUE investigations for the latest two decades and mostly focus on spatial variations. Moreover, our LUE estimates are highly correlated with SIF yield (Figure 8 in the revised manuscript and also stated below), implying that our results are generally reliable in China. Nevertheless, we have expanded the discussion in Section 3.4 (Uncertainties and implications for carbon-cycle assessment) to acknowledge the limitation of not considering CO_2 effects on LUE, which is also stated below.

Line 414-422: "Another source of uncertainty relates to the temporal extrapolation of the RF model. Atmospheric CO_2 concentrations is increasing, and elevated CO_2 can directly stimulate photosynthetic carbon assimilation by enhancing Rubisco carboxylation and suppressing photorespiration, thereby affecting photosynthetic LUE (Ainsworth and Long, 2005; Kang et al., 2025). A global flux-tower analysis identifies CO_2 fertilization as an important contributor to temporal variations in ecosystem LUE (Liu et al., 2024). However, atmospheric CO_2 concentration is not included as a predictor in our RF model, introducing uncertainties into the magnitude of the estimated long-term LUE trend and hence future LUE predictions. Moreover, CO_2 responses vary among plant functional types and different environmental conditions (Ainsworth and Long, 2005). Future studies could incorporate atmospheric CO_2 concentrations or a physiologically based CO_2-response function into the upscaling framework to better constrain long-term LUE dynamics."

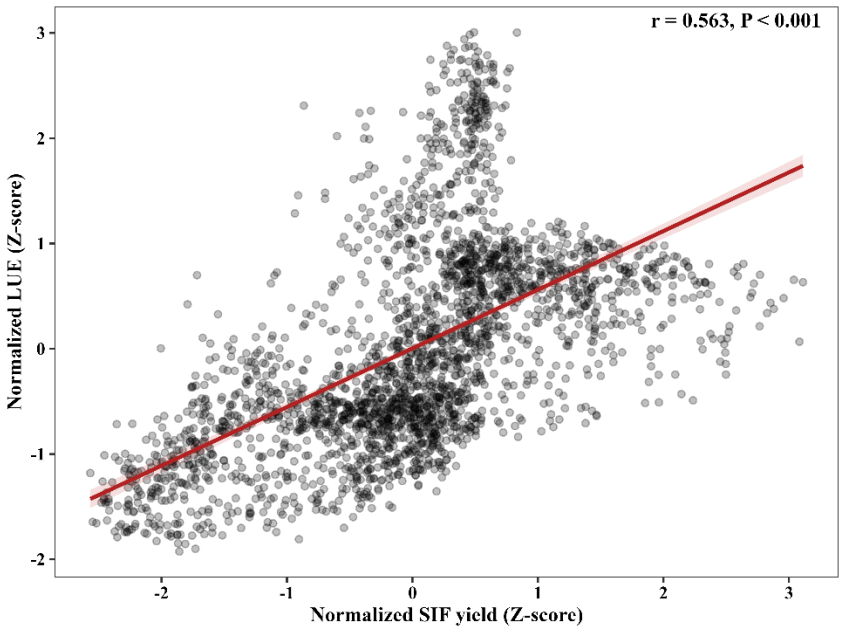

Figure 8: Spatial relationship between multi-year mean normalized LUE and SIF yield across China during 2003–2020. The red line represents the ordinary least squares (OLS) linear regression fit, and the shaded area indicates the 95% confidence interval.