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ORIGINAL ARTICLE

Boreal Forest Sensitivity to Temperature Is Jointly Regulated by Ecosystem Productivity and Seasonality: A Synthesis Based on Carbon Fluxes From FLUXNET Sites

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ABSTRACT

Boreal forests are experiencing rapid global warming, which may amplify the impact of temperature on their carbon sink function. However, the factors influencing the sensitivity of the carbon balance to temperature in boreal forests are still not well understood, especially over short timescales. Leveraging the FLUXNET dataset, we calculated the sensitivities of carbon fluxes to temperature anomalies (T_s) across boreal forest (24 sites) on the seasonal scale. Here, a positive T_s value indicates that the carbon flux increases with temperature anomaly, while a negative value suggests the opposite. Results showed that T_s of NEP in early spring was positive for evergreen needleleaf forests but negative for deciduous broadleaved forests. Although T_s of gross ecosystem production (GEP) remained positive, it tended to decrease with increasing temperature and vapour pressure deficit in spring and summer. Associated with this decrease were relatively small changes in T_s of ecosystem respiration (R_e), so that T_s of NEP decreased with increasing temperature and vapour pressure deficit in spring and summer. Both T_s of GEP and R_e increased with ecosystem productivity (represented by annual GEP) in spring, with T_s of GEP being more sensitive, indicating that carbon sinks in sites with lower productivity tended to negatively respond to higher temperature. Young-aged and low-nutrient forests tended to respond negatively to increasing temperatures. Ecosystem productivity and seasonality played an essential role in regulating T_s of NEP. Our results suggest that significant declines in ecosystem productivity may exacerbate the negative response of NEP to elevated temperatures, further compromising carbon sequestration in boreal forests. This understanding is vital both for improving the predictive accuracy of carbon-climate models and for formulating targeted strategies to bolster resilience in the most vulnerable boreal ecosystems.

1 | Introduction

Boreal forests cover 30% of the global forest area and are an important part of the global carbon sink (Pan et al. 2024a). Therefore, they are recognised as an important element in climate change mitigation policies (Pan et al. 2011; Martínez-García et al. 2024). This region is subject to the fastest climate warming, with annual average temperatures rising by 1.5°C or more and predicted to rise by 4°C–11°C in the end of the century relative to pre-industrial levels (Gauthier et al. 2015; Larson et al. 2023). While the carbon sink of boreal forests is generally expected to

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increase with global warming due to the positive relationship between net ecosystem production (NEP) and temperature (Black et al. 2000; Bonan 2008), decreases in carbon fluxes under high temperature have frequently been observed (Niu et al. 2012; Niu et al. 2021; Ping et al. 2023; Niu et al. 2024; Wang et al. 2024). Concerns have thus been raised about how the carbon sink in boreal forests responds to varying temperatures, as this response could significantly alter carbon-climate feedbacks. However, limited studies have been devoted to the response of NEP sensitivity to temperature anomalies and its underlying mechanisms, leaving a sizeable research gap.

Despite recent advances in boreal forest research (Arain et al. 2022; Liu et al. 2025a), substantial uncertainties persist in quantifying their carbon fluxes. A main source of uncertainty stems from their temperature responses. As the net CO_2 exchange between forest ecosystems and the atmosphere, NEP quantifies the equilibrium between photosynthetic carbon assimilation (gross ecosystem production, GEP) and respiratory carbon efflux (ecosystem respiration, R_e) (Chapin et al. 2006). The distinct biophysical processes of these two components jointly determine the temperature response of NEP. In general, the impact of increased temperature on plant photosynthesis by reshaping canopy architectures, microclimate buffering capacity, and phenology (e.g., timing of leaf-out, senescence, and growing-season length) has been well documented across biomes (Sprintsin et al. 2012; Keenan et al. 2014; De Frenne et al. 2021), and respiration is expected to increase with temperature (Duffy et al. 2021), leading to a projected suppression of carbon sink strength under high temperature. Nevertheless, the optimal temperatures for both photosynthesis (Wang et al. 2024; Pan et al. 2024b) and respiration (Chen et al. 2023; Niu et al. 2024) have been widely observed at the global scale, suggesting that R_e may also decrease under high temperature like GEP. In this context, the convergent response patterns of GEP and R_e to temperature may introduce considerable uncertainty in characterising NEP dynamics under climate change. This uncertainty may be highly variable due to the changing temperature responses of photosynthesis and respiration. Therefore, the explanatory power of common factors like forest types, ecosystem productivity, and nutrient availability may be limited (Xu et al. 2020), highlighting the need to explore the sensitivities of carbon balance components to temperature anomalies (T_s) over short timescales. However, the majority of previous studies have focused on individual components, hindering accurate estimation of regional and global carbon sinks.

To assess the impacts of temperature on carbon fluxes, previous studies have utilised large-scale forest inventory and remote sensing technology (Buermann et al. 2014; Girardin et al. 2016), finding a weakening of the boreal forest's carbon sink strength in response to high temperature. However, both methods exhibit limitations. Forest inventory, typically conducted at multi-year intervals, suffers from coarse temporal resolution limiting its capacity to capture fine-scale dynamics of high temperature impacts (Potapov et al. 2011; Walker et al. 2021). The limited accuracy of remote sensing data at regional scales may confound the assessment of temperature impacts across forest types (Fassnacht et al. 2023), thereby leading to a non-uniform response of carbon sink strength to temperature. Insufficient temporal and spatial precision preclude the detection of heat stress events, for example, short-duration heatwaves and rapid temperature fluctuations that may also impair ecological functioning (Reichstein et al. 2013). Eddy covariance (EC) technology has emerged as a robust methodology for accurately assessing the impact of climate change on carbon fluxes in boreal forest ecosystems (Dunn et al. 2007; Krishnan et al. 2008; Vesala et al. 2010). Although some studies have examined the responses of carbon fluxes to temperature (Welp et al. 2007; McMillan et al. 2008; Liu et al. 2022), they primarily focused on the annual scale rather than the seasonal scale (Xu et al. 2020; Arain et al. 2022). Notably, research indicated that the negative impacts of elevated temperatures on forest carbon sinks occur at temperatures that are often lower than those defined as "extremely high" (i.e., 90% or 95% quantile temperature during the long-term period) (Ping et al. 2023; Niu et al. 2024). This suggests that extreme high temperature is not a prerequisite for heat stress, likely due to the different physiological states of vegetation across various seasons (Richardson et al. 2010; Richardson et al. 2013). Therefore, employing seasonal temperature sensitivity to characterise the responses of carbon fluxes to temperature at the seasonal scale has considerable potential for improving our understanding of how boreal forests respond to climate change.

To fill this knowledge gap, we used carbon flux data and meteorological records from 24 forest sites within the comprehensive FLUXNET dataset to systematically examine the response of carbon fluxes to temperature anomalies in boreal forest (> 45°N). The specific objectives were to (1) examine the seasonal variations in carbon fluxes sensitivity to temperature anomalies; (2) identify which environmental factors make NEP more vulnerable to temperature anomalies; and (3) determine the main driving factors affecting NEP sensitivity to temperature anomalies.

2 | Materials and Methods

2.1 | Data Collection

The study derived carbon fluxes and meteorological data from the FLUXNET 2015 data set (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/). These data cover various ecosystem types and include eddy covariance (EC) and meteorological data (Pastorello et al. 2020). The sites were chosen based on the following criteria: (1) latitude must be greater than 45°; (2) no artificial disturbance has occurred since stand replacement; (3) contains forest age and at least 5 years of data; (4) pure forests (i.e., there is only one dominant tree species in the flux footprint). Focusing on the boreal forest ecosystem, we extracted 24 boreal sites that met these criteria from the FLUXNET 2015 dataset (Figure 1 and Supporting Information: Table S1), and of all 24 forest sites with age ranging from 2 to 240 years. The carbon fluxes of these 24 sites exhibited similar seasonal patterns (Supporting Information: Figure S1). Among them, 17 sites were evergreen needle-leaved forests (ENF) and seven sites were deciduous broadleaved forests (DBF). Forest-stand age was obtained from the GFAD dataset (Poulter et al. 2019) and was divided into three classes (< 40 years, 40–90 years, and > 90 years), namely young (3 sites), middle (9 sites), and old (12 sites) forests (Kuuluvainen and Gauthier 2018; Liu et al. 2025a). Seasonal periods were defined based on standardised mean monthly air-temperature seasonality. Nutrient level was classified

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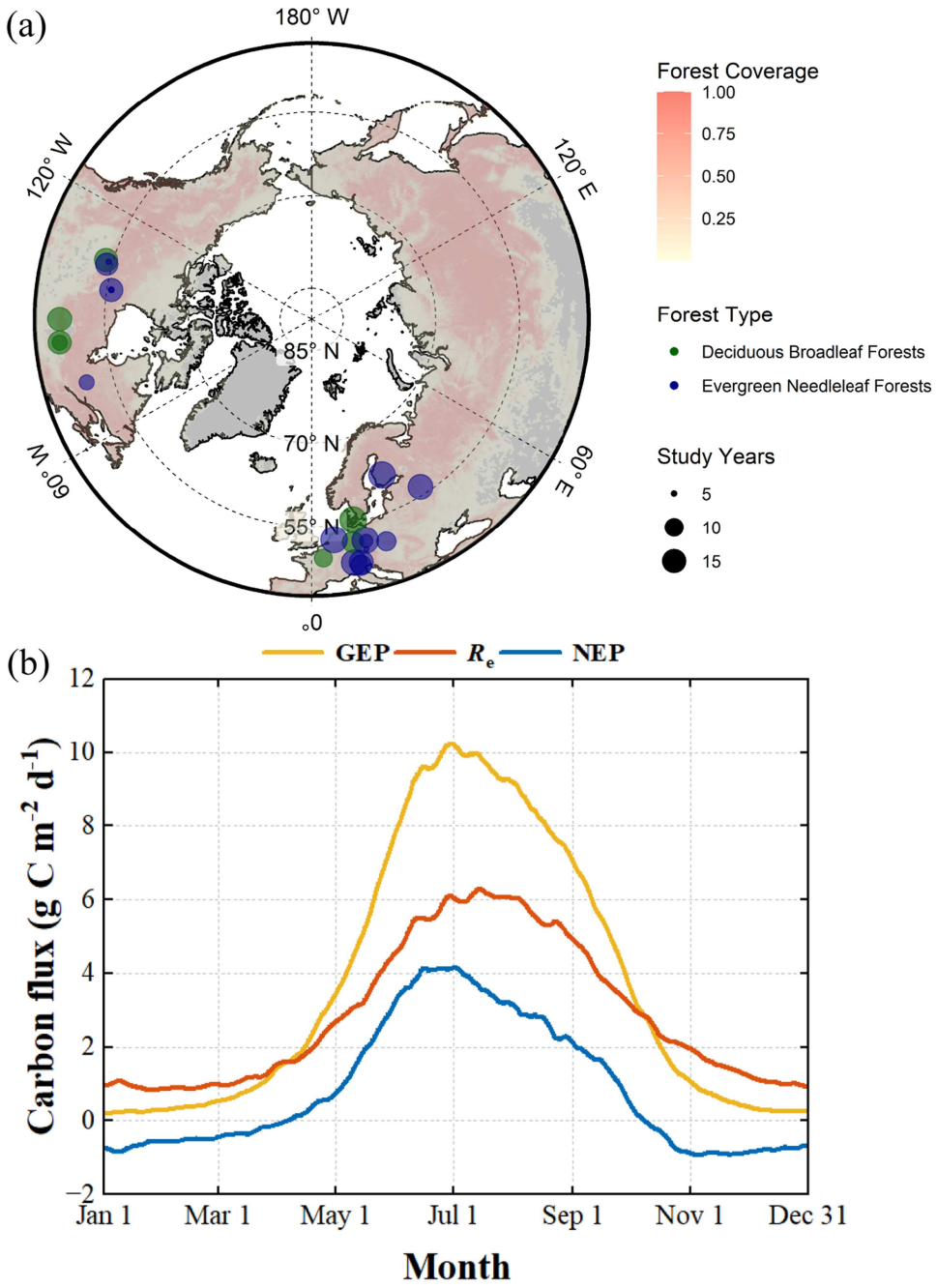

FIGURE 1 | Spatial distribution of eddy covariance flux monitoring sites across boreal forests (> 45°N; a) and seasonal variations in daily carbon fluxes (b). The background illustrates boreal forest cover density derived from Pugh et al. (2019). Green and blue circles indicate deciduous broadleaf and evergreen needleleaf forest sites, respectively. The size of each circle is proportional to the duration of data collection at the site. Carbon fluxes include gross ecosystem production (GEP), ecosystem respiration (R_e), and net ecosystem production (NEP). In panel (b), seasonal variations in daily carbon fluxes represent the mean daily fluxes averaged across all sites. [Color figure can be viewed at wileyonlinelibrary.com]

into three classes, namely low (17 sites), medium (2 sites), and high (5 sites) nutrient availability (Fernandez-Martinez et al. 2014; Liu et al. 2025a). To determine the nutrient availability classes, soil data (e.g., carbon, nitrogen, soil type, soil texture, pH, etc.) were first collected from published literature for nutrient classification (Supporting Information: Table S2). Then, sites were objectively ordered along a nutrient gradient using principal component analysis (PCA). Given the limited number of sites in the medium nutrient availability, we adopted the PCA to assess whether it was necessary to include this nutrient category (Supporting Information: Figure S2). Our analysis revealed a considerable overlap between the medium and other nutrient levels. Notably, the overlap between medium and high nutrient sites was nearly twice as high as that between medium and low nutrient sites (9.5% vs. 5.2%, Supporting Information: Table S3). Therefore, we decided to incorporate the medium nutrient sites into the high nutrient category.

For carbon flux data, uniform quality control and processing methods were used to improve consistency and comparability among sites (Pastorello et al. 2020). Briefly, net ecosystem

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exchange (NEE) data were screened, outliers removed, and gap-filled to derive net ecosystem production (NEP) (i.e., NEP = −NEE). The empirical relationship between nighttime NEE (i.e., nighttime R_e) and temperature was estimated; subsequently, this relationship was applied to daytime to derive daytime R_e and GEP (Reichstein et al. 2005).

2.2 | Data Processing

Carbon fluxes (i.e., GEP, R_e, and NEP) sensitivity to temperature anomalies (T_s of GEP, R_e, and NEP) was calculated followed the methodology proposed by Xu et al. (2020), in which daily mean air temperature was used as an index of heat stress. In brief, the procedure involves three steps (Figure 2): (1) daily GEP, R_e, NEP, and T_a were detrended over their respective study periods using linear regression; (2) the multi-year average of daily T_a and carbon fluxes were calculated and was subtracted from each daily T_a values to obtain their daily anomalies; (3) daily T_a anomalies were fitted with the concurrent responses of GEP, R_e, and NEP using linear mixed-effects models with sites as random effects to separate fixed temperature responses from site-level variations across boreal forests (Liu et al. 2025a). A sliding window of 15-days with a time step of 1 day was employed during the fitting process. Significance was evaluated at the 5% level, where the relationship was considered statistically significant. Considering the reliability of the model, we only retained the regression relationship when $p < 0.05$. Finally, the corresponding slope value (i.e., T_s) represents the sensitivity of the response of carbon fluxes to the short-term temperature anomalies (Xu et al. 2020; Arain et al. 2022). The standard unit of the sensitivity of carbon fluxes to temperature anomalies was g C m^{-2} day^{-1} $°C^{-1}$. Here, positive sensitivity values indicate that carbon fluxes increase with temperature, while negative values indicate that carbon fluxes decrease with increasing temperature (Xu et al. 2020).

2.3 | Data Analysis

Linear regression was used to assess the relationship between the temperature sensitivity of carbon fluxes and continuous variables. Significance was evaluated at the 5% level. Differences between carbon flux sensitivities in various season were assessed using the least significant difference (LSD) test at the $p < 0.05$ significance level. The classification and regression tree (CART) was employed to identify the key factors influencing the T_s of NEP. We considered potential impact variables to include four categorical variables: season, nutrient level, vegetation type, and forest age, and four continuous variables: annual GEP, mean annual temperature (MAT), mean annual precipitation (MAP), and elevation. In the CART model, the proportional reduction in error (PRE) is equivalent to a traditional coefficient of determination (R^2) and is used to evaluate the model's performance. The maximum number of splits and the minimum PRE were set to 8 and 0.01, respectively. The data processing (including extraction, filtering, normalisation, detrending, fitting, etc.) and the CART model were performed in MATLAB R2022b (MathWorks, Natick, MA, USA). Regression analyses were performed in R (https://www.r-project.org/).

3 | Results

3.1 | Seasonal Patterns of Carbon Flux Sensitivity to Temperature Anomalies

Both T_s of R_e and GEP were primarily positive values across both ENF and DBF ecosystems (Figure 3), with little difference observed between the two forest types (Figure S3). T_s of GEP and R_e for DBF peaked in early summer, and T_s of GEP showed an earlier peak in early spring for ENF. As a result, GEP exhibited higher sensitivity to temperature anomalies than R_e ($p < 0.001$), the T_s of NEP for ENF showed positive values in early spring. In contrast, T_s of NEP for DBF exhibited negative values across seasons.

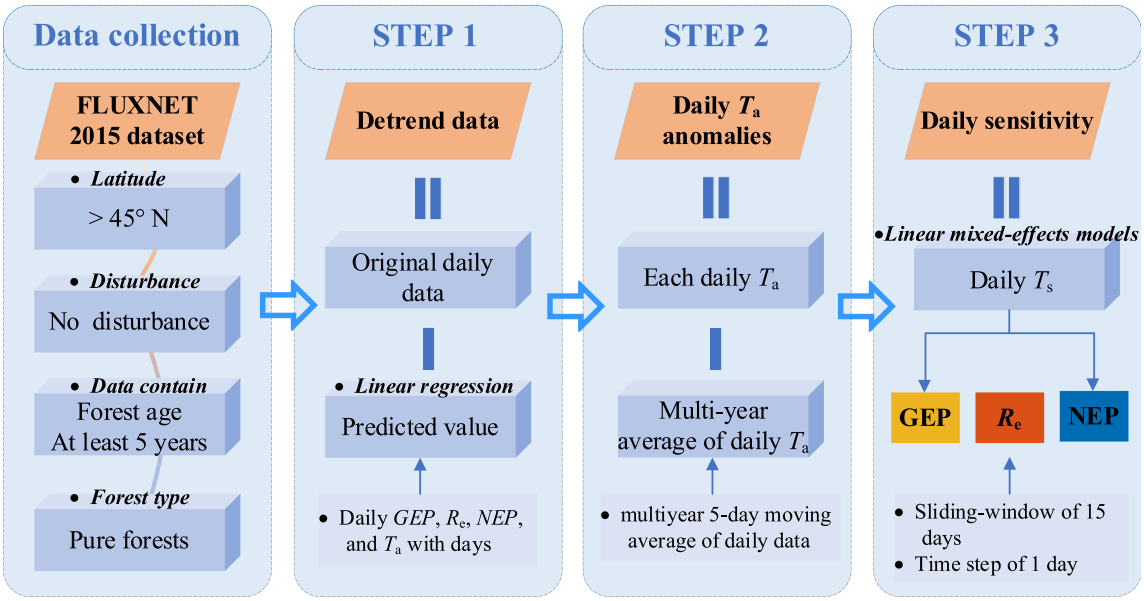

FIGURE 2 | Flowchart with respect to data processing and analysis. [Color figure can be viewed at wileyonlinelibrary.com]

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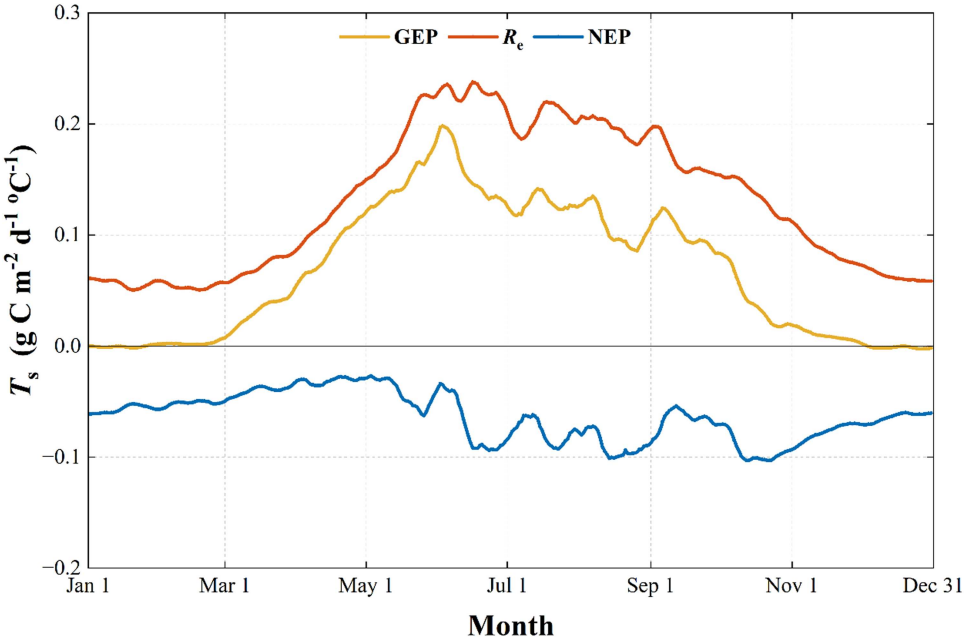

FIGURE 3 | Daily sensitivities of forest carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} °C^{-1}). Carbon fluxes include gross ecosystem production (GEP, orange), ecosystem respiration (R_e, red), and net ecosystem production (NEP, blue). Positive and negative T_s indicate that carbon fluxes increase and decrease with increasing temperature anomalies, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

3.2 | Effects of Climatic Factors on Carbon Flux Sensitivity to Temperature Anomalies

T_s of R_e increased with T_a in all seasons except for summer ($p < 0.001$; Figure 4 and Supporting Information: Table S4). T_s of GEP initially increased with T_a in all seasons except for winter, however, it tended to decrease sharply with increasing T_a when T_a approached a threshold. Furthermore, T_s of R_e was higher than T_s of GEP across different seasons ($p < 0.05$; Supporting Information: Table S5), leading to negative values of T_s of NEP. In summer, T_s of R_e stayed relatively constant at around 0.2 g C m^{-2} day^{-1} °C^{-1}, while T_s of GEP tended to decrease with increasing T_a (Figure 4b).

T_s of R_e increased with VPD in spring and winter ($p < 0.001$), but it decreased with increasing VPD in summer and autumn ($p < 0.05$; Supporting Information: Figure S4 and Table S6). T_s of GEP decreased with increasing VPD in spring and summer ($p < 0.001$), leading to that T_s of NEP decreased with increasing VPD (Supporting Information: Figure S4a,b). Moreover, T_s of GEP increased with precipitation in all seasons except winter ($p < 0.05$), whereas T_s of R_e responded positively in autumn and winter ($p < 0.05$;Supporting Information: Figure S5 and Table S7). Consequently, T_s of NEP increased with precipitation in spring and summer but decreased in winter ($p < 0.05$).

3.3 | Effects of Other Factors on Carbon Flux Sensitivity to Temperature Anomalies

T_s of GEP and R_e showed significant positive correlations with annual GEP across all seasons except for summer ($p < 0.05$; Figure 5). In Spring, T_s of GEP increased more rapidly than that of R_e with rising annual GEP in spring, causing T_s of NEP to shift from negative to positive values around annual GEP of 1500 g C m^{-2} year^{-1} ($p < 0.05$; Figure 5a). In autumn and winter, T_s of NEP exhibited no clear relationship with annual GEP due to similar responses of T_s of GEP and R_e to annual GEP ($p < 0.05$; Figure 5c,d).

Across all seasons, T_s of GEP showed an increasing trend with stand age though this trend was no statistically significant ($p > 0.05$; Figure 6). Although the T_s of R_e exhibited no consistent response pattern with stand age across seasons, it remained numerically higher than that T_s of GEP, leading to negative T_s of NEP in forests of all ages and across all seasons. In spring, summer, and autumn, the negative T_s of NEP in young forests was the lowest compared to that in both middle-aged and old forests, though these differences were not statistically significant (Figure 6a–c). In summer, autumn, and winter, T_s of R_e showed greater values than T_s of GEP for low nutrient forests ($p < 0.001$; Figure 7b–d). The T_s of NEP was lower for low-nutrient forests than that for high-nutrient forests only in summer ($p < 0.05$).

3.4 | Key Factors Affecting the NEP Sensitivity to Temperature Anomalies

Annual GEP and season were the most important variables affecting T_s of NEP among continuous and categorical variables, respectively (Figure 8). The primary split at the root node separated the group of higher productivity sites (GEP ≥ 1900 g C m^{-2} year^{-1}) with the positive T_s of NEP. The lower productivity sites (GEP < 1900 g C m^{-2} year^{-1}) were further divided by elevation, season, MAT, MAP, and GEP. The lowest negative T_s of NEP occurred at less productive sites (GEP < 1900 g C m^{-2} year^{-1}) with low elevation (< 30 m).

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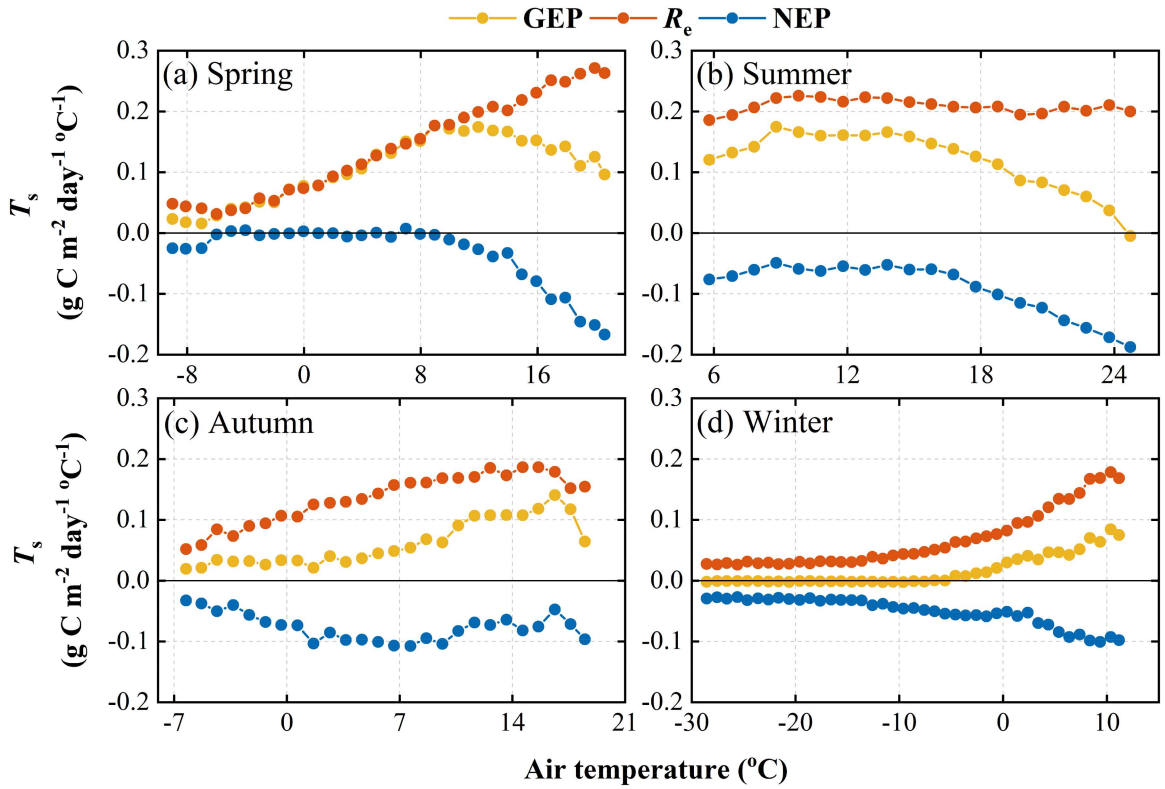

FIGURE 4 | Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} °C^{-1}) and air temperature in (a) spring, (b) summer, (c) autumn, and (d) winter. Carbon fluxes include gross ecosystem production (GEP, orange), ecosystem respiration (R_e, red), and net ecosystem production (NEP, blue). Daily T_s values were sorted into 1-°C air temperature bins. [Color figure can be viewed at wileyonlinelibrary.com]

4 | Discussion

4.1 | Climatic Factors Affecting Carbon Flux Sensitivity to Temperature Anomalies

Our results showed that the T_s of NEP decreased with T_a during spring and summer ($p < 0.001$; Figure 4a,b and Supporting Information: Table S4). This pattern may be attributed to the optimum temperature for respiration is usually higher than that for photosynthesis (Liu et al. 2025a). In spring and summer, the T_s of GEP decreased (but values stayed positive) after reaching its optimum temperature (approximately 9.0°C and 13.8°C, respectively), while the T_s of R_e continued to increase (Figure 4a) or remain unchanged (Figure 4b) with increasing T_a, jointly resulting in a more negative the T_s of NEP. When the temperature exceeds the optimum temperature, the photosynthesis of plants will rapidly decline due to damage from electron transport, rubisco enzymatic capacity, stomatal regulation, and accelerated leaf senescence (Scafaro et al. 2017; Wang et al. 2024). In winter, the T_s of NEP also decreased with increasing T_a ($p < 0.001$; Figure 4d), which is because the greater response to temperature anomalies for R_e compared to GEP. This result aligns with the findings that R_e can be promoted by stimulating soil respiration even if warming occurred in the low temperature range during winter (Monson et al. 2006).

We found that the R_e sensitivity to temperature anomalies remained unchanged with increasing VPD in summer (0.2 g C m^{-2} day^{-1} °C^{-1}, Supporting Information: Figure S4b), paralleling the trend observed in its response to T_a (Figure 4b). But more negative and more sensitive response of GEP to increasing temperature was observed in summer, which was associated with higher VPD. This may be related to stomatal closure (Zhu et al. 2021), which exacerbates the inhibition of NEP by temperature anomalies. While our results showed a relationship between T_s of carbon fluxes and VPD, it should be noted that temperature and VPD are usually closely related (Yuan et al. 2025). Therefore, it's essential for future disentangle the casual effect of VPD on the T_s of carbon fluxes.

Our results showed that the T_s of NEP increased with precipitation during spring and summer but decreased in winter, despite some of its values were negative ($p < 0.05$; Supporting Information: Figure S5 and Table S7). This is primarily attributed to the divergent water-limitation status and contrasting physiological responses between seasons (Chan et al. 2018; Arain et al. 2022). During spring and summer, increased precipitation alleviates water stress, resulting in a greater temperature response of GEP more than that of R_e (Supporting Information: Table S7).

4.2 | Other Factors Affecting Carbon Flux Sensitivity to Temperature Anomalies

Forests with low productivity exhibited negative T_s, while the T_s of NEP was positive in high productivity forests (Figure 5a,b). This finding contrasts with Xu et al. (2020), who observed a more negative NEP sensitivity to temperature anomalies in high productivity in North American forests across temperate and boreal ecosystems. This discrepancy may be attributed to the

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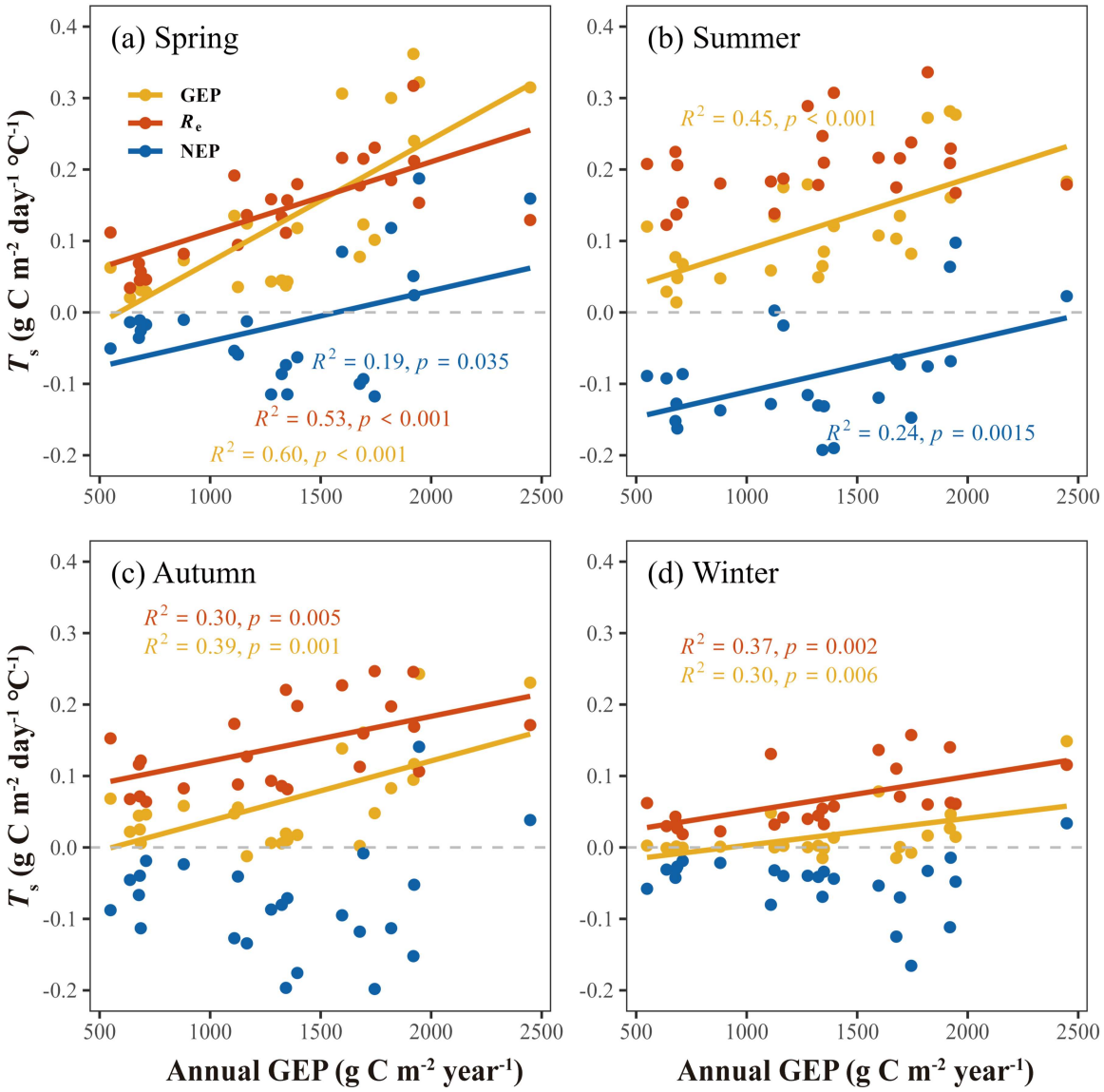

FIGURE 5 | Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} °C^{-1}) and annual gross ecosystem productivity (GEP) in (a) spring, (b) summer, (c) autumn, and (d) winter. Carbon fluxes include gross ecosystem production (GEP, orange), ecosystem respiration (R_e, red), and net ecosystem production (NEP, blue). Only significant liner regression relationships with statistical $p < 0.05$ are shown. Each point represents the mean T_s of GEP, R_e, and NEP during the given season for a given site. [Color figure can be viewed at wileyonlinelibrary.com]

distinct response of GEP and R_e to temperature anomalies in different forest ecosystems. Under experimental warming, boreal forests usually exhibit higher resilience than temperate forests given their higher optimum temperature for photosynthesis (Wu et al. 2025). This implies that the wider thermal safety margin in boreal forests grants them stronger buffering capacity against temperature anomalies than temperate forests. Moreover, while T_s of R_e showed larger values than T_s of GEP, the fluctuations in T_s of GEP were more obvious than T_s of R_e. This leads to negative responses of NEP to temperature anomalies, which were mainly affected by the temperature response of vegetation photosynthesis rather than that of ecosystem respiration (Supporting Information: Table S8). At the same time, caution should be exercised when interpreting this phenomenon in autumn and winter (Figure 5c,d) due to limited photoperiod during these seasons.

We found pronounced seasonal changes in carbon flux sensitivity to temperature anomalies in boreal forests (Figure 3 and Supporting Information: Table S5), with seasons acting as a key categorical variable for explaining T_s of NEP (Figure 8). This is consistent with the results of Xu et al. (2020) in North American forests, but they provided little discussion about why the season is important. Seasonal alternation is usually accompanied by changes in forest phenology (Richardson et al. 2013), thus resulting in different responses of the carbon flux to temperature anomalies in different seasons. Extensive studies have indicated that the growing season of boreal forests is being prolonged due to the advance of spring phenology and the delay of autumn phenology under climate change (Richardson et al. 2013; Liu et al. 2025b). The growth of photosynthetic organs in spring leaves enhance photosynthetic rates and promoted carbon uptake (Pan et al. 2024a), but photoinhibition damage may also occur at low temperatures. Summer leaves

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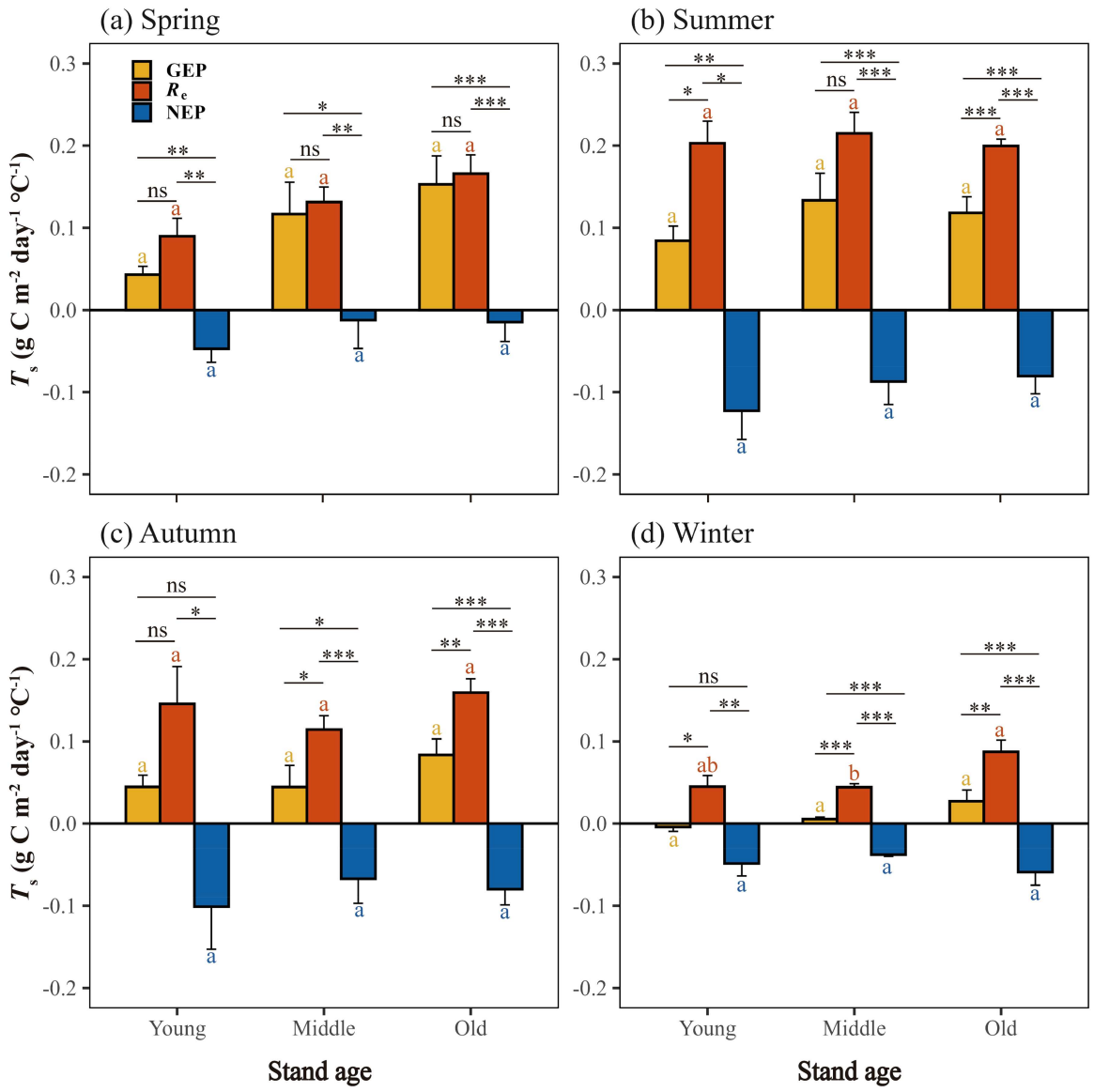

FIGURE 6 | Effect of stand age on the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} °C^{-1}) in (a) spring, (b) summer, (c) autumn, and (d) winter. Carbon fluxes include gross ecosystem production (GEP, orange), ecosystem respiration (R_e, red), and net ecosystem production (NEP, blue). Forest stand-age is divided into young (< 40 years), middle (40–90 years), and old forests (> 90 years) (Kuuluvainen and Gauthier 2018; Liu, Zha, et al. 2025). Daily T_s of GEP, R_e, and NEP were averaged among sites within each age class. Error bars indicate ± 1 standard error. Different lowercase letters indicate significant differences ($p < 0.05$) in a given carbon flux sensitivity across stand ages. The horizontal line indicates the difference in carbon flux sensitivities at the same stand age. *** denotes $p < 0.001$; ** denotes $p < 0.01$; * denotes $p < 0.05$; ns denotes no significant difference. [Color figure can be viewed at wileyonlinelibrary.com]

form thermal adaptation through increasing the maximum rate of carboxylation of Rubisco, adjusting the optimal range of photosynthetic temperature to acclimate to rising temperatures (Hasanuzzaman et al. 2013; Wang et al. 2024; Wu et al. 2025). Meanwhile, the photosynthesis and respiration reached their peak in summer (Supporting Information: Figure S1a–d), but their NEP was also most strongly affected by temperature anomalies. Although delayed autumn defoliation increases photosynthetic period of plants, their photosynthetic capacity decreases due to leaf senescence (Bauerle et al. 2012; Zohner et al. 2023). Considering the whole growing season, vegetation productivity increases more in the late growing season (i.e., the period from the peak to the end of C uptake) due to longer photosynthetic times (Liu et al. 2025b). Furthermore, earlier spring phenology may also cause a dual lagged effect on plant productivity during the subsequent summer and autumn (Buermann et al. 2018). On the one hand, the early growth of plants may promote photosynthesis in subsequent seasons through the development of larger leaves or increased foliar nitrogen (Richardson et al. 2013). On the other hand, it may adversely affect photosynthesis later because of earlier leaf senescence or the build-up of water deficits during autumn (Barnett et al. 2005; Keenan and Richardson 2015; Buermann et al. 2018). Moreover, our results also showed the effects of temperature anomalies on carbon fluxes varied with forest type even in the same season, such as T_s of NEP during early spring exhibited positive values for ENF but negative values for DBF (Figure S3), which could be explained by the differences found

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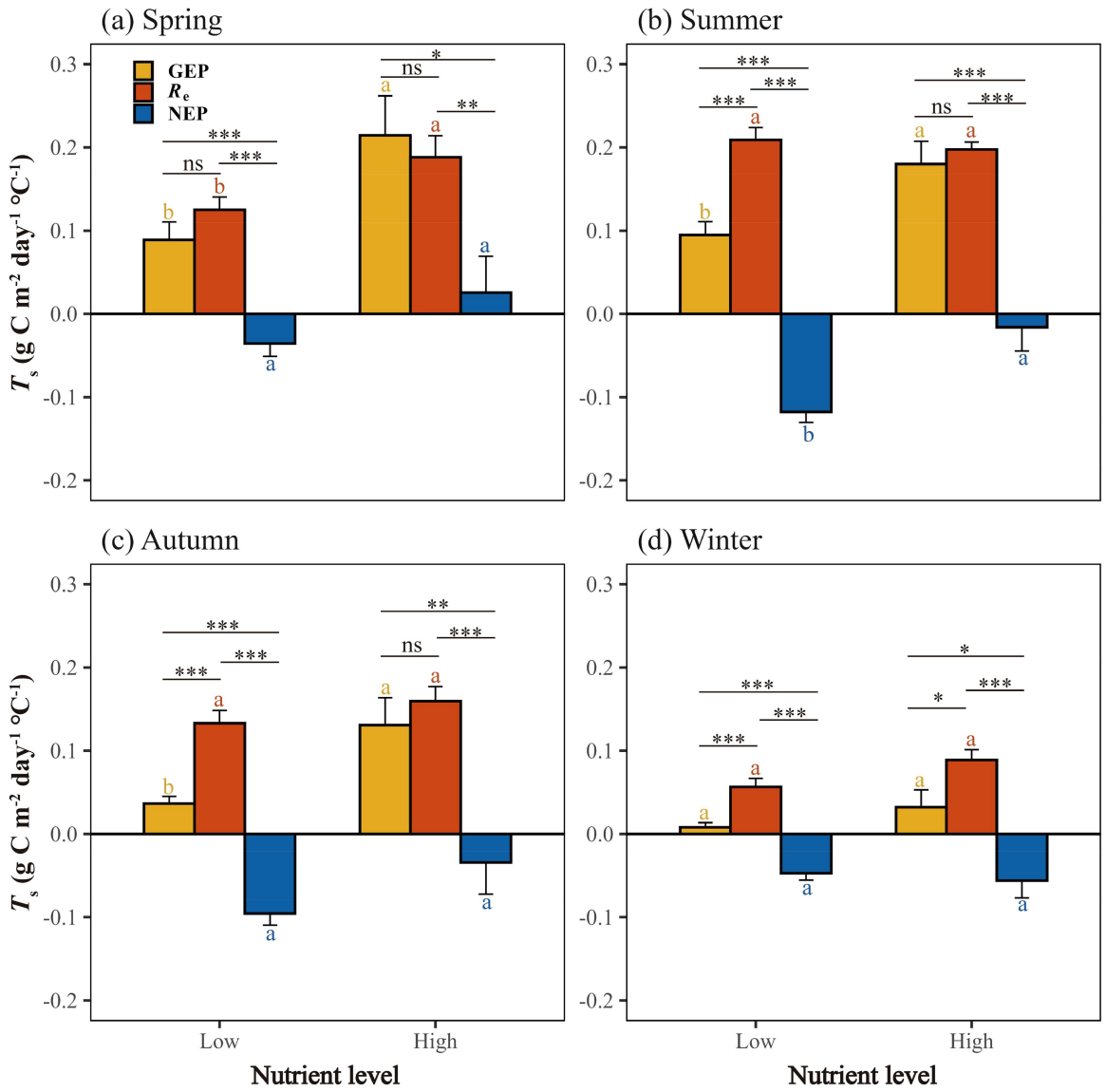

FIGURE 7 | Effect of nutrient availability on the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} °C^{-1}) in (a) spring, (b) summer, (c) autumn, and (d) winter. Carbon fluxes include gross ecosystem production (GEP, orange), ecosystem respiration (R_e, red), and net ecosystem production (NEP, blue). Nutrient availability is divided into low and high forests, which was derived from Liu et al. (2025). Daily T_s of GEP, R_e, and NEP were averaged among sites within each nutrient level. Error bars indicate ± 1 standard error. Different lowercase letters indicate significant differences ($p < 0.05$) in a given carbon flux sensitivity across nutrient levels. The horizontal line indicates the difference in carbon flux sensitivities at the same nutrient level. *** denotes $p < 0.001$; ** denotes $p < 0.01$; * denotes $p < 0.05$; ns denotes no significant difference. [Color figure can be viewed at wileyonlinelibrary.com]

in the strategies for leaf construction and photosynthesis between ENF and DBF (Qi et al. 2021; Shi et al. 2024). Predicted seasonal warming may result in greater CO_2 loss under future temperature scenarios as NEP was limited by temperature anomalies during most seasons (Figure 4). Consequently, translating the understanding of forest type (or mixing ratios) responses into differentiated model parameterisations is essential for enhancing the precision of carbon sink projections under climate change.

Our results showed that NEP in young forests tended to be more susceptible to temperature anomalies (Figure 6), which aligns with previous research (McMillan et al. 2008; Xu et al. 2020; Liu et al. 2025a). In boreal forests, net primary production (NPP) at the early succession stage (young forests) is mainly determined by the understory vegetation, while it is mainly determined by the canopy-dominant tree production at the late succession stage (old forests) (Martínez-García et al. 2024). Young forests with overlapping niches face intense intraspecific competition (e.g., for light, water, and nutrients) (Martínez-García et al. 2024; Liu et al. 2025a), resulting in them being more vulnerable to temperature anomalies. As forests progress from young to old growth, stand structural reorganisation—characterised by density-dependent self-thinning and progressive root system development—enhances hydraulic redistribution capacity and soil water exploitation (Chan et al. 2018; Wu et al. 2018). This means that forests with relatively complex structure may exhibit greater thermal adaptation (Schwarz et al. 2004; Xu et al. 2020).

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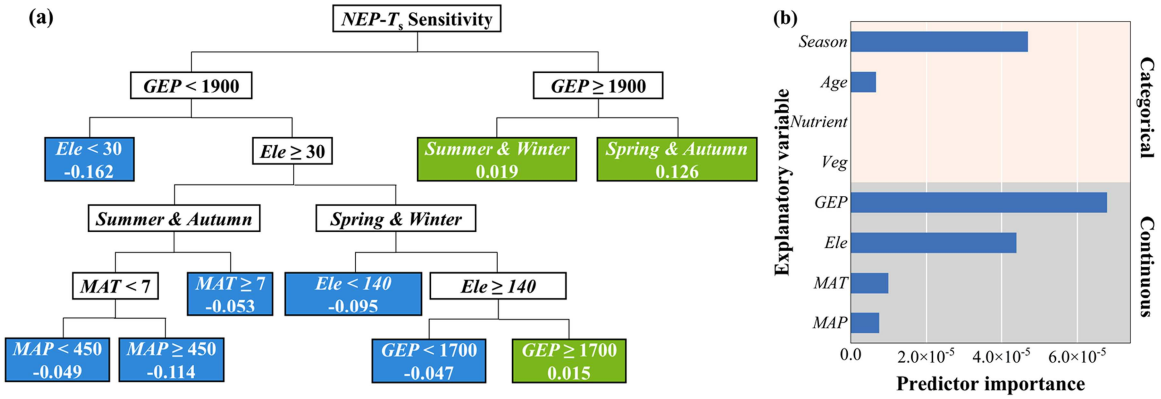

FIGURE 8 | Classification and Regression Tree (CART) analysis on the sensitivity of net ecosystem production to temperature anomalies (T_s of NEP, g C m^{-2} day^{-1} $°C^{-1}$). (a) CART analysis indicates factors affecting the temperature sensitivity of NEP in boreal forests, (b) the importance of potential explanatory factors. GEP is mean annual gross ecosystem production (g C m^{-2} $year^{-1}$); Ele, elevation (m); MAT, mean annual temperature (°C); MAP, mean annual precipitation (mm); Veg, vegetation type (including evergreen needleleaf forest and deciduous broadleaf forest); Age, forest age (including young, middle, and old forests). Season (including spring, summer, autumn, and winter). Nutrient (including low and high nutrient forests). Values below each variable indicate the mean T_s of NEP under the given condition. [Color figure can be viewed at wileyonlinelibrary.com]

Our results showed that NEP in low nutrient forests tended to be more susceptible to temperature anomalies, especially in summer ($p < 0.05$; Figure 7). This may be related to the difference in carbon allocation patterns. Specifically, a greater proportion of GPP was allocated to fine roots to maintain their nutrient requirements in low-nutrient forests (Shan et al. 2001; Goulden et al. 2011; Fernandez-Martinez et al. 2014), thus, R_e may be increased by stimulating autotrophic respiration in response to temperature anomalies. At the same time, low-nutrient forests correspond to lower annual GEP (1148.36 ± 373.53 g C m^{-2} $year^{-1}$), which may result in their limited temperature response (Figure 5). On the contrary, high-nutrient forests preferentially allocate assimilates to aboveground biomass, thereby reducing root-associated respiration (Janssens et al. 2010; Fernandez-Martinez et al. 2014), but possibly increasing aboveground stem-leaf respiration.

4.3 | Implications

Our study suggests that NEP exhibits greater resistance to temperature anomalies in middle-aged and high-nutrient forest sites compared to young-aged and low-nutrient sites, which may be related to optimised resource allocation, structural maturity, and adaptive physiological regulation in these ecosystems. Although some studies have highlighted the CO_2 fertilisation effect in enhancing carbon sequestration (Walker et al. 2021) and the critical role of young and old-aged forests as carbon sinks (Arain et al. 2022; Liu et al. 2025a), these ecosystems conversely exhibited higher suppression and lower resistance to temperature anomalies. This phenomenon underscores that pursuing enhanced productivity in these forests involves a critical trade-off with their ecological resistance, thereby necessitating caution in developing forest management strategies under climate change.

Furthermore, our study also indicates that the negative impact of temperature anomalies on NEP of boreal forest primarily arises from the greater sensitivity of respiration compared to photosynthesis, with this differential sensitivity being closely linked to ecosystem productivity and seasonal dynamics. Although we note that there are some limitations in our study regarding limited dataset, our results still lend support to the context-dependent nature of the "Diversity-Stability Hypothesis" (Vitousek 1977; Liang et al. 2016), wherein high-productivity ecosystems augment their resilience to temperature anomalies (Forzieri et al. 2022; Liu et al. 2025c), while the stability of low-productivity ecosystems is more susceptible to the combined influences of geographic gradients and resource limitations. These results provide valuable insights into how annual GEP and seasonal patterns modulate the vulnerability of ecosystems to temperature anomalies, offering a framework for understanding and predicting boreal forest ecosystem responses to climate change.

5 | Conclusions

By combining eddy-covariance and microclimate data from 24 boreal forest sites, we estimated the carbon flux sensitivity to temperature anomalies on seasonal scales and analysed the driving mechanisms. We found that the negative effects of temperature anomalies on NEP gradually intensified with the concurrent increase of T_a and VPD during spring and summer, primarily attributable to the inhibition of GEP by these combined climate variables. The carbon sink of forests with low annual GEP tend to show negative sensitivity to temperature anomalies, while the carbon sink of forests with high productivity tend to show positive sensitivity. Young and low-nutrient forests were more vulnerable to higher temperature anomalies, suggesting that their carbon sink capacity may be inhibited under projected warming scenarios. Among these factors, ecosystem productivity and seasons were the primary determinants governing T_s of NEP. This can help understand the boreal forest carbon dynamics under warming climates. Given the projected increase in temperature in boreal forests, future research should aim to promote the carbon sink, possibly by targeting forest management specifically in young, low-productivity, and nutrient-poor forests.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Figure S1: Seasonal variations in daily carbon fluxes for evergreen needleleaf forest (ENF; a, c, and e) and deciduous broadleaf forests (DBF; b, d, and f). **Figure S2:** Principal component analysis of the sensitivities of forest carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$) under different nutrient availability conditions in (a, b) spring, (c, d) summer, (e, f) autumn, and (g, h) winter. **Figure S3:** Daily sensitivities of forest carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$). (a) T_s for evergreen needleleaf forest (ENF), (b) T_s for deciduous broadleaf forest (DBF). **Figure S4:** Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$) and vapor pressure deficit (VPD) in (a) spring, (b) summer, (c) autumn, and (d) winter. Carbon fluxes include gross ecosystem production (GEP, orange), ecosystem respiration (R_e, red), and net ecosystem production (NEP, blue). Daily T_s values were sorted into 0.5-hPa VPD bins. **Figure S5:** Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$) and precipitation in (a) spring, (b) summer, (c) autumn, and (d) winter. Carbon fluxes include gross ecosystem production (GEP, orange), ecosystem respiration (R_e, red), and net ecosystem production (NEP, blue). Daily T_s values were sorted into 1-mm precipitation bins. **Table S1:** Information about boreal forest sites (> 45 °N) in this study. **Table S2:** Information on the nutrient availability of the studied forest sites (Fernandez-Martinez et al., 2014). **Table S3:** Proportion of overlapping area in PCA analysis of nutrients. **Table S4:** Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$) and air temperature (T_a). **Table S5:** Differences of the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$) in different seasons. Carbon fluxes include gross ecosystem production (GEP), ecosystem respiration (R_e), and net ecosystem production (NEP). **Table S6:** Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$) and vapor pressure deficit (VPD). **Table S7:** Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$) and precipitation (PPT). **Table S8:** Relationship between the sensitivities of carbon fluxes to temperature anomalies (T_s, g C m^{-2} day^{-1} $°C^{-1}$).

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