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Impact of Fragmentation on Carbon Uptake in Subtropical Forest Landscapes in Zhejiang Province, China

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Abstract: Global changes cause widespread forest fragmentation, which, in turn, has given rise to many ecological problems; this is especially true if the forest carbon stock is profoundly impacted by fragmentation levels. However, the way in which forest carbon uptake changes with different fragmentation levels and the main pathway through which fragmentation affects forest carbon uptake are still unclear. Remote sensing data, vegetation photosynthesis models, and fragmentation models were employed to generate a time series GPP (gross primary productivity) dataset, as well as forest fragmentation levels for forest landscapes in Zhejiang province, China. We analyzed GPP variation with forest fragmentation levels and identified the relative importance of the phenology (carbon uptake period—CUP) and physiology (maximum daily GPP—GPP_{max}) control pathways of GPP under different fragmentation levels. The results showed that the normalized mean annual GPP data of highly fragmented forests during the period from 2000 to 2018 were significantly higher than those of other fragmentation levels, while there was almost no significant difference in the annual GPP trend of forest landscapes with all fragmentation levels. Moreover, the percentage area of the control variable, GPP_{max}, gradually increased with fragmentation levels; the mean GPP_{max} between 2000 and 2018 of high-level fragmentation was higher than that of other fragmentation levels. Our results demonstrate that the carbon uptake capacity per unit area was enhanced in highly fragmented forest areas, and the maximum photosynthetic capacity (physiology-based process) played an important role in controlling carbon uptake, especially in highly fragmented forest landscapes. Our study calls for a better and deeper understanding of the potential of forest carbon uptake, and it is necessary to explore the mechanism by which forest fragmentation changes the vegetation photosynthetic process.

Keywords: forest carbon sequestration; vegetation growth; landscape patterns; gross primary productivity; phenology

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1. Introduction

Forests are a key component in terrestrial ecosystems [1]; globally, they play an important role in providing a variety of ecological services for mankind, such as absorbing and storing carbon, maintaining soil and water, and purifying air [2–4]. However, the world's terrestrial biomes have been significantly affected by human-induced global changes [5]. The global forest area has shrunk by about one-third since the 1850s [6], most of which was induced by natural disturbances and the expansion of the agricultural and urban industries [7]. The rapid and vast loss of forest results in the splitting of spatially contiguous

distributed forest landscape into small patches, leading to worldwide forest fragmentation [8]. Considering that some key functions of forests can be damaged by fragmentation through the degradation of vegetation biomass and biodiversity [9,10], it is necessary to comprehensively understand the impacts of forest fragmentation on ecosystems.

A series of ecological problems, particularly carbon loss and the intensification of the greenhouse effect, are directly induced by forest fragmentation [11–13]. Several studies have indicated that human activities induce more forest edge areas, aggravating fragmentation and decreasing carbon storage [14,15]. However, carbon uptake is also proven to be enhanced in highly fragmented forests [16,17]. The complex variation in carbon up-take under different fragmentation levels proposes a demand for assessing the relationship and the influence pathway between forest fragmentation and vegetation carbon up-take, which can enhance our insights into the future carbon uptake potential of forests in the context of widespread forest fragmentation. In particular, in the context of intense land use caused by urbanization, forests show a high degree of fragmentation [8]. In addition to the direct impact of forest area change on vegetation carbon sequestration, it is unclear how forest distribution patterns affect forest carbon sequestration; this will greatly limit the effectiveness of urban forest management and ecological conservation measures, and will also limit our understanding of regional carbon cycle dynamics.

A number of methods have been used to measure forest fragmentation levels, with the patch or class level's fragmentation-related landscape pattern metrics being adopted by most studies to quantify the levels of forest fragmentation [12,16,18]. However, these approaches have neglected the fact that forest fragmentation is a landscape-scale issue containing complex spatial processes [19]. Although there are some hierarchical approaches, which are based on spatial processes, to measuring the levels of forest fragmentation [20–22], these were mainly used to estimate the status of forest fragmentation, and have rarely been used to study the impacts of fragmentation on ecological functions due to the difficulty of accessing field observation data for relevant fragmentation levels. In reality, the classification results of the fragmentation levels from these methods may have great potential in studies investigating the ecological effects of forest fragmentation, particularly those with the assistance of the remote sensing approach, to estimate ecological function indicators at large spatial scales.

The processes of forest carbon uptake can be simply summarized as the absorption of atmospheric carbon dioxide by plants through photosynthesis [23]; gross primary productivity (GPP), a direct measurement of the total amount of carbon assimilated by vegetation, is generally considered as a reflection of vegetation carbon uptake. In addition, the vegetation carbon stock is highly related to the accumulation of annual GPP over a long period, which is mainly controlled by two factors—the carbon uptake period (CUP) and the maximum daily GPP (GPP_{max}), which are associated with vegetation phenology and physiology, respectively [24,25]. Both of these factors are affected by the climate and soil nutrient change caused by forest fragmentation [26–28]; therefore, detecting the variation in CUP and GPP_{max} under different fragmentation levels is crucial for explaining the pathway or the mechanism of the impact of fragmentation on forest carbon uptake.

In this study, forest landscapes in Zhejiang province, China, were selected as the study area in which to examine the relationship between forest fragmentation and GPP. Multiple sources of remote sensing data were applied to calculate forest fragmentation levels and to simulate vegetation GPP. We have proposed a basic assumption that the GPP and its two components—CUP and GPP_{max}—vary between forest fragmentation levels. Based on the analysis of the variation in GPP, CUP, and GPP_{max} with fragmentation levels, we would like to answer the following two scientific questions: (1) How does forest carbon uptake change with different fragmentation levels? (2) What is the main pathway affecting forest carbon uptake under different fragmentation levels?

2. Materials and Methods

2.1. Study Area

Zhejiang province, China, which extends across 27.03°–31.18°N and 118.02°–123.17°E, was selected as the study area (Figure 1). The forest coverage of Zhejiang province is about 59.4%, most of which is distributed in the mountains and hills. The subtropical monsoon climate is the dominant climate of Zhejiang province; it has hot, rainy summers and cold, dry winters, and has obvious characteristics of seasonal change. The mean annual temperature of Zhejiang is between 15 and 18 °C, while the average annual precipitation ranges between 980 and 2000 mm. The growing season usually starts in March and ends in October. The evergreen broadleaf forests and mixed coniferous–broadleaf forests are the main vegetation types of the study area (Figure 1); there are more than thirty tree species in the forest landscapes of Zhejiang province.

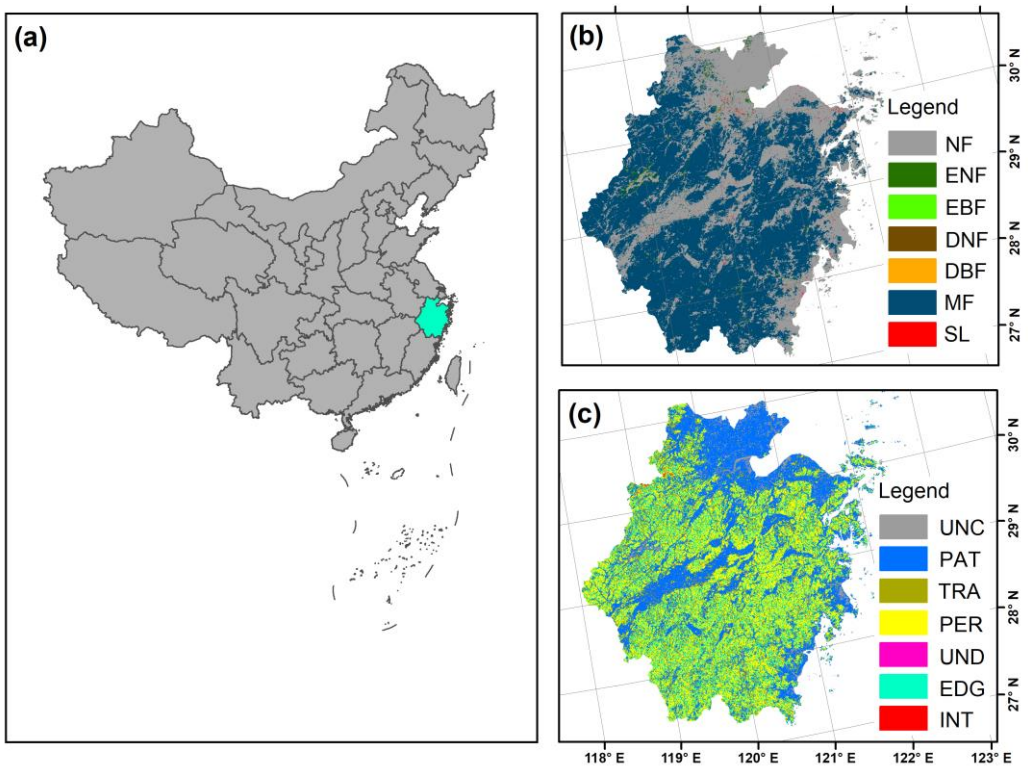


Figure 1. Location, forest type distribution, and classified forest fragmentation levels of forest landscapes in Zhejiang, China. (**a**) The location of Zhejiang, China. (**b**) Distribution of main forest types in Zhejiang. (**c**) Forest fragmentation levels in Zhejiang. UNC: unclassified forest, PAT: patch forest, TRA: transitional forest, PER: perforated forest, UND: undetermined forest, EDG: edge forest, INT: interior forest. The forest type data were derived from the MODIS MCD12Q1 land cover product (from 2010), while the map of fragmentation levels was calculated using the forest fragmentation model (see Section 2.2) in this study.

In this study, the tropical forest landscapes of Zhejiang were selected as the study area primarily for the following reasons: on the one hand, Zhejiang has a developed economy, whereby urbanization and other human activities in Zhejiang have caused drastic land use changes. In addition, Zhejiang has a large forest area and a high forest coverage; these two factors result in the distribution pattern of subtropical forests in Zhejiang containing all types of forest fragmentation, as well as having typical gradients of forest frag-mentation. On the other hand, Zhejiang has turned to the stage of ecosystem protection after its early development; the change in forest cover after 2000 is quite limited compared to that of its neighboring regions, which makes it convenient for this study to compare the productivity and its trend among static fragmentation types.

2.2. Forest Map Data and Fragmentation Levels Classification

Considering the fact that forest cover change may alter the forest fragmentation categories with time, this study requires a temporal stable status of forest cover. In order to exclude the influence from forest coverage change on the accuracy of the classification of forest fragmentation levels, our study only focused on the forest areas in Zhejiang province that have not changed since 2000. We used grids of 500 m in size to calculate the proportion of forest loss between 2000 and 2018 (the ratio of total forest loss pixels to total pixels in a 500 m grid) based on the Global Forest Change dataset [29]; the grids with a forest loss proportion of less than 5% were retained and were representative of unchanged forest landscapes. Moreover, a 50 m resolution forest map from 2010, generated using ALOS PALSAR-2, MODIS, and Landsat-7/8 satellite data [30], was selected as the basic forest cover data to conduct a classification of forest fragmentation levels based on the retained grids (unchanged forest landscapes).

A forest fragmentation model [20,21] that is widely used to estimate the status of forest fragmentation based on satellite-derived forest maps was employed in this study to classify forest fragmentation levels. This fragmentation model was developed based on the consideration of causing forest loss as a result of spatial disturbances; it has been widely applied to estimate forest fragmentation by analyzing forest distribution maps [31,32]. Additionally, forest area density (P_f) and forest connectivity (P_{ff}) are two key indicators in this model for defining the fragmentation type of a given "window" or "landscape" based on a forest/non-forest binary map [20]. The size of the "window" reflects different spatial scales in the estimation of forest fragmentation. P_f and P_{ff} are calculated using the following equations:

$$P_f = \frac{N_f}{N_w} \quad (1)$$

$$P_{ff} = \frac{D_{ff}}{D_f} \quad (2)$$

where P_f is the proportion of forest pixels in a given window, calculated by dividing the number of forest pixels (N_f) by the total number of pixels (N_w) in the window; P_{ff} is the forest connectivity, calculated by dividing the pixel pair number that includes at least one forest pixel (D_{ff}) by the pixel pair number that includes two forest pixels in cardinal directions (D_f).

A look-up table (Table 1) containing the criteria of the two indicators (D_{ff} and D_f) was used to conduct the classification of forest fragmentation levels. Six fragmentation types, including patch (PAT), transitional (TRA), perforated (PER), undetermined (UND), edge (EDG), and interior (INT), were obtained. The fragmentation levels of these six types are shown as PAT > TRA > PER > UND > EDG > INT. However, UND was excluded from our study due to the fact that it only exists in extreme cases. In addition, in order to match the resolution (~500 m) of the GPP data, a 9 × 9 size "window" was adopted in this study.

Table 1. Classification criteria, area, and area percentage of each forest fragmentation level of the forest fragmentation model in forest landscapes in Zhejiang, China. PAT: patch forest, TRA: transitional forest, PER: perforated forest, UND: undetermined, EDG: edge forest, and INT: interior forest.

Fragmentation Categories	Classification Criteria	Area (10^4 ha)	Area Percentage (%)
PAT	$P_f < 0.4$	263.0	33.7
TRA	$0.4 < P_f < 0.6$	129.5	16.6
PER	$0.6 <= P_f < 1$ and $P_f > P_{ff}$	226.1	28.9
UND	$0.6 <= P_f < 1$ and $P_f = P_{ff}$	0.7	0.1
EDG	$0.6 <= P_f < 1$ and $P_f < P_{ff}$	153.0	19.6
INT	$P_{ff} = 1$	9.0	1.2

2.3. Time Series GPP Dataset

A satellite-based light-use efficiency model—the vegetation photosynthesis model (VPM)—was used to simulated time series GPP dataset from 2000 to 2018 for the study area. The VPM was driven using the MODIS MOD09A1 surface reflectance dataset, the MCD12Q1 land cover dataset, the MYD11A2 land surface temperature dataset, and NCEP reanalysis II climate data. The final 500m resolution GPP of each 8-day period during 2000–2018 was obtained. The details of the simulation processes using the VPM have been reported in previous studies [33,34].

Based on the 500 m 8-day period GPP dataset, the annual GPP for each year between 2000 and 2018 was obtained by aggregating all the data in a relevant year. In addition, the GPP_{max} for each year between 2000 and 2018 was obtained by extracting the peak value for each pixel in each year. Since the vegetation in our study area usually has obvious characteristics of seasonal change, the temporal dynamic curve of GPP generally shows a unimodal shape. Therefore, in this study, the growing season is defined using a relative threshold method, as suggested in previous studies [35,36]; the threshold is set as 20% of the GPP_{max} in a given year. The carbon uptake period (CUP) for each year between 2000 and 2018 was obtained by counting the number of days in which the GPP was higher than the value of 20% of the GPP_{max} in each year.

2.4. Data Analysis

2.4.1. Comparison of GPP Trend among Different Fragmentation Levels

In order to explore the impact of forest fragmentation on vegetation productivity, we compared the mean annual GPP and the normalized mean annual GPP among different fragmentation levels from 2000 to 2018. The normalized mean annual GPP throughout 2000–2018 was calculated by dividing the mean annual GPP from 2000 to 2018 by the P_f for each pixel in order to exclude the influence of forest areas on GPP values for a pixel. A one-way ANOVA was adopted to test the significance of the difference between mean annual and mean normalized annual GPP data between 2000 and 2018 among forest fragmentation levels. Meanwhile, the LSD multiple comparison method was used to detect the difference between mean annual and normalized mean annual GPP data between 2000 and 2018 under various fragmentation levels.

The linear trend of the annual GPP during 2000–2018 for each pixel and the entire Zhejiang province was calculated, and the slope value of the linear regression line was represented as the magnitude of the trend. The annual GPP trend of different fragmentation levels throughout 2000–2018 was also compared using a one-way ANOVA.

2.4.2. Detecting the Relative Importance of the Control Pathways of GPP

In order to explore the control pathways of GPP in our study area, we conducted multiple linear regression between GPP and either CUP, GPP_{max}, or a combination of CUP and GPP_{max} for each pixel of the period between 2000 and 2018. A metric assessing meth-od in the "relaimpo" package in the R software [37] was employed to quantify the relative importance of each individual variable in linear models for each pixel in this study; the variable with the highest relative importance value was regarded as the control variable of GPP. The relative importance of each individual control variable was calculated to reflect its degree of control, and the values were normalized from 0 to 100%. In addition, the pixel number percentages of the three control variables were also calculated and were statistically compared for each forest fragmentation level.

2.4.3. Comparison of GPP Control Pathways among Different Fragmentation Levels

In order to answer the question of which pathway of forest fragmentation affects vegetation productivity, the CUP, GPP_{max}, and CUP $\times$ GPP_{max} were calculated and compared among various forest fragmentation levels. A one-way ANOVA was adopted to test the significance of the differences in the three control variables, and the LSD multiple

com-parison method was used to detect the difference between the three control variables un-der various fragmentation levels.

2.4.4. Statistical Analysis and Data Processing Methods

The raster data processing, mapping, and statistical analysis were conducted using ArcGIS10.3 and R software (version 4.4.1) [38]; the significance level of the one-way ANOVA was set to 0.05.

3. Results

3.1. GPP Dynamics of Different Fragmentation Levels

There was a significant ($p < 0.05$) difference in the mean annual GPP in 2000 and 2018 for forest landscapes with various fragmentation levels in Zhejiang (Table 2). Generally, forest landscapes with fragmentation levels of PAT and INT had the lowest and highest mean annual GPP values, respectively, while no significant difference in the mean annual GPP was identified between TRA, PER, and EDG. Although a significant ($p < 0.05$) difference in the normalized mean annual GPP for 2000 and 2018 in Zhejiang was found among all forest fragmentation levels (Table 2), the highest and lowest normalized mean annual GPP values in forest landscapes were represented by the PAT and INT fragmentation levels, respectively. Similarly, there was no significant difference in the normalized mean annual GPP between PER and EDG.

Table 2. Comparison of mean annual GPP and mean normalized annual GPP among different forest fragmentation categories for 2000 and 2018. The mean normalized annual GPP was calculated as the ratio of the mean annual GPP to the proportion of forest pixels in a forest landscape. The characters indicate the results of multiple comparisons between any two categories. PAT: patch forest, TRA: transitional forest, PER: perforated forest, EDG: edge forest, and INT: interior forest.

Fragmentation Categories	**Mean Annual GPP (g C m^{-2})**		**Mean Normalized Annual GPP (g C m^{-2})**	
	2000	**2018**	**2000**	**2018**
PAT	1040.4 ± 319.1 a	1101.6 ± 449.4 a	11,611.3 ± 17,514.1 d	11,337.4 ± 16,718.4 d
TRA	1268.7 ± 256.4 b	1516.8 ± 351.1 b	2979.0 ± 4071.6 c	3505.2 ± 4629.4 c
PER	1366.5 ± 193.1 bc	1643.4 ± 231.5 bc	1870.6 ± 1276.2 b	2246.4 ± 1487.0 b
EDG	1349.8 ± 202.4 bc	1635.2 ± 246.3 bc	2199.1 ± 2681.0 b	2656.5 ± 3158.8 b
INT	1421.4 ± 197.6 c	1693.9 ± 213.9 c	1657.0 ± 1222.9 a	1972.6 ± 1478.9 a

Significant ($p < 0.05$) increasing trends were found in all fragmentation levels and all types of forest landscapes in Zhejiang, except for the PAT landscape (Figure 2a). The in-crease in the rate of annual GPP with regard to various fragmentation levels fluctuated from 10.6 g C m^{-2} year^{-1} in TRA to 13.1 g C m^{-2} year^{-1} in PER. Spatially, the annual GPP trend in Zhejiang generally showed positive values for most pixels (Figure 2b). The annual GPP trend in PAT was significantly lower than those in forest landscapes with other fragmentation levels, but there was no significant difference in the annual GPP trend among TRA, PER, EDG, and INT. The higher values (>30 g C m^{-2} year^{-1}) of the annual GPP trend were mainly distributed in the west and central part of Zhejiang, while the lower values (<−45 g C m^{-2} year^{-1}) of the annual GPP trend were mainly distributed in the north and coastal areas of Zhejiang.

3.2. Relative Importance of Different GPP Control Pathways

CUP × GPP$_{max}$ was identified as being the control variable for about 61.8% of the entire Zhejiang province; the area percentages of the control variables for CUP and GPP$_{max}$ were 19.7% and 18.5%, respectively (Figure 3a). The control variable for CUP was mainly distributed in some parts of western and central Zhejiang, while the control variable for GPP$_{max}$ was mainly distributed in central and eastern Zhejiang. The relative importance of the three control variables ranged from 0 to 82%, and most of them were distributed in the range of 5~35% (Figure 3b). The area percentages of the control variables for CUP

× GPP_{max} were maintained at approximately 60% among various fragmentation levels (Figure 3c). However, the control variable for CUP (13.2~27.8%) and GPP_{max} (11.1~25.0%) still accounted for a certain proportion of area among various fragmentation levels. There was no significant ($p > 0.05$) difference in the relative importance between any two fragmentation levels, and the mean relative importance of various fragmentation levels ranged between 25% and 28% (Figure 3d).

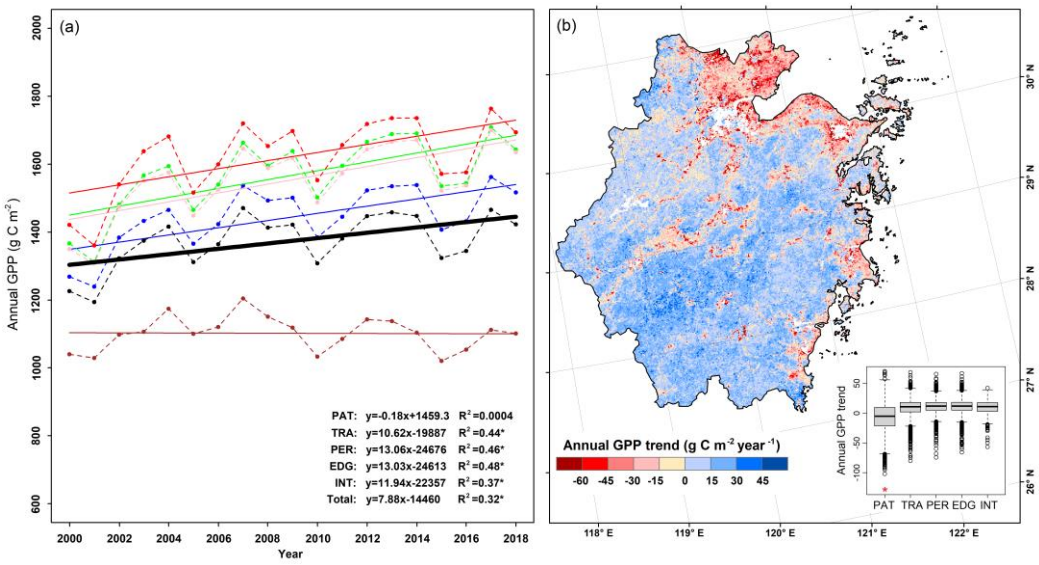


Figure 2. (**a**) Annual GPP dynamics of different fragmentation levels and (**b**) linear trend distribution of annual GPP of forest landscapes in Zhejiang between 2000 and 2018, and the comparison of the annual GPP trend values among different fragmentation levels. The red asterisk indicates the annual GPP trend of PAT is significantly ($p < 0.05$) than that of other fragmentation categories. PAT: patch forest, TRA: transitional forest, PER: perforated forest, EDG: edge forest, and INT: interior forest.

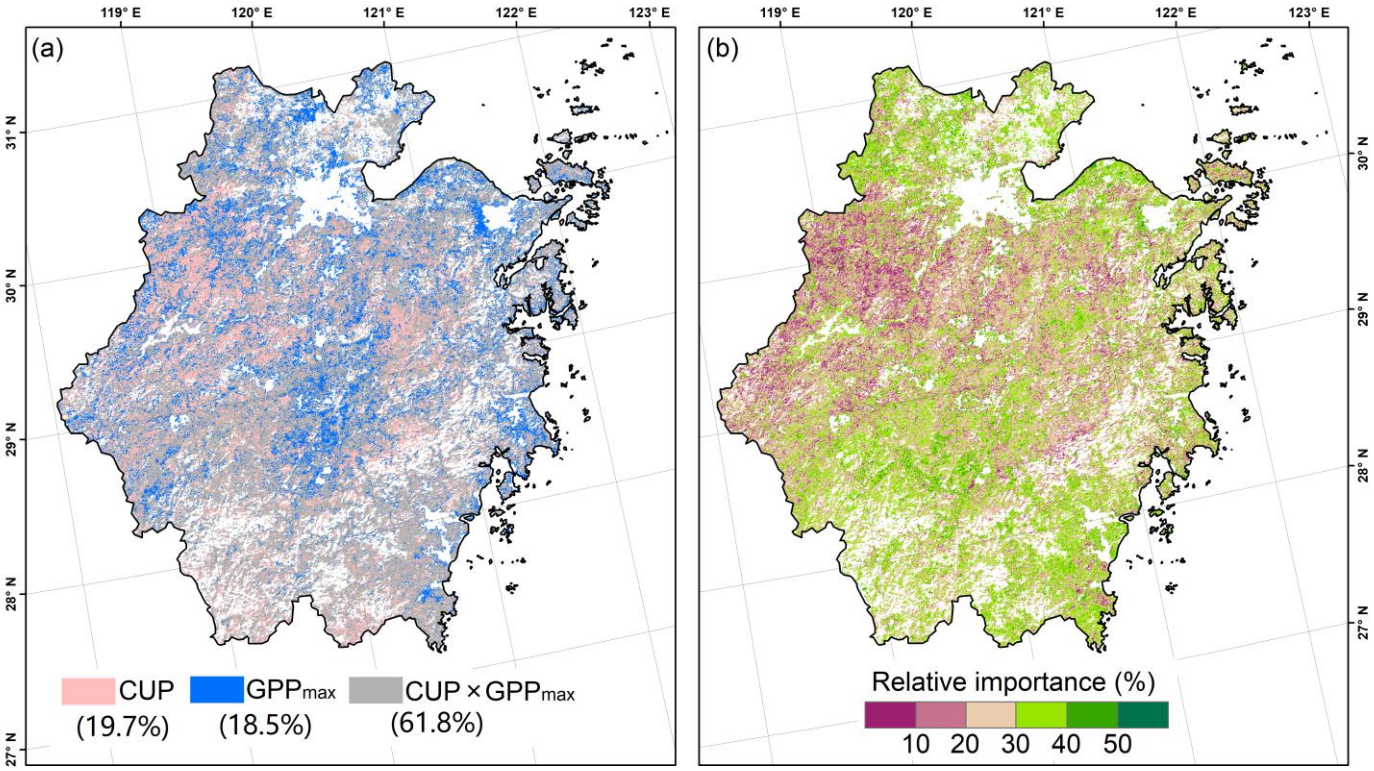


Figure 3. *Cont.*

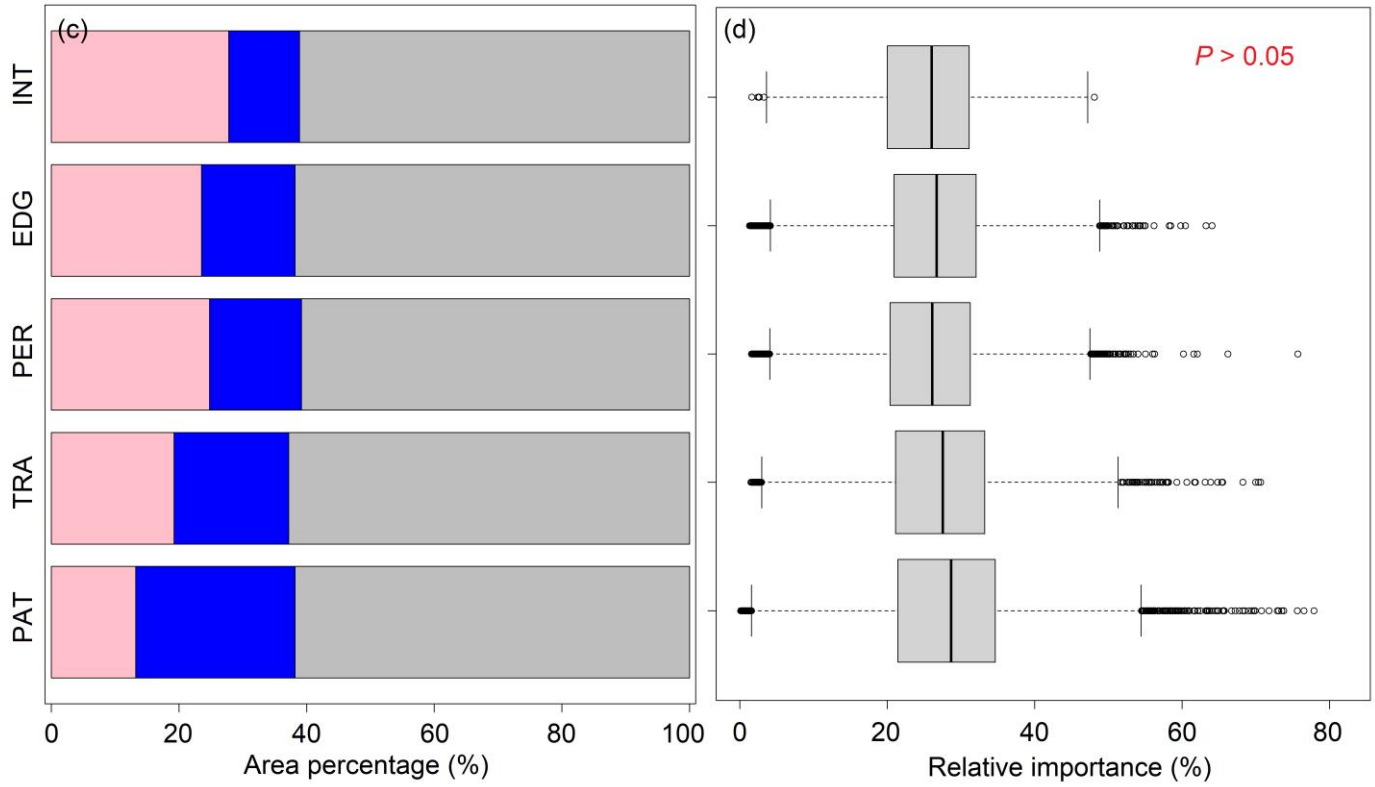


Figure 3. Distribution of different control variables and their relative importance. (**a**) Spatial distribution of different control variables, (**b**) spatial distribution of their relative importance on annual GPP during 2000–2018, (**c**) comparison of relative importance among three control variables, and (**d**) pixel number percentages of three control variables for different fragmentation levels. PAT: patch forest, TRA: transitional forest, PER: perforated forest, EDG: edge forest, and INT: interior forest.

3.3. GPP Control Pathways of Different Fragmentation Levels

A significant ($p < 0.05$) difference in the mean CUP of forest landscapes in Zhejiang during 2000–2018 was detected among all fragmentation levels (Table 3). The highest and lowest mean CUP were represented by the INT and PAT forest landscapes, respectively, and there was no significant ($p > 0.05$) difference in the mean CUP between TRA, PER, EDG, and INT. Moreover, the mean GPP_{max} of INT forest landscapes was significantly ($p < 0.05$) higher than that for the PAT and TRA landscapes; no significant ($p > 0.05$) difference in the mean GPP_{max} existed in forest landscapes in Zhejiang between TRA, PER, and EDG, or between PER, EDG, and INT. Similarly, a significant ($p < 0.05$) difference in the mean CUP × GPP_{max} of forest landscapes in Zhejiang during 2000–2018 was detected among all forest fragmentation levels (Table 3). The highest and lowest mean CUP × GPP_{max} values existed in the INT and PAT landscapes, respectively, and there was no significant ($p > 0.05$) difference in the mean CUP × GPP_{max} between PER and EDG.

Table 3. Comparisons of mean CUP, mean GPP_{max}, and mean CUP × GPP_{max} of forest landscapes in Zhejiang among different fragmentation categories during 2000–2018. The characters indicate the results of multiple comparisons between any two categories. PAT: patch forest, TRA: transitional forest, PER: perforated forest, EDG: edge forest, and INT: interior forest.

Fragmentation Categories	CUP (days)	GPP_{max} (g C m^{-2} day^{-1})	CUP × GPP_{max}
PAT	256.1 ± 73.4 a	8.7 ± 2.2 a	2339.4 ± 949.7 a
TRA	310.7 ± 49.7 b	9.6 ± 1.6 b	3041.2 ± 737.1 b
PER	329.8 ± 28.5 b	10.2 ± 1.3 bc	3369.1 ± 548.5 c
EDG	327.8 ± 30.3 b	10.1 ± 1.3 bc	3320.6 ± 551.2 bc
INT	332.9 ± 28.1 b	10.7 ± 1.5 c	3547.7 ± 524.7 d

Spatially, the mean values of CUP and GPP_{max} in the forest landscapes of Zhejiang during 2000–2018 both have high heterogeneities. The higher mean CUP values (>330 days) were generally found in the south and east parts of Zhejiang, while the lower mean CUP values (<210 days) were generally found in the north part of Zhejiang (Figure 4a). Among the regions with a high forest coverage, there was little difference in the mean CUP throughout 2000–2018, but the mean GPP_{max} during 2000–2018 presented obvious spatial variations. In particular, the highest values (>12.5 g C day^{-1}) of the mean GPP_{max} during 2000–2018 were concentrated in dense forest landscapes in the east and northwest parts of Zhejiang (Figure 4b); however, the values of mean GPP_{max} during 2000–2018 were generally less than 10 g C day^{-1} in the south dense forest landscapes in Zhejiang.

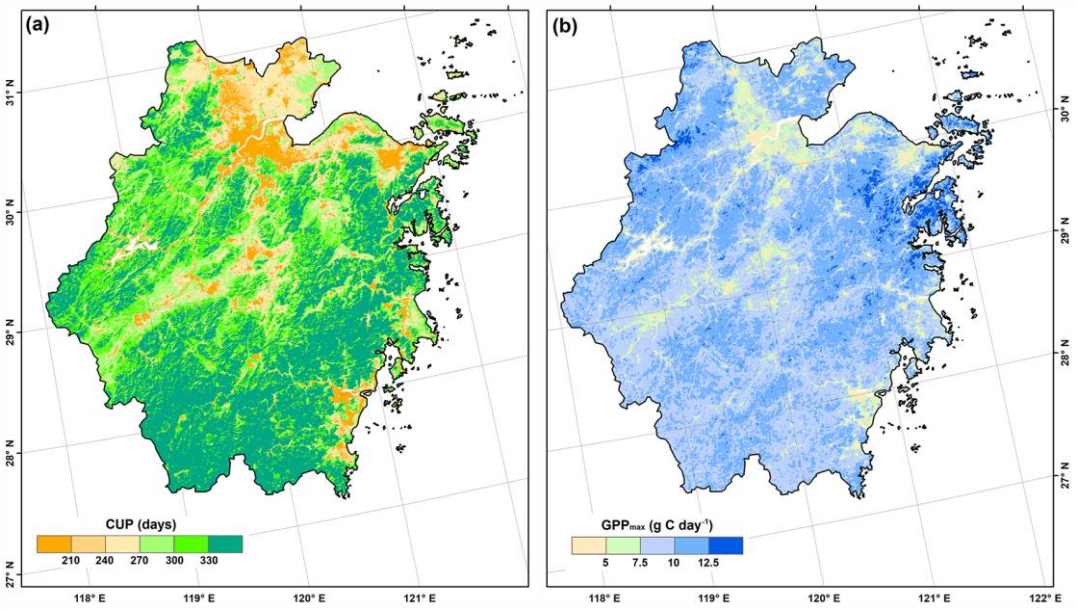


Figure 4. Spatial distribution of the mean values of carbon uptake period (CUP) and maximum daily GPP (GPP_{max}) for subtropical forest landscapes in Zhejiang Province during 2000–2018. (**a**) The spatial map of the mean CUP during 2000–2018. (**b**) The spatial map of the mean GPP_{max} during 2000–2018.

4. Discussion

4.1. Impacts of Forest Fragmentation on Carbon Uptake

The mean annual GPP throughout 2000–2018 generally declined from INT to PAT forest landscapes (Table 2); this is in line with previous studies, which suggest that carbon loss in forests is aggravated by fragmentation level [39–41]. The carbon loss is directly attributed to the forest loss under forest fragmentation, which may be mainly caused by natural and human disturbances, such as logging, fire, and agriculture and urban expansion [5,27,42]. However, our results also showed that the normalized mean annual GPP of PAT forest landscapes during 2000–2018 was significantly higher than that of other fragmentation levels (Table 2), which implies that the carbon uptake of higher fragmented forest areas was enhanced when excluding the influence of forest area density. A similar result was found in a temperate broadleaf forest of north America [16], where the forest growth rate decreased with the distance from forest edge. The variations in light availability [43] and the sensitivity to climate [44,45] of the forests with different fragmentation levels are likely to be responsible for their differences in carbon uptake.

In this study, except for the PAT forest landscapes, there was no significant difference in the annual GPP trend throughout 2000–2018 among fragmentation levels (Figure 3); this could be attributed to two possible reasons. On the one hand, forest landscapes with a high fragmentation level are more likely to be distributed near urban areas, and the changed environment with a higher temperature and CO2 concentration and better hu-

man management and protection (e.g., artificial irrigation) had a positive influence on forest carbon uptake. On the other hand, forest landscapes with different forest fragmentation levels (except PAT) were evenly distributed in Zhejiang (Figure 1), which led to parallel forest age structures existing in different fragmentation levels; this result suggests that the impact of forest fragmentation on the change rate of vegetation productivity is very limited.

4.2. Impacts of Forest Fragmentation on Control Pathways of Carbon Uptake

Since vegetation carbon uptake processes can be divided into phenological and physiological factors, the control pathway of GPP is either phenological, physiological, or both. Our results showed that CUP $\times$ GPP_{max} was the most widespread control variable of GPP, at mostly more than 60%, during 2000–2018 for all fragmentation levels (Figure 3), which is consistent with a previous study that reported that GPP was jointly controlled by phenology and physiology processes [24]. However, the individual CUP or GPP_{max} still controlled the GPP in some forest landscapes in Zhejiang. For example, forest carbon uptake was mainly controlled by the CUP in mountain areas, while the controlling role of GPP_{max} on GPP usually occurred in the central and coastal areas with a flat terrain (Figure 3). Our study indicates that the dominant pathways of forest carbon uptake are closely related to topographic conditions.

Moreover, our results showed that the percentage area of the GPP_{max} control variable gradually increases with fragmentation level; the mean GPP_{max} of PAT during 2000–2018 was found to be higher than that of other fragmentation levels (Table 3). This means that the maximum photosynthetic capacity of vegetation, mainly reflected by GPP_{max}, is important in controlling carbon uptake in highly fragmented forest landscapes. The factors of less inter-individual competition [46,47] and more carbon dioxide fertilization [48,49] are likely possible drivers of the observed importance of GPP_{max} at higher fragmentation levels.

In addition, the control variables of the CUP and CUP $\times$ GPP_{max} of INT forest landscapes were obviously higher than those of other fragmentation levels. This suggests that phenology-based processes benefit from less fragmented forest landscapes and are most likely to be attributed to the warming conditions caused by the edge effect [50] in highly fragmented forests.

4.3. Insights on Local Forest Management under Forest Fragmentation

Historically, forests in Zhejiang, China, have experienced severe logging disturbances, causing a grim status of forest fragmentation. However, the results of this study may still provide useful insights into local forest management. Firstly, a higher carbon uptake capacity per unit area exists in highly fragmented forest landscapes, reminding us to explore the potential of forest carbon uptake in the context of the widespread existence of forest fragmentation. In particular, as one of the most developed regions in China, Zhejiang is subject to intense human activities, such as rapid urbanization and economic development, which have significantly affected the distribution pattern of natural ecosystems, such as forests. The positive relationship between forest fragmentation and carbon sequestration provides an opportunity for Zhejiang to balance development and ecological protection. Secondly, although the forest carbon uptake may be enhanced under fragmentation, there is still a great need to protect the forests due to the fac that any loss of forest coverage will lead to a further loss of carbon stock. Finally, this relationship is also based on the implication that the increase in the maximum photosynthetic capacity may induce the enhancement of carbon uptake in highly fragmented forest landscapes. Therefore, it is necessary to explore the mechanism by which forest fragmentation changes the vegetation photosynthetic process, which will play an important role in formulating forest management measures. In addition, although subtropical forests in Zhejiang Province were selected as being representative in this study, considering the universality of research approaches and the widespread availability of research objects, our results have great potential values for understanding how the carbon uptake of subtropical forests responds to forest fragmentation in other subtropical regions.

4.4. Research Uncertainties and Prospects

In this study, we explored how forest carbon uptake changes with different fragmentation levels and what the main pathway is in which fragmentation affected forest carbon uptake throughout 2000–2018 in forest landscapes in Zhejiang, China. Some uncertainties may exist in our study. Firstly, although forest protection and suspended logging disturbances have been implemented since 2000 in the study area [51,52], we assumed that the forest coverage was kept stable when the forest loss proportion was less than 5% in the period between 2000 and 2018; this may still induce some uncertainties, since the succession of forests themselves may have caused some changes in forest cover [53]. Secondly, the datasets of forest cover and GPP were produced on a large scale (the whole of China) and have a high accuracy. However, we only used some parts of the datasets, inducing uncertainties in the accuracy of the datasets. Lastly, although the forest fragmentation level classification and GPP estimation were obtained based on certified methods [20,29,54], the accuracy of these data may also have some impacts on the study results.

5. Conclusions

Compared to previous studies, this study has revealed the variation in carbon uptake with forest fragmentation levels at both landscape and regional scales, and the forest landscape pattern was found to have certain impacts on forest productivity. In addition, the control pathways of carbon uptake under forest fragmentation were also identified. These findings have enhanced the understanding of vegetation carbon uptake processes in the context of widespread forest fragmentation.

Our results demonstrate that carbon uptake capacity per unit area was enhanced in highly fragmented forest landscapes. However, there was almost no significant difference in the annual GPP trend throughout 2000–2018 among forest landscapes with different fragmentation levels. Additionally, although forest carbon uptake was jointly controlled by phenology- and physiology-based processes, the maximum photosynthetic capacity of vegetation—the physiology-based process—played an important role in controlling car-bon uptake, particularly in highly fragmented forest landscapes. Hence, the results and findings from this study call for a better and deeper understanding of the potential of forest carbon uptake in connection to fragmentation. There is an emerging need to pay serious attention to sustainable forest conservation and protection in the context of the widespread existence of forest fragmentation. Moreover, in order to formulate appropriate forest management and planning activities, it is necessary to explore the mechanism in which forest fragmentation changes the vegetation photosynthetic process in connection to carbon uptake and release.

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