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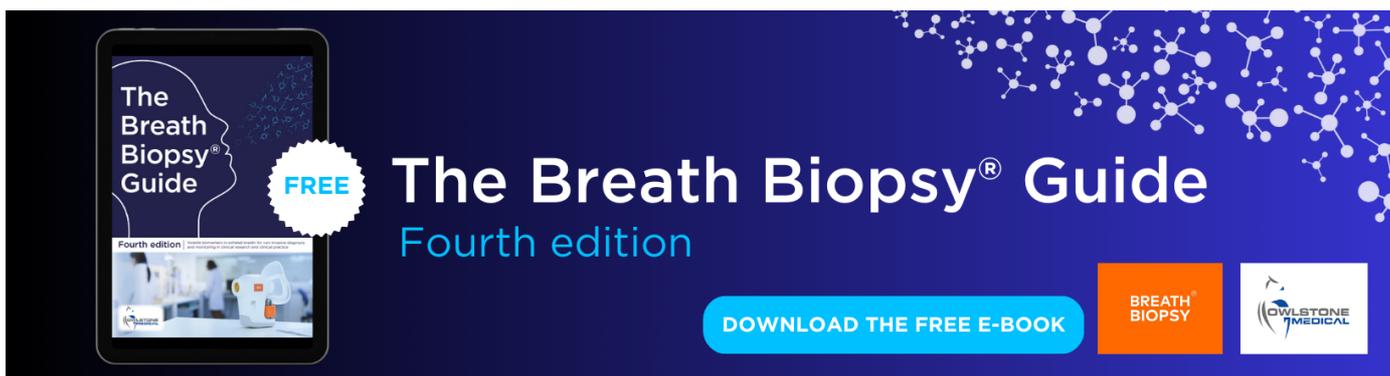
## Space evidence of enhanced photosynthetic carbon uptake under fragmented temperate forests

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## LETTER

## Space evidence of enhanced photosynthetic carbon uptake under fragmented temperate forests

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E-mail: [ma\\_jun@fudan.edu.cn](mailto:ma_jun@fudan.edu.cn)**Keywords:** forest fragmentation, photosynthetic carbon uptake, climate change, landscape pattern, remote sensingSupplementary material for this article is available [online](#)**Abstract**

Global changes arouse large-scale fragmentation of forests, which has a profound impact on the balance of the global carbon cycle. However, the effect and process of temperate forest fragmentation on photosynthetic carbon uptake are not clear. We used remote sensing datasets to describe the degree of forest fragmentation and clarify the relationship between fragmentation and photosynthetic carbon uptake in the temperate forests of northeastern China. The results show that forest fragmentation has high spatial heterogeneity and promotes photosynthetic carbon uptake by 14% in the cold temperate zone and 10% in the middle temperate zone. Hydrothermal conditions are the dominant influencing path, explaining 60% of the variation in the cold temperate zone and 49% of the variation in the middle temperate zone. In addition, temperature is the dominant driver of the cold temperate zone, and water is the dominant driver of the middle temperate zone. Our research calls for a deeper understanding of the carbon cycle of fragmented temperate forests, and it is necessary to consider appropriate human intervention in forest management.

**1. Introduction**

Due to the impacts of deforestation, farmland expansion and natural disturbances, global forests have experienced rapid and vast losses (Arora and Boer 2010, Curtis *et al* 2018), which has caused large-scale forest fragmentation (Haddad *et al* 2015). Currently, only approximately 30% of global forests are more than 1000 m away from the edge (Haddad *et al* 2015), and forest fragmentation has become a severe and prominent global ecological issue. It is a great threat to forest ecosystem functions, which leads to degradation of habitat quality (Wickham *et al* 2008), loss of biodiversity (Ries *et al* 2004), limited flow of ecosystem processes and services (Burkhard *et al* 2009), and reduction of carbon sequestration potential (Ramachandra *et al* 2016, Vieilledent *et al* 2018). In particular, the influence of forest fragmentation on regional and global carbon cycle has attracted extensive attention in recent years (Smith *et al* 2018, Taubert *et al* 2018, Vieilledent *et al* 2018).

Forest ecosystem is an important carbon sink on Earth and plays a leading role in the dynamics of the terrestrial carbon cycle (Dixon *et al* 1994, Pan *et al* 2011). Forest carbon inventories often only consider the calculation of deforestation (Field *et al* 2014), but the impact of forest degradation on carbon accounting methods has been proven to be non-negligible (Smith *et al* 2018). It is urgent to explore how fragmentation affects the carbon cycle of the remaining forests. Many studies have discussed the effects of forest fragmentation on carbon sequestration in the tropics and generally reported negative relationships (Chaplin-Kramer *et al* 2015, Ordway and Asner 2020). However, global attention on temperate forests is not intimate (Staus *et al* 2002), although the fragmentation of temperate forests is also very serious (Morreale *et al* 2021) and the internal area and loss rate of temperate forests are close to those of tropical forests (Riitters *et al* 2016). Between tropical and temperate zones, there are tremendous differences in species composition, community structural

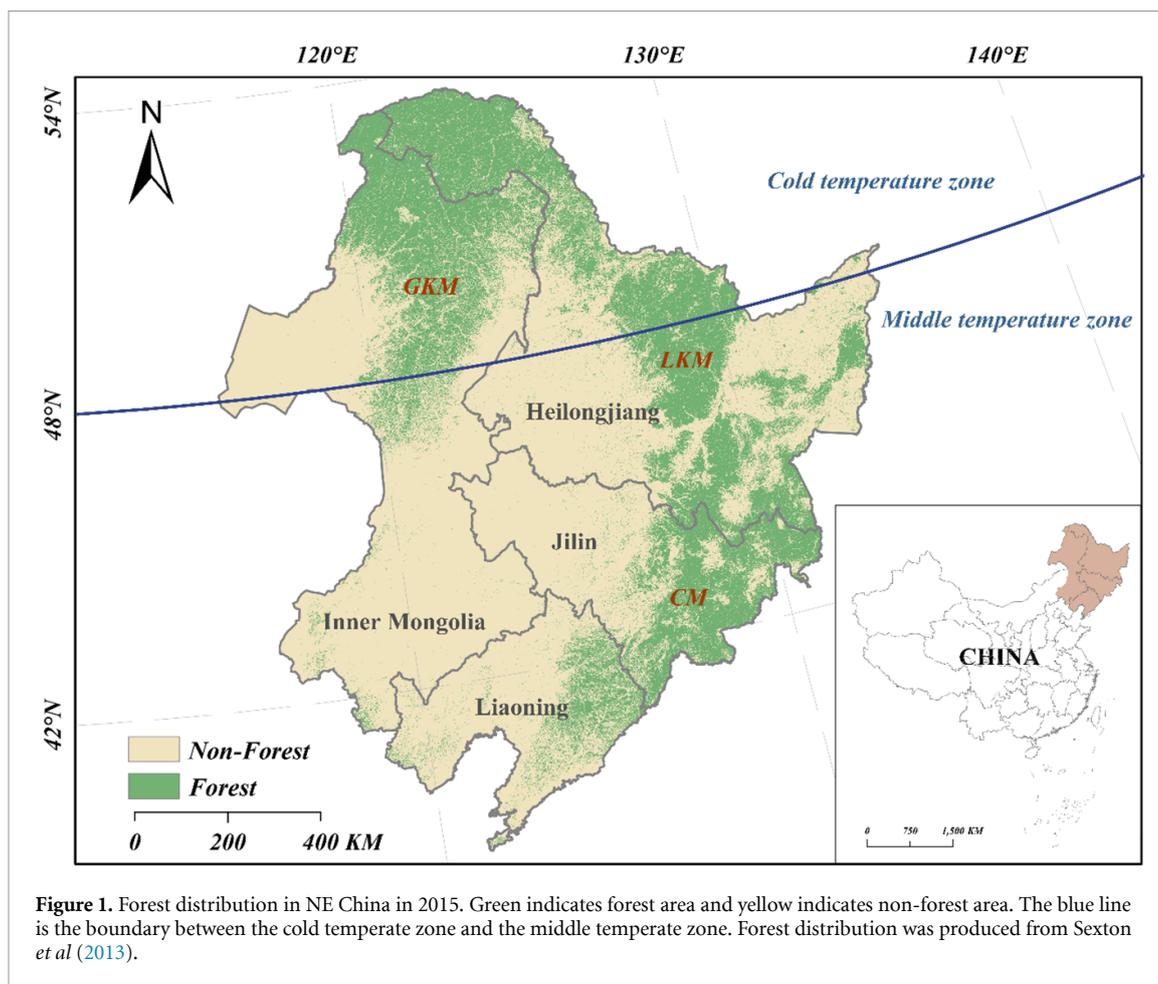
characteristics and limiting factors on productivity, which may result in different aggregate responses to forest carbon dynamics (Smith *et al* 2018). At present, at the regional scale, the effect by which fragmentation of temperate forests affects the carbon cycle remains unclear. Temperate forests are an important part of accurately assessing the global forest carbon budget, and the uncounted carbon caused by fragmentation may be huge (Morreale *et al* 2021). There is therefore an urgent need to understand whether forest fragmentation promotes or inhibits carbon cycle and how fragmentation affects the carbon cycle.

Forest fragmentation changes the growth conditions of vegetation communities, such as the increase of wind turbulence (Laurance and Curran 2008), the decrease of vapor pressure deficit (Laurance 2000), the rise of temperature (Ritter *et al* 2005), and drought (Ritter *et al* 2005). Due to local growth constraints (Nemani *et al* 2003) and vulnerability to stress (Reinmann and Hutrya 2017), the effect of these changes on plant growth and carbon storage is uncertain in different regions. Moreover, there is significant spatial heterogeneity of the dominant climatic factors restricting forest growth, such as temperature and water (Nemani *et al* 2003). For example, water and light are the main factors affecting forest growth in tropical areas, while temperature gradually becomes the dominant factor in temperate areas (Smith *et al* 2018). Therefore, distinguishing the influence path of forest fragmentation affecting the carbon cycle is the premise of understanding the internal mechanism. Despite some studies have proven that temperate forest edges enhance forest growth according to local-scale plot investigations (Bowering *et al* 2006, Reinmann and Hutrya 2017), they did not explore the specific internal mechanism. Filling the research gap of the influence path of forest fragmentation on carbon sequestration in different forest regions is conducive to better understanding the process and mechanism between forest fragmentation and carbon sequestration and specifying more appropriate policies.

Forest fragmentation and the carbon cycle are complex spatiotemporal processes. An accurate understanding of how the spatial pattern of fragmentation affects the entry of carbon into the ecosystem is crucial for understanding the relationship between them more conveniently, and quantifying fragmentation and carbon reasonably is the basis. Previously, most of the studies on the ecological effects of forest fragmentation usually adopted gradients of patch or class levels' fragmentation-related landscape metrics, such as the distance from the edge or patch size or patch number, to characterize the degree of fragmentation (Haddad *et al* 2015, Remy *et al* 2016, Ma *et al* 2017, Taubert *et al* 2018). Nevertheless, these methods cannot fully reflect the state of fragmentation and downplay the fact that forest fragmentation

is a landscape scale problem with complex spatial processes (Fahrig 2003). In addition, forest annual growth reflected by tree ring width and forest above-ground biomass are two commonly used indicators to estimate carbon (Chaplin-Kramer *et al* 2015, Silva Junior *et al* 2020). However, access to these data generally reflects the carbon status at local scale and is time- and labor-consuming (Barbosa *et al* 2014, Latifi *et al* 2015). Considering that the environmental changes caused by fragmentation directly affect photosynthesis, using photosynthetic carbon uptake might be more appropriate to detect the relationship between forest fragmentation and the process of carbon entry into ecosystems. Gross primary productivity (GPP) and solar-induced chlorophyll fluorescence (SIF) have great potential in estimating carbon uptake by terrestrial plants through photosynthesis (Ma *et al* 2018). Consequently, the development of remote sensing and spatial analysis technology provides important data and method bases for the estimation of forest fragmentation and carbon parameters at landscape and above scales, which will greatly promote the researches on the relationship and mechanism of forest fragmentation and the carbon cycle.

There are extensive temperate forests in north-eastern (NE) China and this region is the largest natural forest area in China, accounting for about one-third of China's forest areas (Shi 2010). In the past, anthropogenic disturbances, such as harvesting and farmland expansion, have led to serious forest fragmentation in NE China, yet there are also well-preserved forest areas, especially in some protected areas (Yu *et al* 2011, Chen *et al* 2015, Liu *et al* 2018). Existing studies have demonstrated that the NE forest region is a potential carbon sink, and its forest change has a significant impact on the global carbon cycle (Myneni *et al* 2001, Shi 2010, Pan *et al* 2011). Understanding the impact of forest fragmentation on photosynthetic carbon uptake and their internal influence path are helpful to assess its importance and is of great significance for maintaining forest ecosystem service function and value. In this study, the degree of forest fragmentation was quantified by landscape pattern indices, and the remote sensing datasets of land surface temperature (LST), soil moisture (SM), GPP and SIF were used as indicators of regional environmental conditions and forest photosynthetic carbon uptake. The main objectives of this research were to: (a) evaluate the status of forest fragmentation in NE China using multiple landscape pattern indices; (b) explore the effects of forest fragmentation on photosynthetic carbon uptake and their differences in different temperate zones; (c) investigate the dominant influence paths of fragmentation affecting the photosynthetic carbon uptake dynamics in temperate forests.



**Figure 1.** Forest distribution in NE China in 2015. Green indicates forest area and yellow indicates non-forest area. The blue line is the boundary between the cold temperate zone and the middle temperate zone. Forest distribution was produced from Sexton *et al* (2013).

## 2. Materials and methods

### 2.1. Study area

The forest regions in NE China were selected as the study area (figure 1). The terrain of the study area is mainly mountainous, with an altitude of 300–1940 m. It spans from the cold temperate zone to the middle temperate zone with a north–south direction. The annual average temperature is 3.0° centigrade. The average temperature in July is 18°–20° centigrade, and the average temperature in January is lower than –20° centigrade. The annual total precipitation ranges between 400 and 1100 mm. The main forest types in this area are temperate deciduous broad-leaved forest, temperate coniferous broad-leaved mixed forest and cold temperate coniferous forest.

There are mainly four provinces, including Heilongjiang, Jilin, Liaoning and eastern Inner Mongolia in NE China. The population and economic development levels of the four provinces are different (table S1 available online at [stacks.iop.org/ERL/17/044011/mmedia](https://stacks.iop.org/ERL/17/044011/mmedia)). NE China is divided into three forest regions, including the Great Khingan Mountains (GKM), the Lesser Khingan Mountains (LKM) and the Changbai Mountains (CM). *Larix gmelinii*, *Pinus koraiensis*, *Taxus cuspidate* and *Quercus* spp. are the dominant tree species in this study area.

### 2.2. Data

#### 2.2.1. Forest cover data

The Global Forest Cover Change forest cover map product of 2015, with a spatial resolution of 30 m, was used in this study (Sexton *et al* 2013). The dataset contains estimates of the percentage of horizontal ground in each 30 m pixel covered by woody vegetation greater than 5 m in height. The forest distribution map was produced into a binary forest/non-forest map (figure 1) and used as the basis for the calculation of forest landscape metrics.

#### 2.2.2. Photosynthetic carbon uptake data

The time series GPP dataset in 2015, with a spatio-temporal resolution of 500 m and 8 d, was used in this study. The GPP dataset was produced using a satellite-based light use efficiency model (vegetation photosynthesis model, VPM), which was driven by moderate resolution imaging spectroradiometer (MODIS) MOD09A1 surface reflectance dataset, MCD12Q1 land cover dataset, MYD11A2 LST dataset, and National Centers for Environmental Prediction reanalysis II climate data. The details of the VPM simulation processes can be acquired from previous studies (Zhang *et al* 2017, Ma *et al* 2018). In this study, the annual GPP was obtained by adding all 8 d GPP data in the whole year through the cumulative method to reflect the annual

amount of forest photosynthetic carbon uptake (figure S1).

To verify the accuracy of the GPP data, it is fitted with SIF data to ensure reliable accuracy (figure S2). The daily OCO-2 SIF in 2015 was publicly available at <http://globalecology.unh.edu> (Li and Xiao 2019). The final SIF data were quality-controlled and aggregated to annual mean values at a spatial resolution of 0.05° to reflect the mean annual value of forest photosynthetic carbon uptake.

### 2.2.3. Climate data

In order to explore the process of the impacts of fragmentation on photosynthetic carbon uptake, climatic indicators including LST and SM were used to build a link between fragmentation degrees and annual carbon uptake. The MODIS MYD11A2 LST dataset product and TerraClimate SM dataset product (Abatzoglou *et al* 2018) were adopted in this study. To distinguish seasonal differences in forest growing conditions, the annual mean and growing season (April to October) mean values of LST and SM were calculated respectively (figures S3 and S4).

## 2.3. Methods

### 2.3.1. Mapping the distribution of forest fragmentation degrees

Forest fragmentation includes three characteristics: increased edge, increased isolation and reduced area (Haddad *et al* 2015). Based on these three characteristics, three corresponding landscape pattern indices, including edge density (ED), patch density (PD) and mean patch area (MPA), were combinedly used to describe the degree of forest fragmentation in NE China. All of NE China was divided into a series of square grids (25 km × 25 km), and three landscape pattern indices were calculated based on the binary forest/non-forest map for each grid at class level using FRAGSTATS software (McGarigal and Marks 1995). ED means the sum of the lengths of all edge segments involving the corresponding patch type, divided by the total landscape area. ED was calculated as follows:

$$ED = \frac{\sum_{k=1}^m e_{ik}}{A} \times 10000$$

where  $e_{ik}$  is the total edge length in meters and  $A$  is the total landscape area in square meters. MPA means the sum of the area of patches of the corresponding patch type divided by the number of patches of the same type. MPA was calculated as follows:

$$MPA = \text{mean}(\text{AREA}[\text{patch}_{ij}])$$

where  $\text{AREA}[\text{patch}_{ij}]$  is the area of each patch in hectares. PD means the number of patches of the corresponding patch type divided by the total landscape area. PD was calculated as follows:

$$PD = \frac{n_i}{A} \times 10000 \times 100$$

where  $n_i$  is the number of patches and  $A$  is the total landscape area in square meters. More details about the landscape pattern metrics were fully explained in previous studies (McGarigal and Marks 1995, Riitters *et al* 1995, Mcgarigal *et al* 2002).

Due to the artificial cause of the deviation of the three landscape pattern indices from real status by divided grids, *Kriging* interpolation method was used to smooth the three low-resolution (25 km) landscape pattern indices and generate high-resolution (5 km) raster layers of ED, PD and MPA. In addition, considering any single landscape pattern index is insufficient to reflect the real status of forest fragmentation, the three indices were combinedly to build a forest fragmentation index (FFI) using the following equations:

$$FFI_n = (ED_n + (1 - MPA_n) + PD_n) / 3$$

where  $n$  is the number of each grid, and ED, MPA and PD were standardized in advance. The general form of the standardized formula is shown below:

$$Y_n = \frac{x_n - x_{min}}{x_{max} - x_{min}}$$

where  $n$  is the number of each grid,  $x$  is ED, PD or MPA and the value of  $Y$  is between 0 and 1. In this study, the FFI was classified into five categories, including little fragmentation (0–0.2), low fragmentation (0.2–0.4), medium fragmentation (0.4–0.6), high fragmentation (0.6–0.8) and extreme fragmentation (0.8–1), to represent the forest fragmentation degree in NE China.

### 2.3.2. Comparison of the forest fragmentation in different provinces

For testing the spatial heterogeneity of forest fragmentation degree, the mean values of ED, PD, MPA, and FFI were compared among the four provinces in NE China. Kolmogorov–Smirnov (KS) test is a non-parametric test with a wide application range and low requirements for the data itself. KS test was used in advance to evaluate the distribution normality of landscape pattern indices, and the results were negative. Hence we chose two nonparametric tests, the Kruskal–Wallis test and Mann–Whitney U test. They were used to evaluate whether there were significant differences in the landscape indices among the four provinces.

### 2.3.3. Assessing the relationship between forest fragmentation and photosynthetic carbon uptake

Linear correlations were used to explore the relationships between landscape pattern indices and photosynthetic carbon uptake separately of both cold temperate zone and middle temperate zone, in order to eliminate the impact of photosynthetic carbon uptake differences between the two zones on the regression models (figure S5). The landscape pattern

indices were converted by natural logarithm for their non-normal distributions. The  $R$ -square values were used to assess the strength of the linear correlations. In addition, according to the five divided levels of FFI, we counted the mean value of photosynthetic carbon uptake of forest landscape with  $FFI > 0.6$  and  $FFI < 0.4$  in different climate zones, so as to evaluate the enhancement effect (EE) of forest fragmentation on photosynthetic carbon uptake. The calculation formula is as follows:

$$EE = \frac{x_{FFI>0.6} - x_{FFI<0.4}}{x_{FFI<0.4}}$$

where EE is the enhancement effect,  $x$  is the mean value of GPP or SIF.

#### 2.3.4. Distinguishing the influence path of forest fragmentation on photosynthetic carbon uptake

A piece-wise structural equation model (SEM) based on bivariate relationships was established to understand how fragmentation affects the photosynthetic carbon uptake of temperate forests through water (SM) and temperature (LST) conditions. The maximum likelihood estimation method was used to fit the data. The accuracy of the model was evaluated by low standardized root mean square residual (SRMR,  $< 0.09$ ), high comparative fit index (CFI,  $> 0.95$ ) and Tucker–Lewis index (TLI,  $> 0.90$ ) (Fan et al 2016).

Considering that not all grids contain forests, according to the mean value of percentage of forests of all grids, we regard the grids with percentage of forests higher than 45% as forest grids (figure S6) for sections 2.3.2–2.3.4.

## 3. Results

### 3.1. The spatial patterns of forest fragmentation

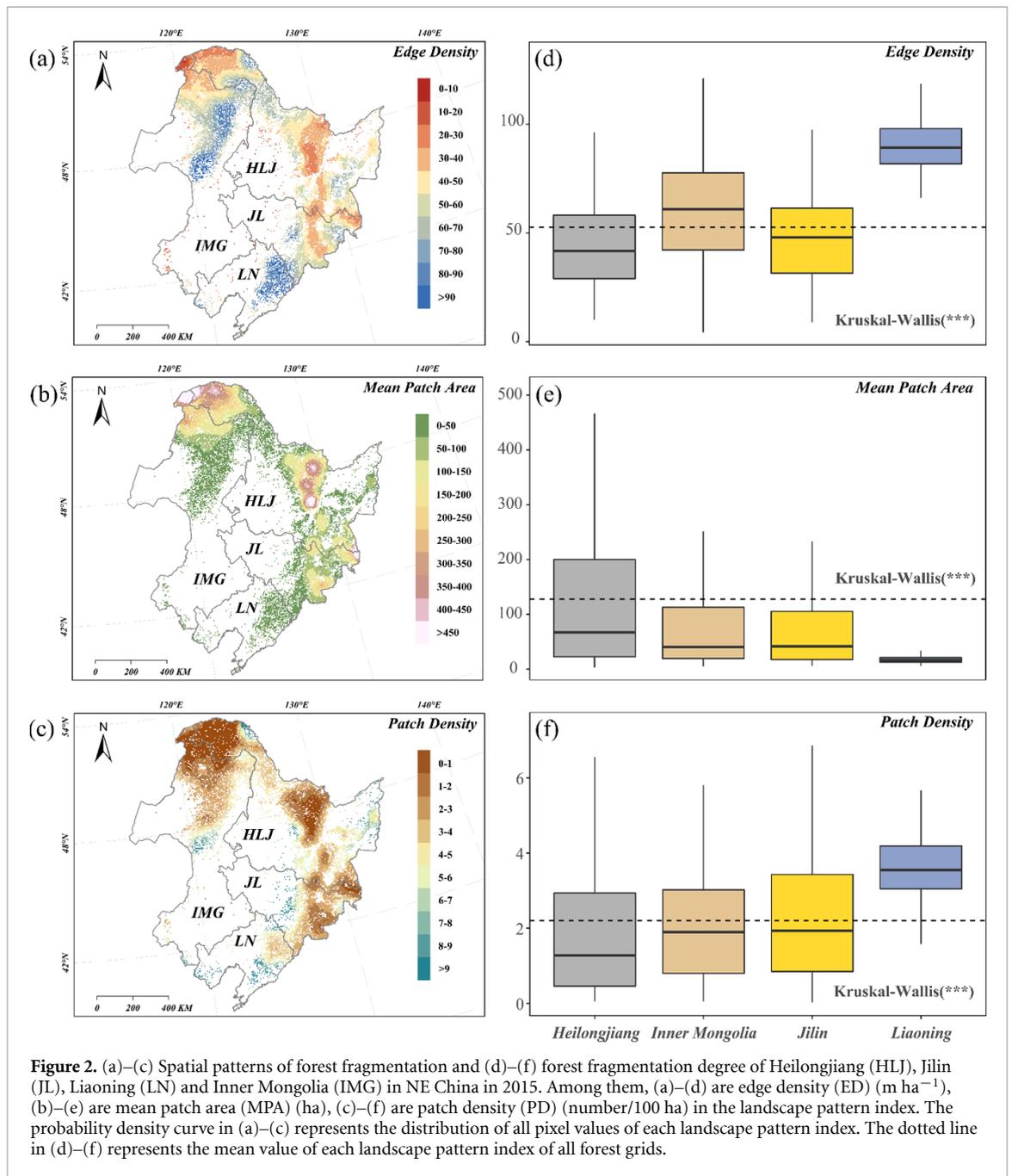
For single landscape pattern metrics, the spatial patterns of ED, PD, and MPA were similar in general, and they all had large spatial heterogeneities (figures 2(a)–(c)). The high values of ED ( $> 70 \text{ m ha}^{-1}$ ), PD ( $> 7$  number/100 ha), and the low value of MPA ( $< 150$  ha) in NE China was mainly concentrated in the south of GKM and southwest of CM, while the low values of ED ( $< 30 \text{ m ha}^{-1}$ ), PD ( $< 3$  number/100 ha), and the high value of MPA ( $> 350$  ha) were mainly distributed in the north of GKM and the middle part of LKM and CM (figure 2). In forest edges, the values of ED and PD were relatively high, and the values of MPA were relatively low. In addition, the ED, PD, and MPA in Liaoning were significantly different from those in the other three provinces in NE China (figures 2(d)–(f) and table S2). However, there were no significant differences in the ED, PD, and MPA between Inner Mongolia, Jilin, and Heilongjiang except the ED between Heilongjiang and Jilin, as well as the PD and MPA between Inner Mongolia and Jilin (table S2). Overall,

Liaoning had the highest values of ED ( $89 \text{ m ha}^{-1}$ ) and PD (4 number/100 ha) but the lowest values of MPA (19 ha), while Heilongjiang had the lowest values of ED ( $45 \text{ m ha}^{-1}$ ) and PD (2 number/100 ha) but the highest values of MPA (155 ha).

For the integrated forest landscape fragmentation index, the spatial pattern of FFI was similar to ED, PD, and MPA, and high FFI values usually distributed in forest edges (figure 3). The total landscape areas of the five degrees of forest fragmentation, from little fragmentation to extreme fragmentation, were 4241.59, 80 309.31, 208 259.26, 73 764.34, 3735.97  $\text{km}^2$ , respectively (table 1). In Jilin, Inner Mongolia, and Heilongjiang, forests with little, low and medium fragmentation degrees accounted for the majority of the total forest landscape area, and their area percentages in the three provinces were 83.4%, 90.4%, 73.5%, respectively. However, there were almost no forests below medium fragmentation degree in Liaoning, and the high fragmentation degree forest landscape, with a percentage of 87.5%, was the main part in Liaoning.

### 3.2. Relationship between forest fragmentation and photosynthetic carbon uptake in different climate zones of northeastern (NE) China

According to the linear-log correlation analysis between annual GPP and annual mean SIF of forest and landscape fragmentation indices, there were significant ( $P < 0.05$ ) correlations between GPP/SIF and ED, PD, MPA, and FFI for both the cold temperate zone and middle temperate zone in NE China (figure 4). The annual GPP and annual mean SIF were positively correlated with ED, PD, and FFI but negatively correlated with MPA. The linear-log correlations between GPP and ED, PD, MPA, and FFI were stronger in the cold temperate zone ( $R^2 = 0.31, 0.28, 0.30$  and  $0.24$ , respectively) than in the middle temperate zone ( $R^2 = 0.19, 0.11, 0.13$  and  $0.13$ , respectively). The linear-log correlations between SIF and ED, PD, MPA, and FFI were stronger in the cold temperate zone ( $R^2 = 0.21, 0.31, 0.30$  and  $0.21$ , respectively) than in the middle temperate zone ( $R^2 = 0.05, 0.09, 0.12$  and  $0.10$ , respectively). Although the values of annual GPP in the cold temperate zone were obviously higher than those in the middle temperate zone, the linear-log regression models for the two temperate zones were all almost parallel. However, the linear-log regression models of SIF data did not show such a trend. Furthermore, according to the five FFI levels, in the cold temperate zone, the average GPP and SIF in the higher fragmentation area ( $FFI > 0.6$ ) were 14% and 23% higher than those in the lower fragmentation area ( $FFI < 0.4$ ), respectively. In the middle temperate zone, the average GPP and SIF in the higher fragmentation area ( $FFI > 0.6$ ) were 10% and 7% higher than those in the lower fragmentation area ( $FFI < 0.4$ ) (table 2).



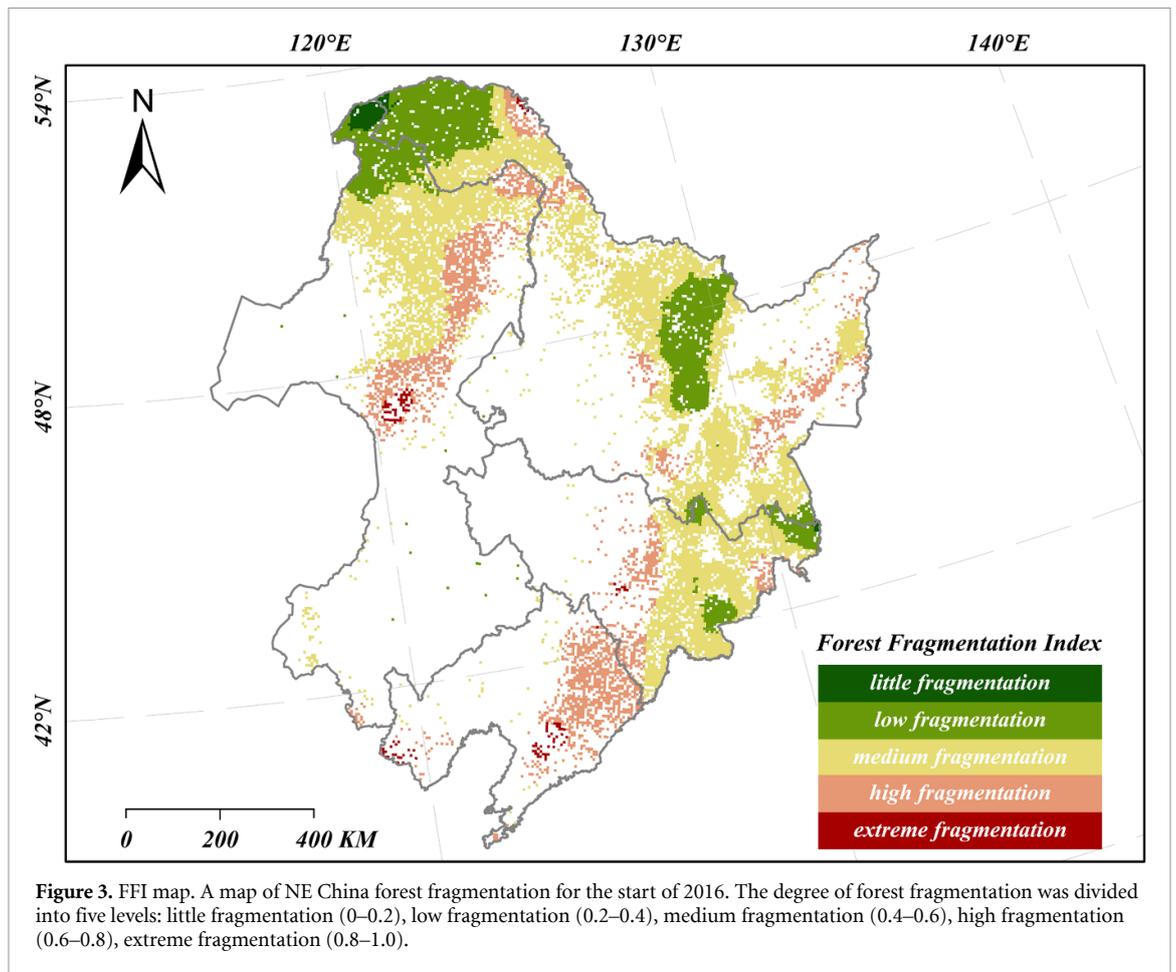
**Figure 2.** (a)–(c) Spatial patterns of forest fragmentation and (d)–(f) forest fragmentation degree of Heilongjiang (HLJ), Jilin (JL), Liaoning (LN) and Inner Mongolia (IMG) in NE China in 2015. Among them, (a)–(d) are edge density (ED) ( $\text{m ha}^{-1}$ ), (b)–(e) are mean patch area (MPA) (ha), (c)–(f) are patch density (PD) (number/100 ha) in the landscape pattern index. The probability density curve in (a)–(c) represents the distribution of all pixel values of each landscape pattern index. The dotted line in (d)–(f) represents the mean value of each landscape pattern index of all forest grids.

### 3.3. Influence path of forest fragmentation on photosynthetic carbon uptake

The results of SEM analysis showed that there was a significant ( $P < 0.05$ ) positive relationship between forest fragmentation and photosynthetic carbon uptake in both the cold temperate zone and middle temperate zone (figure 5). Three landscape pattern indices (ED, MPA, PD) were selected as potential variables of forest fragmentation, and annual and growing season mean values were selected as potential variables of temperature and water. Moreover, forest fragmentation has a significant direct positive influence on temperature and a significant direct negative influence on water. Meanwhile,

there was a direct positive relationship between temperature and photosynthetic carbon uptake, and a direct negative relationship between water and photosynthetic carbon uptake, but the strength of these relationships was inconsistent in the two regions.

In the cold temperate zone, forest fragmentation had significantly positive effects on temperature and water, which explained 50% of the variation in temperature but only 2% of the variation in water. The coefficient of the strong positive relationship (0.764) between temperature and photosynthetic carbon uptake was much larger than that of the non-significant negative relationship ( $-0.055$ ) between



**Table 1.** Landscape area and proportion of different forest fragmentation degree in NE China by province in 2015. Landscape area refers to the pixel area of forest landscape dominated by forest.

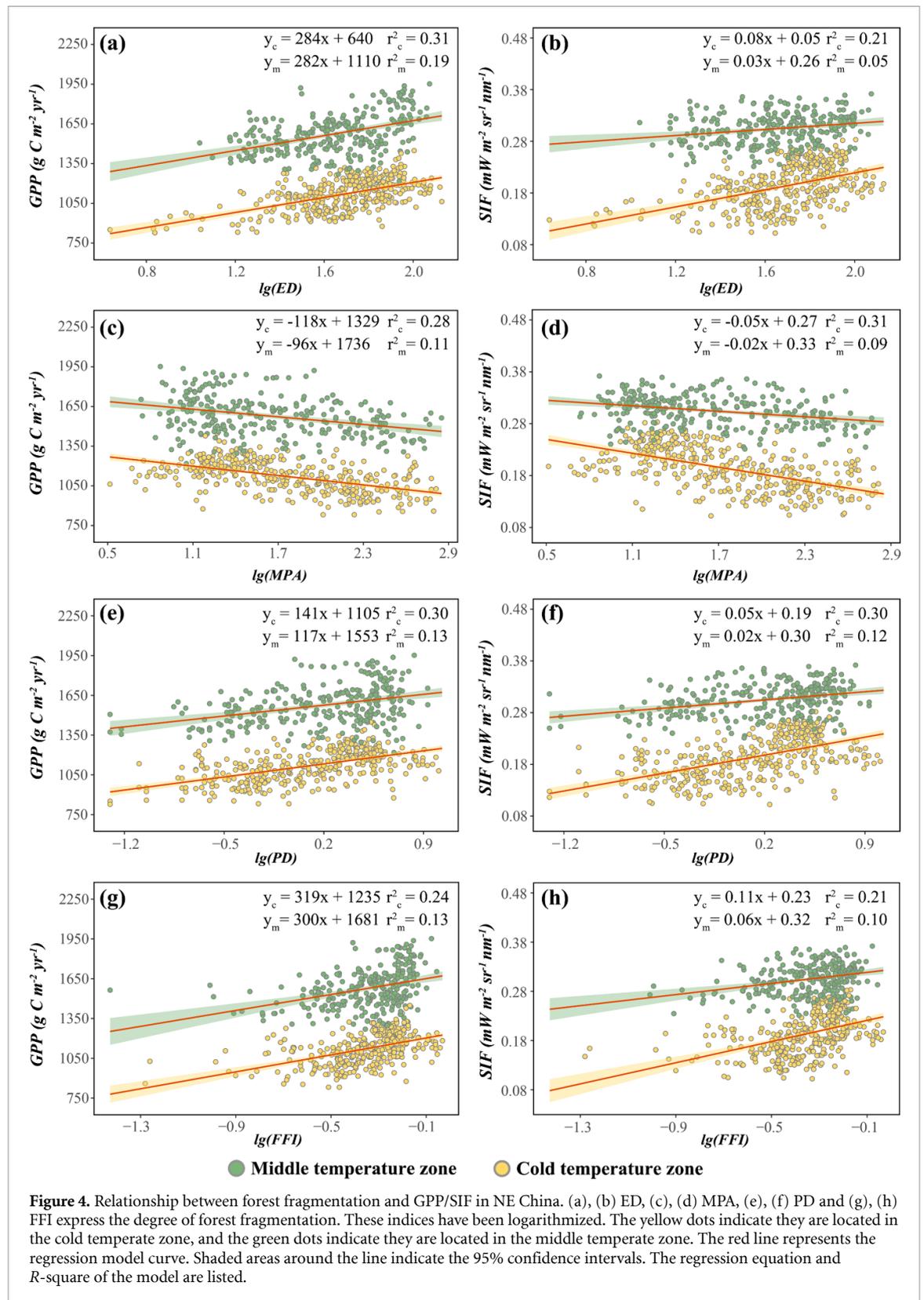
Province		Forest fragmentation degree					Total
		Little	Low	Medium	High	Extreme	
Heilongjiang	Landscape area (km <sup>2</sup> )	3202.3	15 898.9	58 005.9	26 348.4	1404.5	104 860.0
	Percentage (%)	3.05	15.16	55.32	25.13	1.34	—
Inner Mongolia	Landscape area (km <sup>2</sup> )	814.6	55 702.5	103 792.6	16 713.6	337.1	177 360.4
	Percentage (%)	0.46	31.41	58.52	9.42	0.19	—
Jilin	Landscape area (km <sup>2</sup> )	224.7	8707.9	45 365.4	10 589.9	224.7	65 112.6
	Percentage (%)	0.35	13.37	69.67	16.26	0.35	—
Liaoning	Landscape area (km <sup>2</sup> )	0.0	0.0	1095.5	20 112.4	1769.7	22 977.6
	Percentage (%)	0.00	0.00	4.77	87.53	7.70	—

water and photosynthetic carbon uptake. The temperature and water altogether explained 60% of the change in forest photosynthetic carbon uptake. In the middle temperate zone, forest fragmentation was significantly related to temperature and water, which explained 75% of the variation in temperature and 22% of the variation in water. The coefficient of the non-significant positive relationship (0.055) between temperature and photosynthetic carbon uptake was much smaller than that of the strong negative relationship (−0.677) between water and photosynthetic carbon uptake. Temperature and water accounted for 49% of the change of photosynthetic carbon uptake in all.

## 4. Discussion

### 4.1. The impact of forest fragmentation on photosynthetic carbon uptake is inconsistent in different regions

In NE China, forest photosynthetic carbon uptake is significantly positively correlated with forest fragmentation degrees, reflected by landscape pattern metrics, in both the cold temperate zone and middle temperate zones (figure 4). This is in accordance with some studies in temperate forests, for instance, the carbon uptake and storage in edges of a temperate broadleaved forest in southern New England are 13% and 10%, respectively, higher than that of the internal

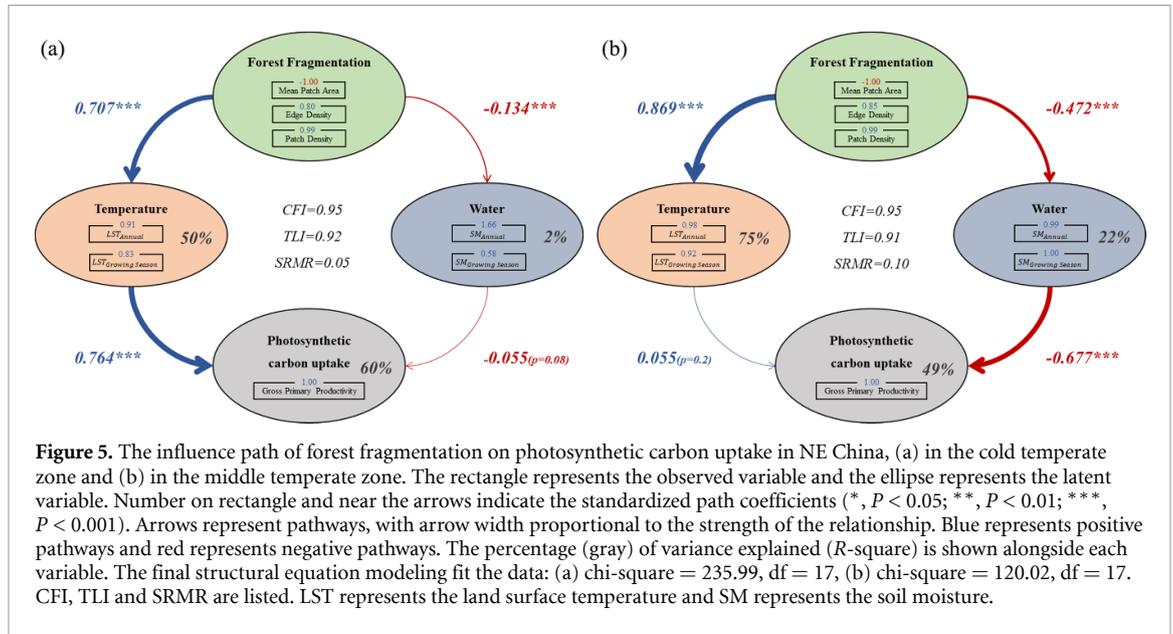


(Reinmann and Hutrya 2017). Besides, forest growth and biomass increased by 36.3% and 24.1% at forest edges adjacent to anthropogenic land covers in the NE US (Morreale et al 2021). These are similar to our results that at the regional scale, temperate forest fragmentation will increase the GPP by 14% and 10% in the cold temperate zone and middle temperate

zone, respectively. It is worth mentioning that some of these studies used remote sensing data and others used forest resource inventory data at different scales, and there were also differences in the study area and research designs. Hence there might be uncertain errors in estimating the enhancement of photosynthetic carbon uptake by forest fragmentation,

**Table 2.** Mean value of photosynthetic carbon uptake of forest fragmentation degree. CTZ refers to the cold temperate zone. MTZ refers to the middle temperate zone.

Data type	Climate zone	Fragmentation degree		Enhancement effect (EE)
		FFI < 0.4	FFI > 0.6	
GPP (g C m <sup>-2</sup> yr <sup>-1</sup> )	CTZ	1041.1	1186.8	14%
	MTZ	1508.1	1666.4	10%
SIF (mW m <sup>-2</sup> sr <sup>-1</sup> nm <sup>-1</sup> )	CTZ	0.17	0.21	23%
	MTZ	0.29	0.31	7%



but the EE of temperate fragmented forests is consistent. In contrast, sufficient studies have indicated that the carbon sequestration of forests has decreased significantly with increasing forest fragmentation in the tropics (Chaplin-Kramer *et al* 2015, Brinck *et al* 2020), species composition (Myers *et al* 2013) and phenology (Tang *et al* 2016) of temperate forests and tropical forests had different responses to fragmentation, which may also lead to differences in the carbon uptake capacity of different regions. Lastly, in addition to these internal factors that depend on the forests themselves, the climatic conditions of the forest external environment were considered as a possible key role. Changes in environment often promote the carbon storage of temperate forest edge relative to the interior (Remy *et al* 2016), but they always create unfavorable conditions in tropical forests, resulting in the overall negative response of carbon pools near the forest edge (Laurance *et al* 2011). For instance, forest biomass is easily lost due to drought and heat stress caused by rising temperature in the Brazilian Amazon (Qin *et al* 2021), whereas the productivity of trees increases rapidly in New York, because the increase of temperature will make the vegetation closer to the optimal temperature of photosynthetic efficiency saturation in temperate regions limited by temperature (Briber *et al* 2015).

Moreover, we only focused on how the spatial pattern of forest fragmentation affects photosynthetic

Currently, there is no clear conclusion about the different responses of forest carbon dynamic to fragmentation in tropical and temperate zones. Firstly, the difference of physiological and biochemical characteristics of forest vegetation may be an important reason. Compared with tropical forests, the above-ground part of temperate forests had higher photosynthetic rate and leaf mass per unit area (Xiang *et al* 2013), and the underground part of them was deeper into the soil layer (Bonan 2008). These characteristics enabled temperate forests to obtain more environmental resources, such as available light (Canham

*et al* 1990) and deeper soil water (Bonan 2008), and have stronger resilience to external disturbances, such as wind (Matlack 1993, Bell *et al* 2017, Smith *et al* 2018). Secondly, the spatial and age structure (Spicer *et al* 2020), species composition (Myers *et al* 2013) and phenology (Tang *et al* 2016) of temperate forests and tropical forests had different responses to fragmentation, which may also lead to differences in the carbon uptake capacity of different regions. Lastly, in addition to these internal factors that depend on the forests themselves, the climatic conditions of the forest external environment were considered as a possible key role. Changes in environment often promote the carbon storage of temperate forest edge relative to the interior (Remy *et al* 2016), but they always create unfavorable conditions in tropical forests, resulting in the overall negative response of carbon pools near the forest edge (Laurance *et al* 2011). For instance, forest biomass is easily lost due to drought and heat stress caused by rising temperature in the Brazilian Amazon (Qin *et al* 2021), whereas the productivity of trees increases rapidly in New York, because the increase of temperature will make the vegetation closer to the optimal temperature of photosynthetic efficiency saturation in temperate regions limited by temperature (Briber *et al* 2015).

carbon uptake. In fact, fragmentation is a dynamic process in time scale, so the relationship between fragmentation and photosynthetic carbon uptake still needs to be further studied.

#### 4.2. Climate driven effects of forest fragmentation on photosynthetic carbon uptake

The mechanism of forest fragmentation on photosynthetic carbon uptake has not been well studied in the past. In this study, water and temperature conditions explained almost half of the effects of temperate forest fragmentation on photosynthetic carbon uptake (figure 5). This is consistent with many studies that have proven that water and temperature are important control paths of forest growth and phenology (Keenan *et al* 2014, Martin-Benito and Pederson 2015, Tang *et al* 2016, Green *et al* 2019). Moreover, the latitudinal pattern of photosynthetic carbon uptake in response to forest fragmentation is driven by different major climatic factors. Our results showed that temperature is the central way for forest fragmentation to affect photosynthetic carbon uptake in the cold temperate zone, and water condition has gradually become the dominant factor controlling this process in the middle temperate zone. This is basically consistent with the spatial pattern distribution provided by previous studies (Nemani *et al* 2003). In addition, there are also some other climatic factors that may contribute to the process of forest fragmentation and photosynthetic carbon uptake. For instance, wind (Chen *et al* 1993) and light (Islam *et al* 2017) effects make use of more gaps generated by fragmentation to penetrate deeper forest interiors, resulting in more complex tree growth patterns (Hylander 2005, Laurance and Curran 2008). Climate changes caused by forest fragmentation are important drivers of photosynthetic carbon uptake, but the specific influencing factors have significant spatial heterogeneity.

Climate change often needs to consider the interaction of multiple factors to judge whether it is a positive or negative effect (Chen *et al* 1993, Smith *et al* 2018). In this study, from the cold temperate zone to the middle temperate zone, the effect of fragmentation on temperature and water increased significantly, but the change in photosynthetic carbon uptake explained by temperature and water decreased from 60% to 49%. This may be due to the interaction between water and temperature conditions partially offsets each other's effect on photosynthetic carbon uptake (Smith *et al* 2018). In other words, the relative importance of temperature and water conditions has changed (Myers *et al* 2013). As latitudes change, there may be an unclear delicate trade-off between this combination of climatic conditions stimulating productivity or creating more severe drought pressures at warmer and lower moisture forest edges (Martin-Benito and Pederson 2015, Smith *et al* 2018). Consequently, it is still a difficult

problem to understand and clarify the internal driving factors and the synergy between forest fragmentation and photosynthetic carbon uptake.

#### 4.3. The spatial patterns of forest fragmentation in NE China and its ecological insights

Our results showed that the fragmentation degree of Liaoning is much higher than that of the other three provinces, while Heilongjiang, Jilin and Inner Mongolia are slightly different under various indicators (figure 2 and table 1). From the single landscape pattern index, Heilongjiang is the province with the lowest degree of fragmentation; from the comprehensive fragmentation index, the degree of fragmentation in Inner Mongolia is lowest. The population and economy are important drivers of the formation of the current spatial pattern of forest fragmentation (Gong *et al* 2013). The population and economy of Liaoning is significantly higher than others, and Liaoning is the most developed region in NE China (table S1). Overall, a higher level of economic development or population will significantly increase the degree of forest fragmentation. The increase of population and the development of the economy often mean more human activities, and forest degradation, deforestation and fire caused by human activities are all considerable causes of fragmentation (Matricardi *et al* 2020). Contrarily, the areas with low degree of fragmentation are mainly concentrated in the north of GKM and the east of LKM, which are mainly distributed in the scope of the nature reserve. This demonstrates that increasing the area of the nature reserve and improving the protection intensity and quality of the nature reserve may be an efficient way to alleviate the fragmentation phenomenon in the future (Morales-Hidalgo *et al* 2015).

Although this study demonstrates that forest fragmentation in temperate regions can enhance photosynthetic carbon uptake, it does not mean that we support habitat fragmentation as a forest management strategy. The enhanced photosynthetic carbon uptake can hardly reverse the carbon loss caused by deforestation in a certain region. Moreover, there are still many known unavoidable and buffering hazards of forest fragmentation to ecosystem services and functions. For example, a large number of species are facing the threat of extinction (Echeverria *et al* 2006), the distribution of surrounding habitat conditions has changed (Latimer and Zuckerberg 2017), and cultural and regulatory services have been negatively affected (Uddin *et al* 2015). Therefore, it might be more important for human intervention to balance the impact of forest fragmentation. However, in land use, land-use change and forestry (LULUCF) activities, the process of accounting carbon inventory often pays no attention to the part of the carbon budget caused by forest degradation such as fragmentation. The impact of forest degradation on the carbon cycle cannot be ignored compared with deforestation or

afforestation (Silva Junior *et al* 2020, Fischer *et al* 2021). So, there is still a crucial gap in the accurate quantification of the carbon cycle and the response to LULUCF activity management policies. Overall, it is urgent to formulate relevant forest management policies and seek the balance between human activities and the forest carbon cycle, as well as ecosystem services and functions.

## 5. Conclusion

Our findings show that, contrary to the tropical forest paradigm, the photosynthetic carbon uptake of temperate forests in NE China is significantly enhanced with the increase in fragmentation (14% in the cold temperate zone and 10% in the middle temperate zone). In this process, environmental change is an important driving force, and hydrothermal conditions can explain at least half of the change in photosynthetic carbon uptake caused by fragmentation. The fragmentation of temperate forests will lead to the increase of LST and the decrease of SM in small areas to improve the level of photosynthetic carbon uptake. Meanwhile, regional differences will lead to changes in the importance of environmental conditions in different climatic zones. In the cold temperate zone, temperature is the key to this process, while in the middle temperate zone, water becomes the dominant influence path. The correlation between water and temperature as the influence paths in this process was clarified. However, there is still great uncertainty in the internal mechanism between forest fragmentation and photosynthetic carbon uptake and this mechanism can play an important role in understanding the forest carbon cycle and maintaining the carbon balance. Although forest fragmentation plays a positive role in promoting photosynthetic carbon uptake, it does not mean that it is necessary to use man-made forest fragmentation as a management strategy and forest fragmentation still has many known negative effects. Therefore, the extent and magnitude of human intervention in forest management needs to be further studied and quantified.

## Data availability statement

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

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