

Article

Spatial Heterogeneity and Driving Mechanisms of Forest Carbon Storage in Wuyi Mountain National Park

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Abstract

Forest aboveground live biomass carbon storage (hereafter referred to as “forest carbon storage”) is an important indicator of forest vegetation carbon sequestration, and its spatial patterns and associated factors are highly heterogeneous. Identifying these variations can improve the understanding of carbon accumulation in complex mountain forests and support fine-scale carbon assessment in similar ecosystems. The results showed the following. (1) The total forest carbon storage in the study area was 3.75×10^6 t C, with a carbon density of 44.83 t C·hm^{−2}. *Pinus massoniana* and hard broad-leaved tree species were the main contributors, and carbon storage peaked at the mature forest stage. (2) Carbon storage exhibited significant spatial clustering (Moran’s I = 0.312), with high-value areas concentrated within the national nature reserve and low-value areas distributed in regions with frequent human activities. (3) The GWR model outperformed the ordinary least squares model, with R^2 increasing to 0.88 and residual spatial autocorrelation reduced by 42.22%. (4) The positive effect of stand volume increased from northeast to southwest, the effect of stand age differed between eastern and western areas, and shrub layer height, soil depth, and slope exhibited region-specific positive and negative effects, with significant interactions among factors.

Keywords: Wuyi Mountain National Park; forest carbon storage; spatial distribution characteristics; geographically weighted regression; spatial heterogeneity of influencing factors



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1. Introduction

In the context of global climate change, forests serve as critical carbon reservoirs and play an essential role in regulating the carbon cycle, mitigating greenhouse gas emissions, and supporting carbon neutrality goals [1,2]. The accurate estimation of forest carbon storage and its economic value is therefore important for assessing carbon sequestration capacity and can provide a scientific basis for carbon trading and ecological compensation. Current approaches for estimating forest carbon storage mainly include remote sensing, geostatistical methods, and traditional spatial models [3]. Remote sensing is advantageous for large-scale assessment but is constrained by spatial resolution and environmental conditions, which may limit its ability to capture fine-scale variation within forests [4].

Geostatistical methods generally rely on assumptions of stationarity and normality, limiting their capacity to accommodate multiple factors and complex nonlinear relationships [5]. Traditional spatial models can account for residual spatial autocorrelation but do not explicitly characterize spatial heterogeneity and therefore may fail to reveal local variation [6].

Forest ecosystems usually exhibit pronounced spatial heterogeneity. The distribution of carbon storage is jointly influenced by multiple ecological and environmental factors, including stand structure, topography, and soil conditions [7]. Among these, stand characteristics such as stand age, species composition, and canopy density regulate carbon storage by influencing vegetation structure and biomass accumulation. Topographic conditions alter soil properties and the growing environment by affecting the redistribution of water and nutrients [8–11]. Soil conditions, in turn, influence forest biomass accumulation through water and nutrient supply, thereby shaping the spatial pattern of forest carbon storage [12,13]. From a mechanistic perspective, stand structure, topography, and soil environment correspond to biomass formation, environmental regulation, and nutrient supply processes in the forest carbon cycle. These three pathways jointly determine the spatial distribution of carbon storage. Ignoring such spatial heterogeneity may bias carbon storage estimates, compromise the accurate assessment of regional carbon sink capacity, and weaken the scientific basis for ecological conservation decisions [14].

Geographically weighted regression (GWR) has been widely applied in the spatial analysis of forest carbon storage and related ecological indicators, as it effectively captures spatial nonstationarity in variable relationships. For example, Liu et al. [15] used a GWR model to analyze the relationships between forest carbon storage, stand structure, and topographic factors in Heilongjiang Province. Their results showed that variables such as mean diameter at breast height (DBH), stand density, elevation, and slope exhibit significant spatial heterogeneity in their effects on carbon storage. Li et al. [16] constructed multiple models integrating topographic features, remote sensing bands, vegetation indices, and texture information to estimate aboveground biomass. Their findings indicate that the extended GWR model achieves higher accuracy than traditional linear regression models in biomass estimation. In addition, Mitran et al. [17] applied an extended GWR model to examine the spatially differentiated contributions of soil types and land use in semi-arid regions. Their study revealed that variations in soil conditions and land use patterns have significant impacts on regional carbon sink distribution. Overall, existing studies have primarily explored the spatial patterns of forest carbon storage and their driving factors from single or dual perspectives, such as stand structure, topography, or soil properties, using GWR models. However, there is still a lack of comprehensive analysis that integrates these three key ecological dimensions—stand, topography, and soil—to explain the driving mechanisms of forest carbon storage and their spatial nonstationarity. Moreover, the understanding of how interactions among different types of factors influence carbon storage remains insufficient and requires further investigation.

Wuyi Mountain supports a representative mid-subtropical forest ecosystem at its latitude and is a biodiversity region of international conservation importance in southeastern China. Its complex mountainous terrain provides a suitable setting for investigating the spatial heterogeneity of forest carbon storage and its associated factors. Previous studies have examined carbon storage in Wuyi Mountain National Park from different perspectives. Chen et al. [18] used land-use data and the InVEST model and found a U-shaped temporal trend in regional carbon storage. High-value areas were mainly concentrated in forested land. Their study characterized the spatiotemporal dynamics of carbon storage under land-use change but did not further examine its associated factors or spatial heterogeneity. Jin et al. [19] estimated forest carbon storage using forest resource data. They focused on its relationships with dominant tree species, stand age classes, and topographic conditions.

Their results identified dominant tree species and stand age classes as the main influencing factors. However, the spatial heterogeneity of these relationships and the interactions among factors were not further explored. Accordingly, this study focuses on the spatial heterogeneity of forest carbon storage in Wuyi Mountain National Park. Particular attention is given to the spatial variation in the relationships between major influencing factors and carbon storage, as well as interactions among these factors.

All data on stand structure, topographic conditions, and soil properties were obtained from the forest resource inventory and recorded at the forest subcompartment level. In GWR modeling, inconsistencies in spatial scale and analytical units may affect the identification of local spatial relationships [20]. Because all variables in this study were recorded and analyzed at the subcompartment scale, the need for additional scale transformation and spatial matching was reduced, providing a consistent spatial basis for characterizing spatial heterogeneity in local relationships. This study considered only aboveground live biomass carbon storage (hereafter “forest carbon storage”) and excluded other forest ecosystem carbon pools, including deadwood, litter, and soil organic carbon. Accordingly, this study aims to: (1) quantify the spatial differentiation pattern of forest vegetation carbon storage in Wuyi Mountain National Park; (2) reveal the spatial nonstationarity characteristics of the effects of driving factors; and (3) explore the influence mechanisms of multi-factor interactions on the spatial pattern of carbon storage. This study aims to deepen understanding of the spatial variation and underlying mechanisms of forest carbon storage and to provide a case study for the fine-scale assessment of similar forest ecosystems worldwide.

2. Study Area and Data Preprocessing

2.1. Study Area

This study covered the entire area of Wuyi Mountain National Park. The study area is located in the northwest of Fujian Province ($27^{\circ}33'–27^{\circ}54' \text{ N}$, $117^{\circ}27'–117^{\circ}51' \text{ E}$), covering an area of 1001.41 km^2 , with a forest cover of 96.7%. It is one of the first national parks established in China. Wuyi Mountain National Park comprises the Wuyi Mountain National Nature Reserve, the Scenic Area, the Upper Reaches of the Jiuqu Stream Protection Area, and newly incorporated areas (Figure 1).

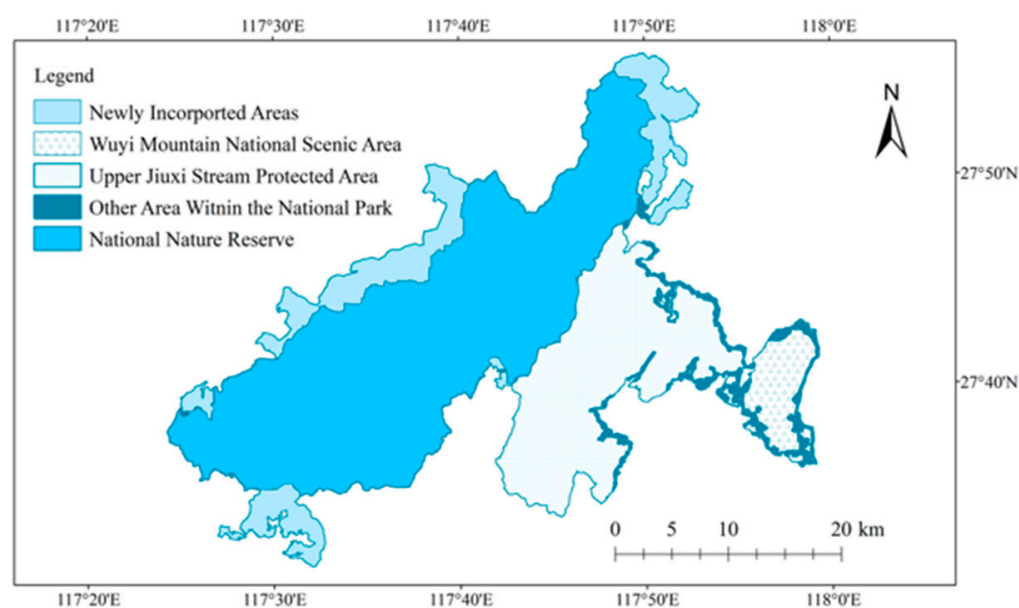


Figure 1. Location and main protected areas of Wuyi Mountain National Park.

The region preserves one of the most intact mid-subtropical evergreen broadleaved forest ecosystems at this latitude worldwide and exhibits pronounced vertical zonation. Major vegetation types include evergreen broadleaved forests, mixed coniferous–broadleaved forests, temperate coniferous forests, and alpine meadows. The dominant tree species include *Phyllostachys edulis*, *Pinus massoniana*, *Cunninghamia lanceolata*, *Quercus* spp., *Pinus hwangshanensis*, and *Castanea mollissima*, as well as other hard and soft broadleaved species.

2.2. Data Sources and Preprocessing

This study was based on the 2018 forest resource inventory data provided by the Wuyi Mountain National Park Research and Monitoring Center. For the inventory, forest sub-compartments were delineated using 1:1000 high-resolution aerial imagery in combination with 1:10,000 topographic maps. Field surveys were then conducted with forest subcompartments as the basic inventory units, generating a forest resource inventory database containing information on stand structure, topographic conditions, soil properties, and related attributes. Accordingly, forest subcompartments were used as the basic spatial units of analysis in this study.

First, to systematically examine the factors associated with forest carbon storage, variables were compiled from three dimensions—stand structure, topographic conditions, and soil properties—based on previous studies [21–24] and the processes of biomass formation, environmental regulation, and nutrient supply involved in forest carbon accumulation (Table 1). Together, these three groups of variables represent distinct pathways within the forest carbon cycle and provide a broad characterization of the ecological processes related to carbon storage. During data preprocessing, measurement units were standardized and the original data were normalized. Forest subcompartments with zero values for all stand inventory variables were excluded to reduce interference from non-vegetated land-cover types. The remaining variables were then further screened according to variable type, data quality, and the results of multicollinearity tests.

Table 1. Specific index detail.

Factor Category	Specific Indicators
Stand Factors	Subcompartment area, canopy density, stand age, age class, mean diameter at breast height, mean tree height, number of trees per hectare, stand volume, scattered tree volume, number of scattered trees, shrub layer height, shrub layer cover, herb layer height, herb layer cover
Topographic Factors	Elevation, slope, slope length, slope position, slope aspect
Soil Factors	Humus layer depth, soil depth, soil type

3. Methods

3.1. Estimation of Carbon Stocks and Their Economic Value

This study adopts the generalized biomass–volume regression equations (Table 2) developed by Fang, Liu, Zheng, and others to estimate forest biomass in China [25–27]. These models are constructed based on national forest inventory data and have been widely validated and applied in regional-scale studies of forest carbon sinks in China [28,29]. They provide a consistent and comparable methodological framework for large-scale biomass estimation across multiple tree species.

Table 2. Regression equations of biomass for various tree species.

Tree Species Type	Biomass Regression Equation (t/hm ²)	Carbon Fraction (%)	Source of Equation
<i>Cunninghamia lanceolata</i> <i>Tsuga chinensis</i>	$B = 0.3999V + 22.5410$	51.27	Fang et al. 2007 [26]
<i>Cryptomeria japonica</i> <i>Metasequoia glyptostroboides</i>	$B = 0.4158V + 41.3318$	53.31	Fang et al. 2001 [25]
<i>Pinus massoniana</i>	$B = 0.52V$	52.71	Fang et al. 2007 [26]
Other Pine Species	$B = 0.5168V + 33.2378$	49.63	Fang et al. 2007 [26]
<i>Schima superba</i>	$B = 0.6255V + 91.0013$	51.15	Fang et al. 2001 [25]
<i>Quercus</i> spp.	$B = 0.6096V + 33.8060$	47.98	Fang et al. 2001 [25]
Other Hard Broadleaved Species	$B = 0.6255V + 91.0013$	49.01	Fang et al. 1998 [27]
Other Soft Broadleaved Species	$B = 0.4754V + 30.6034$	45.02	Fang et al. 2001 [25]
General Biomass Equation	$B = 0.8873V + 4.5539$	50.00	Zheng et al. 2013 [28]

Note: B represents stand biomass with units in t/hm²; V represents stand volume with units in m³/hm².

Because no bamboo-specific biomass regression equation compatible with the present inventory data was available, *Phyllostachys edulis* biomass was estimated using the general vegetation biomass model listed in Table 2 [30]. This approach was adopted to maintain methodological consistency across forest types and comparability in data processing at the forest subcompartment scale. Field measurements from Fujian Province indicate that the carbon fractions of different *P. edulis* organs generally range from 46.3% to 52.1%, which is broadly consistent with the average carbon fraction of 0.50 commonly used for forest vegetation in China [31]. A carbon fraction of 0.50 was therefore used for *P. edulis* to ensure complete estimation of forest carbon storage.

In the forest resource inventory used in this study, several hard broadleaved species, including *Schima superba*, *Quercus* spp., and *Castanea mollissima*, were listed separately. Species not individually identified were grouped as “other hard broadleaved species”. Based on previous vegetation surveys in the Wuyi Mountain region [32], this group mainly includes *Castanopsis carlesii*, *Castanopsis eyrei*, *Cyclobalanopsis* spp., and *Machilus* spp. The regression equation for “other hard broadleaved species” was used for species within this category. It was also applied to separately listed hard broadleaved species for which no compatible species-specific biomass regression equation was available. The equation was developed from mixed broadleaved forest samples and characterizes the volume–biomass relationship of stands composed of multiple hard broadleaved species. It has also been used to estimate biomass for “other hard broadleaved species” and similar composite broadleaved species groups [33,34]. Therefore, the equation was applied consistently to the relevant hard broadleaved species in this study.

Based on individual tree biomass, the carbon storage of each tree was calculated using a carbon conversion factor. The total carbon storage at the subcompartment scale was then calculated through weighted integration based on the proportion of tree species. Finally, total carbon storage for the statistical area was aggregated.

$$\text{Carbon Storage} = B \times CF \quad (1)$$

In the equation, B represents stand biomass, and CF represents the carbon fraction for each tree species.

The economic value of forest carbon storage can be assessed using several approaches, including the carbon tax method, the social cost method, and the carbon emissions trading market price method. Among these, the carbon market price directly reflects the exchange value of carbon sinks within real-world emission reduction mechanisms. Given that China

has established regional carbon markets, and that the Fujian carbon market is relatively mature with well-developed mechanisms, it can effectively represent the actual economic value of regional carbon sinks. Therefore, this study adopts the carbon emissions trading market price method for valuation. The calculation equation is shown in Equation (2):

$$Y = V_c \times A \times 3.67 \times 10^3 \quad (2)$$

In the equation, Y represents the economic value of plant carbon storage (RMB); 3.67 is the conversion coefficient from carbon to CO₂ equivalent; V_c denotes plant carbon storage (10³ t C); and A is the unit carbon price (RMB/tCO₂). The carbon storage estimation in this study was based on the 2018 forest resource inventory data. Therefore, the results represent a static valuation for the base year and do not reflect current market price levels. To ensure consistency in data standards, the unit carbon price was taken as the average transaction price of forestry carbon sink projects in the Fujian carbon emissions trading market in 2018, which was 14.69 RMB/tCO₂ [35].

3.2. Selection and Fitting of Independent Variables

To better examine the spatial heterogeneity and interactions of the main influencing factors, continuous numerical variables were first selected as candidate predictors. Pearson correlation analysis and the variance inflation factor (VIF) were then used to assess multicollinearity, reduce information redundancy, and improve model stability. Random forest was subsequently used to evaluate the relative importance of the candidate variables (Figure 2). Stand volume, stand age, soil depth, elevation, shrub layer height, and slope showed relatively high importance, with a decline in variable importance after slope (Figure 2). Considering both the importance ranking and the representation of stand structure, topographic conditions, and soil properties, these six variables were selected for the subsequent GWR and interaction analyses.

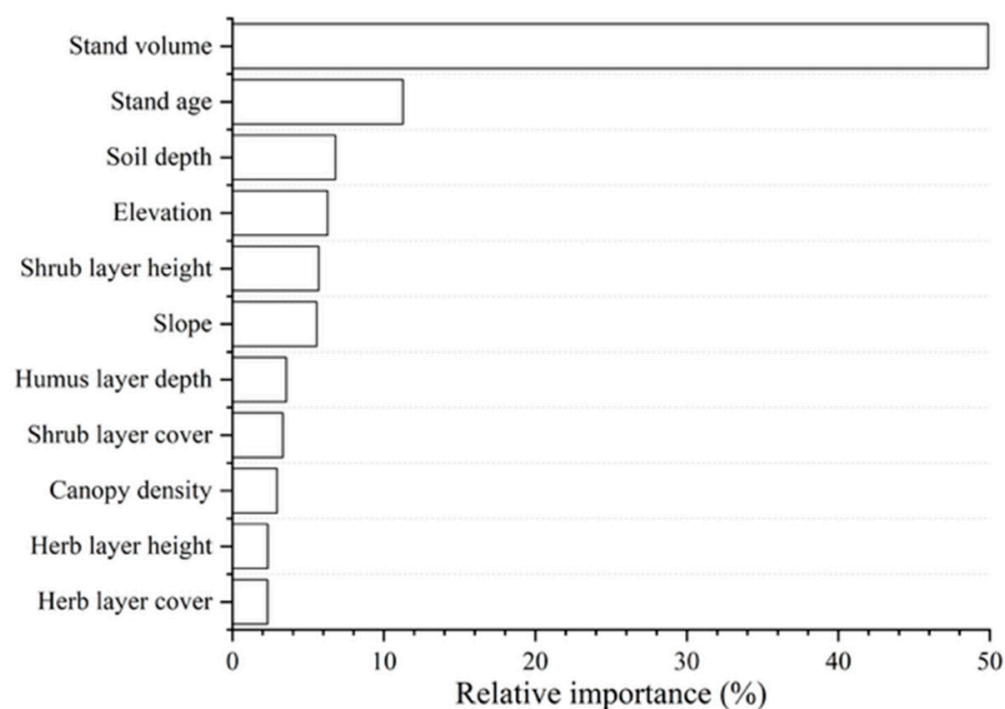


Figure 2. Relative importance of explanatory variables based on the random forest model.

3.3. Spatial Correlation Analysis

This study used Moran's I to test the global spatial autocorrelation of forest carbon storage. It also evaluated spatial autocorrelation in GWR residuals to assess the model's ability to reduce spatial dependence. The equation for global Moran's I is shown in Equation (3):

$$I = \frac{n \sum_{i=1}^n \sum_{j=1}^n w_{ij}(d) (x_i - \bar{x})(x_j - \bar{x})}{\sum_{i=1}^n \sum_{j=1}^n w_{ij}(d) (x_i - \bar{x})^2} \quad (3)$$

In the equation, x_i and x_j represent the observed values at sample points i and j , respectively; $\bar{x}$ is the mean of all observed values within the study area; n is the total number of samples; and $w_{ij}(d)$ denotes the spatial weight calculated based on the distance between sample points i and j .

3.4. OLS Model

The OLS model assumes that regression coefficients are constant across the entire study area. Its mathematical expression is given by Equation (4):

$$Y = \sum_{i=1}^p X_i \beta + \varepsilon \quad (4)$$

where β is the vector of estimated unknown fixed-effect model coefficients; ε denotes the model residuals, assumed to follow a normal distribution $N(0, \sigma^2)$; X_i represents the i -th independent variable; p is the total number of independent variables.

3.5. GWR Model

The GWR model is an extension of the OLS model, incorporating geographical spatial information as weights into the traditional global regression framework, forming a local regression approach. The model is expressed in Equation (5):

$$y_i = \beta_0(u_i, v_i) + \sum_{k=1}^n \beta_k(u_i, v_i) x_{ik} + \varepsilon_i \quad (5)$$

where y_i denotes the carbon storage value of the i -th subcompartment; x_{ik} is the value of the k -th explanatory variable at location i ; (u_i, v_i) represents the geographical coordinates of location i ; $\beta_k(u_i, v_i)$ is the regression coefficient of the k -th explanatory variable at location i ; $\beta_0(u_i, v_i)$ is the local intercept; ε_i is the random error term.

GWR was implemented in ArcGIS 10.8 using Euclidean distance. Spatial weights were constructed using a fixed Gaussian kernel, and the optimal bandwidth was selected by minimizing the corrected Akaike information criterion (AICc). The resulting optimal fixed bandwidth was 4.6 km and used to estimate the local regression parameters.

3.6. Comparison of Model Goodness-of-Fit

Three widely used metrics—coefficient of determination (R^2), root mean square error (RMSE), and mean absolute error (MAE)—were employed to assess the predictive accuracy of the models and compare the goodness-of-fit between the OLS and GWR models. The equations for these metrics are provided below:

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (6)$$

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2} \quad (7)$$

$$MAE = \frac{1}{n} \sum_{i=1}^n |y_i - \hat{y}_i| \quad (8)$$

where n is the number of samples; y_i is the true observed value of the i -th sample; $\hat{y}_i$ is the predicted value of the i -th sample; $\bar{y}$ is the mean of the observed values.

4. Results and Analysis

4.1. Estimated Carbon Storage and Its Economic Value

The total forest biomass in the study area was 7,465,142.98 t, with a total carbon storage of 3,754,409.73 t C and a carbon density of 44.83 t C·hm⁻². Table 3 further presents forest carbon storage and its economic value across different tree species and stand age classes. Stand age classes were taken from the 2018 forest resource inventory and determined based on the dominant tree species, mean stand age, and the corresponding rotation-age standards for each forest subcompartment. Following the Age-Class and Age-Group Division of Main Tree Species (LY/T 2908–2017) [36], stands were classified as young, middle-aged, near-mature, mature, or over-mature.

Table 3. Forest carbon storage and economic value by tree species and stand age class.

Tree Species	Carbon Storage (10 ³ t C)	Economic Value (10 ⁴ CNY)	Stand Age Class	Carbon Storage (10 ³ t C)	Economic Value (10 ⁴ CNY)
<i>Phyllostachys edulis</i>	251.12	1353.85	Young	422.58	2278.05
<i>Pinus massoniana</i>	1078.08	5812.28	Middle-aged	456.25	2459.89
<i>Cunninghamia lanceolata</i>	296.51	1598.54	Near-mature	468.71	2527.12
<i>Quercus</i> spp.	48.93	263.79	Mature	1819.85	9812.93
<i>Pinus hwangshanensis</i>	5.44	29.33	Over-mature	587.02	3165.65
<i>Castanea mollissima</i>	0.40	2.16			
Other Tree Species	0.71	3.83			
Other Hard Broadleaved Species	2067.40	11,145.83			
Other Soft Broadleaved Species	5.83	31.43			

Among these, other hard broadleaved species and *P. massoniana* had the highest carbon storage and were the main contributors to regional forest carbon storage. In contrast, *C. mollissima*, *P. hwangshanensis*, and other soft broadleaved species had relatively low carbon storage and made limited contributions to the total. Among the stand age classes, mature forests had the highest carbon storage and economic value, followed by over-mature, near-mature, middle-aged, and young forests. Forest carbon storage and its economic value therefore differed among stand age classes.

4.2. Analysis of Spatial Distribution Characteristics of Carbon Storage

Forest carbon storage in Wuyi Mountain National Park showed significant spatial clustering, with a global Moran's I of 0.312 ($p < 0.05$), indicating positive spatial autocorrelation. To further identify local spatial clusters, hotspot analysis was conducted using the Getis–Ord G_i^* statistic, which identifies clusters of high and low values. The results revealed distinct hot spots and cold spots. Hot spots formed a continuous northeast–southwest distribution, whereas cold spots were mainly concentrated in the eastern part of the study area. To visualize the spatial distributions of forest carbon storage and its influencing factors, variable values were classified using the natural breaks method. This method determines class thresholds by minimizing within-class variance and maximizing between-class differences, thereby identifying natural groupings in the data [37].

The results (Figure 3b) show that high carbon storage areas are mainly distributed within the national nature reserve, where the terrain is dominated by moderate slopes (12–27°). Such slope conditions help reduce soil erosion risk and improve drainage, creating favorable hydrothermal conditions for vegetation growth and biomass accumulation. As shown in Figure 4, these areas are primarily composed of near-mature and mature forests

with a high stand volume and a relatively complex vertical structure of the shrub layer. Together, these characteristics enhance carbon sequestration efficiency and lead to high carbon storage.

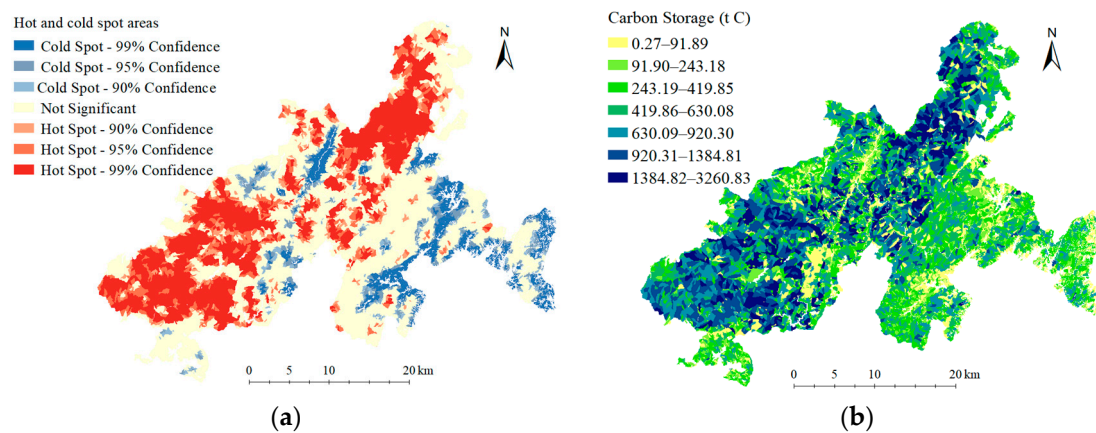


Figure 3. Carbon storage spatial distribution characteristics map. (a) Cold and hot spot distribution; (b) Carbon storage distribution.

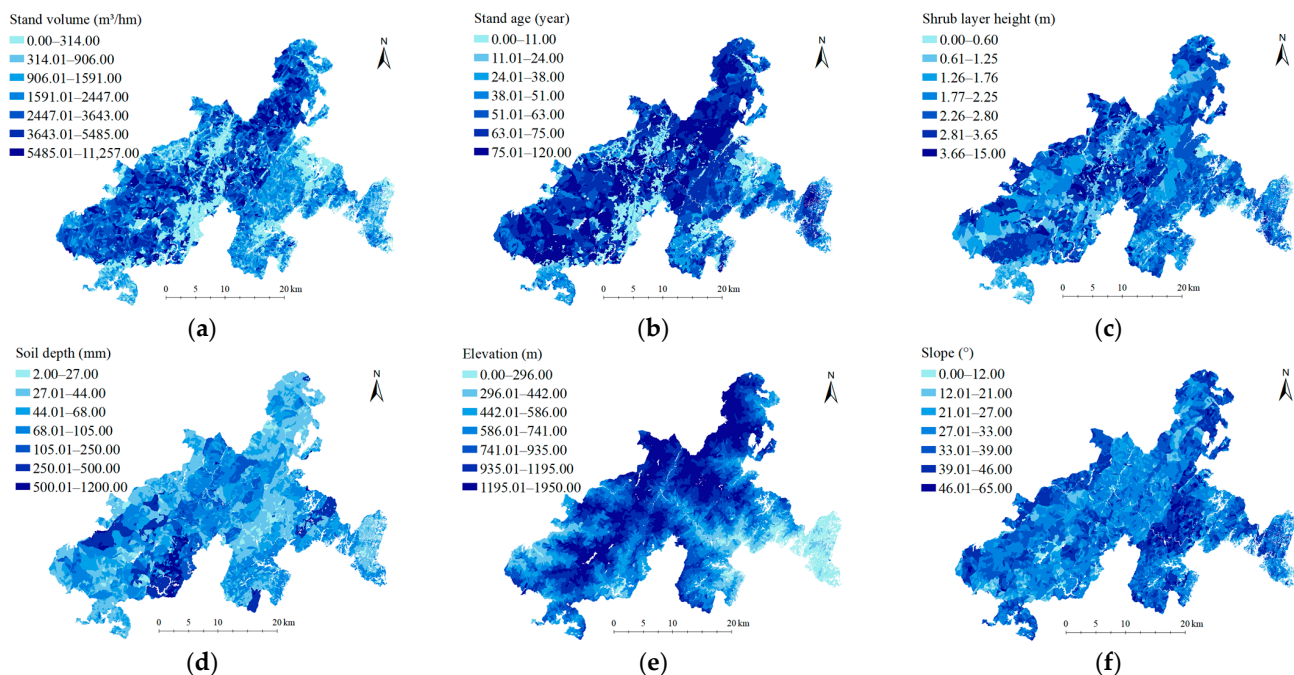


Figure 4. Spatial distribution of various variables. (a) subcompartment stand volume; (b) stand age; (c) shrub layer height; (d) soil depth; (e) elevation; (f) slope.

Low carbon storage areas are mainly located in the national scenic area, which is characterized by relatively flat terrain and lower elevation. However, long-term human activities have led to vegetation degradation. The stands are dominated by young and middle-aged forests, with a lower shrub layer, resulting in a significantly reduced carbon accumulation capacity.

The newly designated protected area in the upper reaches of the Jiuqu Stream serves as an ecological transition zone for carbon storage. Due to its relatively recent establishment, its carbon storage level is still lower than that of the national nature reserve, but it is significantly higher than that of surrounding unprotected areas. Overall, forest carbon storage in the study area shows a decreasing gradient from the national nature reserve to surrounding regions. This forms a spatial pattern with high-value clusters as the core area,

the newly protected area as the transition zone, and the scenic area as the peripheral zone. This pattern is highly consistent with the variation in regional protection intensity.

4.3. Analysis of Heterogeneity in Key Drivers of Carbon Storage

4.3.1. Comparison of Model Fitting Results

As shown in Table 4, the GWR model achieved an R^2 of 0.88, representing a 2.33% improvement over the OLS model. RMSE and MAE were reduced by 4.17% and 6.72%, respectively. All three evaluation metrics therefore indicated better model fit for GWR. The overall difference in model fit was further assessed using the $F(2)$ test proposed by Leung et al. [38]. The result was highly significant ($F(2) = 7.75$, $df_1 = 157.25$, $df_2 = 12,779$, $p < 0.001$), confirming that the improvement in GWR fit was statistically significant. In terms of spatial coverage, the global R^2 of the OLS model was used as a descriptive reference. GWR local R^2 values exceeded this reference in 69.09% of forest subcompartments, accounting for 70.01% of the total study area. In addition, 67.48% of forest subcompartments had lower absolute residuals under GWR, corresponding to 64.56% of the study area. These results indicate that the improvement in GWR fit covered a large proportion of the study area but was not spatially uniform.

Table 4. The results of the goodness-of-fit evaluation index.

Model	Coefficient of Determination (R^2)	Root Mean Square Error (RMSE)	Mean Absolute Error (MAE)
OLS	0.86	143.03	62.48
GWR	0.88	137.07	58.28

Residual spatial autocorrelation also differed between the two models. Moran's I was 0.045 for the OLS residuals and 0.026 for the GWR residuals, representing a 42.22% reduction. A paired randomization test showed that this difference was statistically significant ($p < 0.001$). This indicates that GWR significantly reduced residual spatial autocorrelation. This improvement likely reflects the ability of GWR to capture local variation in the relationships between forest carbon storage and the explanatory variables, thereby allowing parameter estimates to better reflect spatial differences. In addition, the ranges of the GWR coefficient estimates encompassed the corresponding OLS estimates. For all six variables, the interquartile ranges of the local coefficient estimates extended beyond the intervals defined by the corresponding OLS estimates ± 1 standard deviation, indicating pronounced spatial nonstationarity and clear spatial heterogeneity in their relationships with forest carbon storage.

The standardized residuals of the GWR model were concentrated around zero, with most falling within ± 1 . Their distribution was approximately symmetric and contained few extreme values, indicating no obvious systematic bias and an overall stable error structure. All local condition numbers were below 30, suggesting no serious local multicollinearity and good stability of the parameter estimates. Together with the improved goodness-of-fit and the significant reduction in residual spatial autocorrelation, these diagnostic results indicate that the GWR model effectively characterized the spatial heterogeneity of forest carbon storage and provided reliable model estimates.

4.3.2. Analysis of Spatial Distribution Characteristics of Carbon Storage

As shown in Figure 5, forest carbon storage is jointly influenced by multiple factors, including stand structure, soil conditions, and topographic characteristics. The strength and direction of these driving factors exhibited clear spatial heterogeneity. The coefficients of stand volume were statistically significant across all locations. They were consistently

positive and increased from northeast to southwest, indicating a stable and strengthening positive effect on carbon storage. This spatial pattern is closely related to hydrothermal gradients. The northeastern region has higher elevation, lower temperatures, and a shorter growing season, which limit biomass accumulation. In contrast, the southwestern region is warmer and more humid, promoting tree growth and increasing carbon storage.

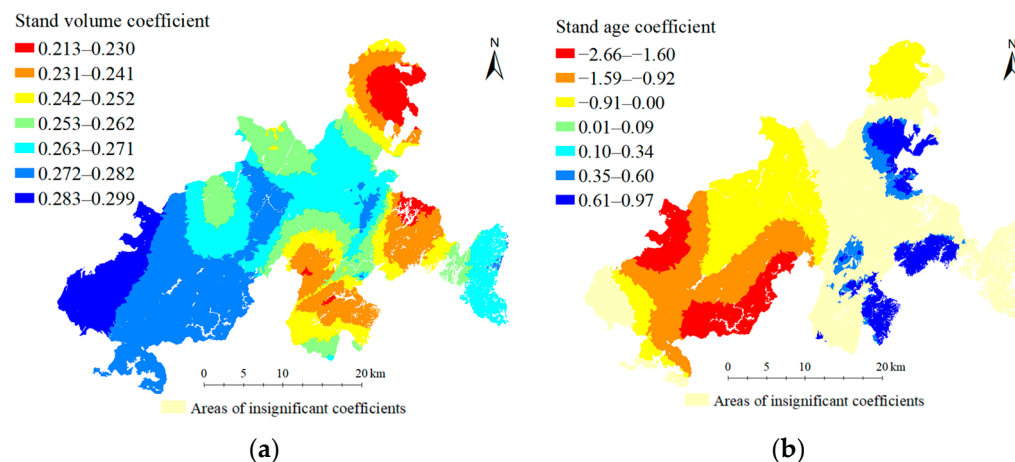


Figure 5. Distribution map of GWR model coefficients. (a) Distribution map of subcompartment stand volume coefficients; (b) Distribution map of stand age coefficients.

The coefficients of stand age showed a pattern of positive effects in the east and negative effects in the west. In the eastern region, forests are mainly young and middle-aged stands, which are in a rapid growth stage and have strong carbon sequestration capacity. In the western region, forests are dominated by mature stands. Due to high elevation, low temperature, and stand senescence, stand age exhibited a negative effect on carbon storage.

In the transitional zone between the eastern and western regions, the effect of stand age on carbon storage was not significant. This may be due to complex terrain and varying slopes in this area, as well as the interspersed distribution of stands of different age classes. The interaction between stand age and topographic factors weakens the independent contribution of stand age to carbon storage.

The spatial effect of shrub layer height on carbon storage showed significant heterogeneity (Figure 6). The results indicate a significant positive effect in areas extending from the central region toward the southwest and northeast. This is attributed to the synergy between a well-developed shrub layer, favorable hydrothermal conditions, and complex community structure, which enhances carbon accumulation. In contrast, some areas in the eastern region exhibited a significant negative effect. This is likely due to intensified competition for resources between the shrub and tree layers, which constrains tree growth and weakens the carbon sink function. In other areas, the effect was not statistically significant, suggesting that the influence of shrub layer height on carbon storage is highly context-dependent. It becomes significant mainly in regions where the shrub layer is well-developed or where inter-layer competition is pronounced.

Local significance tests show that the effect of soil depth on carbon storage varied markedly in direction. Positive effects were observed in parts of the southern and northwestern regions, while negative effects appeared in the central southwestern and some eastern areas. Notably, this variation did not fully correspond to the spatial distribution of soil depth itself. This indicates that the impact of soil depth on carbon storage is not determined solely by its magnitude, but is jointly regulated by site conditions, stand structure, and other factors.

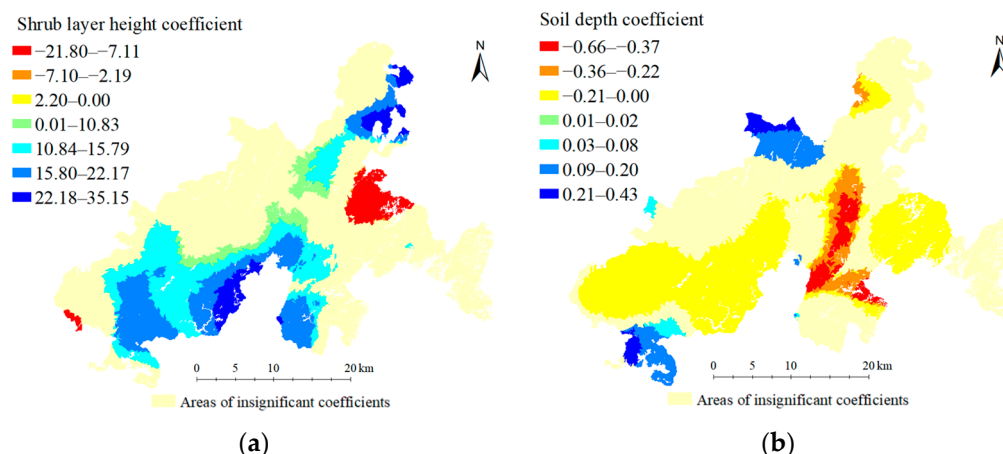


Figure 6. Distribution map of GWR model coefficients. (a) Distribution map of shrub layer height coefficients; (b) Distribution map of soil depth coefficients.

The spatial influence of elevation on forest carbon storage showed clear regional variation (Figure 7). Local significance tests indicate that most areas in the northeast exhibited a significant positive effect, whereas the southwestern region showed a significant negative effect. In other areas, the coefficients were small and not statistically significant, suggesting a weak direct influence of elevation on carbon storage. This may be explained by two reasons. First, the study area is located in a mid-subtropical climate zone, where terrain variation does not create extreme environmental conditions. Second, elevation mainly affects carbon storage indirectly by regulating hydrothermal conditions, vegetation types, and soil properties.

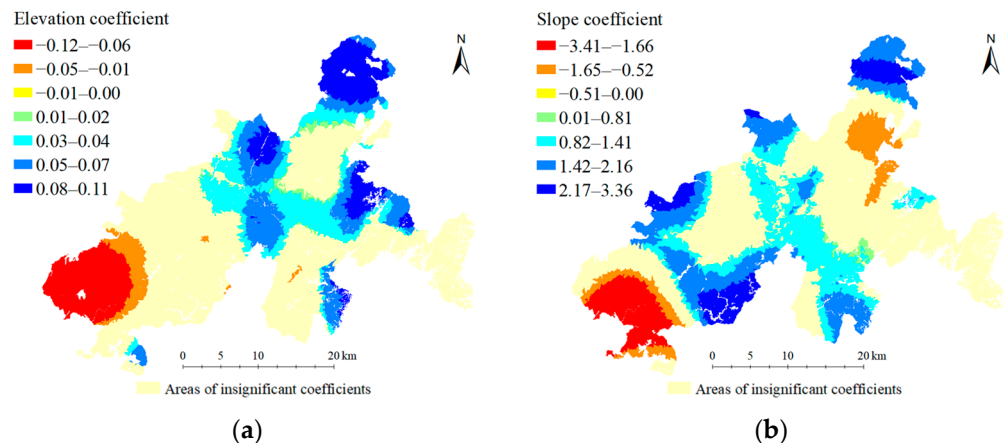


Figure 7. Distribution map of GWR model coefficients. (a) Distribution map of elevation coefficients; (b) Distribution map of slope coefficients.

Local significance tests show that the effect of slope on carbon storage varied across regions. It was significantly negative in the southern area, significantly positive in the northeastern, central, and southeastern areas, and not significant in most other regions. In the continuous zone from northeast to southwest, where terrain is mainly composed of gentle to moderate slopes, the direction and magnitude of coefficients varied notably across segments. This suggests that the effect of slope is not determined solely by its magnitude, but depends on local conditions such as vegetation type, soil properties, and stand structure. Overall, the driving factors exhibit clear spatial partitioning, with no single dominant factor identified, indicating that forest carbon storage in the study area is jointly regulated by multiple factors.

4.4. Analysis of Factor Interactions

The GWR results revealed certain discrepancies between the spatial distributions of some explanatory variables and the patterns of their local regression coefficients, suggesting that forest carbon storage is likely influenced by synergistic interactions among multiple factors. To further identify potential interactions between variables, an interaction dependence plot (IDP) was introduced as a supplementary analysis on the basis of GWR. While controlling for other variables, the IDP visualizes the interactive effect of two explanatory variables on carbon storage through a three-dimensional response surface, where the horizontal axes represent the values of the two variables and the surface height reflects the response intensity of carbon storage. Changes in surface morphology allow for an intuitive identification of nonlinear interactions between variables, thereby providing additional evidence for interpreting the mechanisms underlying forest carbon storage formation.

Interactions were observed among factors from different groups. Notably, slope and stand age exhibited a pronounced interactive effect (Figure 8a). In areas with gentle slopes, carbon storage initially increased and then decreased with increasing stand age; as slope steepness increased, the overall carbon storage level declined, and the positive effect of stand age on carbon storage gradually weakened. An interactive relationship was also found between shrub layer height and elevation (Figure 8b). At low shrub layer heights, carbon storage showed an upward trend with increasing elevation, indicating that when understory competition is weak, changes in hydrothermal conditions along the elevation gradient favor stand growth and carbon accumulation. In contrast, when shrub layer height was high, the trend of carbon storage with elevation tended to flatten, possibly because intensified understory vegetation competition weakened the influence of the elevation gradient on carbon storage. As shown in Figure 8c, under conditions of shallow soil, carbon storage first increased and then decreased with increasing shrub layer height, suggesting that a moderate shrub layer structure helps improve the understory micro-environment, whereas an excessively high shrub layer may intensify understory competition and inhibit tree layer growth. This interactive effect was more pronounced under conditions of relatively limited soil resources and weak understory competition, exhibiting a stronger synergistic regulatory role. In addition, an interactive effect existed between slope and soil depth (Figure 8d). In areas with shallow soil, carbon storage remained relatively stable initially with increasing slope, then increased, and declined again when the slope became excessively steep, indicating that a moderate slope facilitates the improvement of soil water–air conditions and promotes stand growth and carbon accumulation, whereas an overly steep slope may suppress vegetation growth due to intensified soil erosion and nutrient loss. In areas with deeper soil, the regulatory effect of slope on carbon storage was markedly weakened.

Within-factor interactions were also evident. A significant synergistic effect was observed between shrub layer height and stand age (Figure 8e). At low shrub layer heights, carbon storage displayed a clear upward trend with increasing stand age; as shrub layer height increased, understory vegetation competition gradually intensified, the positive effect of stand age on carbon storage was notably weakened, and the interactive effect correspondingly diminished. Under different elevation conditions, carbon storage generally exhibited a trend of first increasing and then decreasing with increasing slope (Figure 8f), but the slope range at which the trend reversed differed across elevation gradients, indicating that the synergistic variation of elevation and slope jointly influences the spatial distribution of forest carbon storage. Taken together, the results from the GWR and IDP analyses demonstrate that GWR reveals spatial heterogeneity in the intensity of influencing factors, while IDP further characterizes the interactive relationships among and within ecological factors. Overall, the formation of forest carbon storage results from the

synergistic effects of multiple factors, including stand structure, topographic conditions, and soil environment.

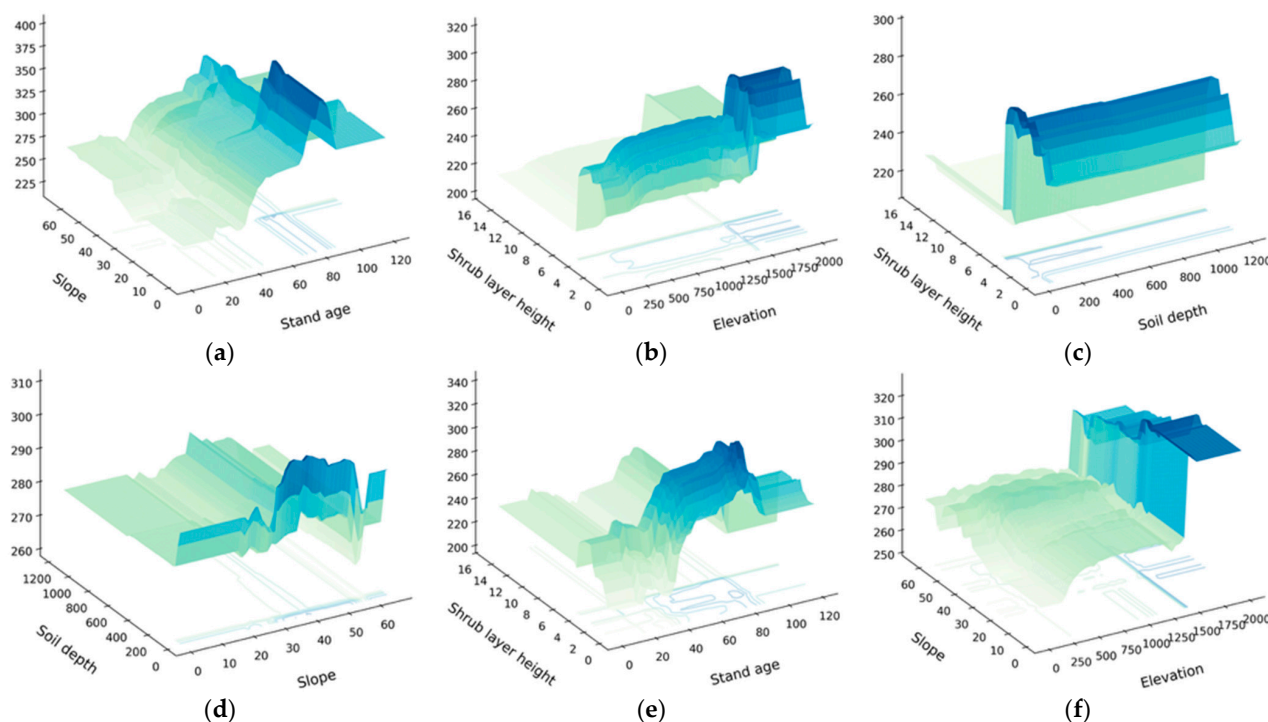


Figure 8. Factor interaction dependence diagram. (a) Slope–stand age; (b) Shrub layer height–elevation; (c) Shrub layer height–soil depth; (d) Soil depth–slope; (e) Shrub layer height–stand age; (f) Slope–elevation.

5. Discussion

5.1. Carbon Storage Estimation and Spatial Distribution

First, the estimated forest aboveground live biomass carbon storage in the study area was 3,754,409.73 t C. This value was higher than the 2020 aboveground carbon storage predicted by Chen et al. [18] using the InVEST model (2.69×10^6 t C), but lower than the estimate of 4.85×10^6 t C reported by Jin et al. [19], who applied a uniform carbon fraction of 0.50 to all tree species. Because all three studies mainly quantified forest aboveground biomass carbon storage, their results are broadly comparable. The differences among estimates may largely reflect differences in methods and parameter settings. The InVEST model is based on a static correspondence between land-use types and carbon density. It may therefore have limited ability to reflect the dynamic effects of land-use change and forest growth on carbon storage. In addition, the use of uniform carbon-density parameters may not adequately capture regional ecological differences, potentially leading to the underestimation of carbon storage [39,40]. Jin et al. [19] used the same biomass regression equations as those applied in this study but converted biomass to carbon using a uniform carbon fraction of 0.50. This approach did not account for interspecific variation in carbon fractions. The biomass equations developed by Fang, Liu, Zheng, and colleagues [25–27] indicate that the carbon fractions of *Quercus* spp., *P. hwangshanensis*, other hard broadleaved species, and other soft broadleaved species were all below 0.50. Together, these species accounted for 58.10% of the total forest biomass in the study area. Applying a uniform carbon fraction of 0.50 may therefore overestimate regional forest carbon storage.

In addition, *P. edulis* carbon storage was estimated using the general biomass equation, with a carbon fraction of 0.50. This may introduce some estimation error. However, *P. edulis* accounted for only 6.72% of the total forest biomass, and its measured carbon fraction

ranges from 46.3% to 52.1%. Sensitivity analysis showed that varying the carbon fraction by $\pm 2\%$ changed the total regional carbon storage by less than 0.27%. This indicates that the uncertainty associated with this parameter assumption has only a limited effect on the estimated regional carbon storage and its spatial pattern.

Second, the aboveground live biomass carbon density in this study was $44.83 \text{ t C} \cdot \text{hm}^{-2}$. This value was lower than those reported for the Great Smoky Mountains National Park and Shenandoah National Park in the southern Appalachian Mountains of the United States, both of which are protected humid montane forest areas. However, it was higher than the values reported for most forest areas of Bai Tu Long National Park in Vietnam, which is also located in the Asian monsoon region [41,42]. Yang et al. reported aboveground live tree carbon densities of 91.1 and $76.4 \text{ t C} \cdot \text{hm}^{-2}$ in the Great Smoky Mountains and Shenandoah National Parks, respectively, both higher than the value estimated in this study. In the Great Smoky Mountains National Park, *Quercus–Carya* forests and *Picea–Abies* forests had carbon densities of 97.3 and $135.5 \text{ t C} \cdot \text{hm}^{-2}$, respectively. The presence of these high-carbon-density forest types may have contributed to the higher regional average. In contrast, bamboo forests and shrublands in Wuyi Mountain National Park had relatively low carbon densities and may have lowered the overall forest carbon density. These differences may therefore be partly related to the relative proportions of forest types with different carbon densities. Aboveground biomass carbon density in Bai Tu Long National Park ranged from 11.90 to $51.87 \text{ t C} \cdot \text{hm}^{-2}$, with most areas ranging from 20 to $40 \text{ t C} \cdot \text{hm}^{-2}$, lower than the value in this study. Low values there were mainly distributed on limestone islands with shallow soils and limited water-holding capacity. In comparison, Wuyi Mountain has a warm and humid climate with abundant precipitation and relatively favorable soil moisture conditions, which may be more conducive to tree growth and biomass accumulation.

In addition, high-carbon-storage core areas were mainly located within the National Nature Reserve and were dominated by near-mature and mature forests, consistent with the findings of Jin et al. [19] for mature vegetation in the Wuyi Mountain region. Low-carbon-storage areas were mainly distributed in the Scenic Area, the Upper Reaches of the Jiuqu Stream Protection Area, and newly incorporated areas. Their relatively low carbon storage was associated with low-lying terrain and human disturbance, in agreement with previous findings on the ecological pressure of forest tourism [43] and the weakening of carbon-density clustering under lower elevation and greater human disturbance [44]. Carbon storage in the Upper Reaches of the Jiuqu Stream Protection Area has gradually increased following ecological restoration and management, consistent with the view that targeted forest restoration can enhance carbon sequestration capacity [45]. Overall, forest carbon storage exhibited a spatial gradient from the core area to the transition and peripheral areas. Aboveground live biomass carbon is a relatively dynamic carbon pool that responds sensitively to forest growth and management disturbance. Its spatial variation therefore reflects differences in vegetation carbon accumulation under contrasting protection and management conditions and may partly indicate the positive role of conservation and ecological restoration in forest carbon sequestration.

5.2. Key Driving Factors of Carbon Storage

The results identified stand volume, stand age, elevation, slope, soil depth, and shrub layer height as the main influencing factors of forest carbon storage in Wuyi Mountain National Park, reflecting the combined roles of stand structure, topographic conditions, and soil properties. Stand volume was significantly positively associated with carbon storage, indicating that biomass accumulation is fundamental to forest carbon storage. The relationship between stand age and carbon storage varied among age classes: carbon

storage increased rapidly in young and middle-aged forests but slowed or even declined in mature and over-mature forests. A similar pattern has been reported along a chronosequence of Moroccan cork oak forests, where carbon storage accumulated at earlier stages but increased more slowly in older stands [46]. The relationship between shrub layer height and carbon storage exhibited pronounced spatial heterogeneity. Interaction analysis further showed that this relationship varied with topographic and soil conditions, consistent with Chen et al. [47]. Slope showed contrasting relationships with carbon storage. Moderate slopes may be associated with more favorable light and drainage conditions, whereas steep slopes may constrain vegetation establishment and productivity, consistent with previous findings [40,48]. The relationship between elevation and carbon storage varied along a northeast–southwest gradient. This pattern may reflect not only elevation itself, but also associated differences in light, temperature, and water availability [49]. Soil depth also showed a nonlinear relationship with carbon storage. Moderate soil depth may favor nutrient supply and root development, whereas greater soil depth may be associated with reduced soil aeration and lower carbon accumulation [50]. A study of Himalayan forests in India likewise reported complex direct and indirect relationships among forest carbon storage, topography, vegetation characteristics, and soil conditions, consistent with the interactions among stand structure, topographic conditions, and soil properties observed in this study [51].

Beyond stand structure, topographic conditions, and soil properties, previous studies have identified climate variables such as temperature and precipitation as important influences on forest carbon cycling and storage [52]. At regional and larger scales, climatic gradients often dominate spatial variation in forest productivity and carbon sink capacity. However, ecological processes are scale dependent, and the relative importance of influencing factors may shift in small mountainous systems [53]. Climate variables were therefore not included separately in the model for two reasons. First, climate data at the forest subcompartment scale are difficult to obtain, whereas coarser climate data may introduce spatial-scale mismatches and weaken the representation of local variation. Second, in mountainous ecosystems, elevation is closely related to temperature and precipitation and can partly represent local climatic gradients.

Previous studies have shown that climatic constraints on tree growth vary with elevation. Tree growth at high elevations is more strongly limited by low temperatures, whereas warming-induced increases in evaporative demand may intensify drought stress at low elevations [54]. This suggests that under current climatic conditions, elevation can partly integrate differences in hydrothermal conditions affecting forest growth and biomass accumulation. Future climate change, however, may alter growth constraints and forest distributions across elevation zones. Based on 24 major mountain systems worldwide from 1990 to 2020, Zhang and An [55] found that natural treelines generally shifted upslope in temperate regions during rapid warming, whereas those in tropical and subtropical regions tended to shift downslope. Elevation therefore remains an important indicator of spatial variation in forest carbon storage under current climatic conditions, although the strength and spatial pattern of its relationship with carbon storage may change under future climate change. Climate factors may also affect carbon storage while being correlated with topographic variables such as elevation. Their omission from the model may therefore cause some climatic effects to be reflected in related variables and influence the estimated effects of those variables. Nevertheless, both OLS and GWR showed high explanatory power, and residual spatial autocorrelation was substantially reduced in GWR, suggesting that the major spatial structure was reasonably well-captured. Future studies should incorporate high-resolution or downscaled climate data to examine the factors associated with forest carbon storage in greater detail.

5.3. Spatial Model Fit and Limitations

GWR showed better overall fit than OLS and significantly reduced residual spatial autocorrelation, indicating a stronger ability to characterize spatial nonstationarity in the relationships associated with forest carbon storage. However, this improvement was not uniform across the study area. Some forest subcompartments showed no clear local fitting advantage, highlighting the limitations of GWR in representing complex spatial processes.

These local differences in model fit may arise from two factors. First, GWR captures spatial nonstationarity through spatially varying coefficients but has limited ability to directly represent nonlinear responses and multifactor interactions. Linear relationships may therefore fail to fully reflect ecological processes in some areas [56]. Random forest and interaction dependence analysis provided complementary information on variable importance and factor interactions, but these analyses were independent of the GWR estimation and therefore could not directly improve its local fit. Second, spatial variation in forest carbon storage may also be influenced by climatic conditions and other local environmental factors not included in the model. GWR has limited ability to account for such unobserved spatial processes, which may also constrain local model fit in some areas.

6. Conclusions

Based on the 2018 forest subcompartment data of Wuyi Mountain National Park, this study estimated aboveground live biomass carbon storage and its economic value using biomass regression equations and the carbon emission trading market price method. Random forest regression was used to identify key variables, and OLS and GWR models were compared in terms of predictive performance. The spatial heterogeneity of the main influencing factors was then examined. The main conclusions are as follows. (1) The total forest biomass in Wuyi Mountain National Park was 7,465,142.98 t, with a carbon storage of 3,754,409.73 t C and a carbon density of 44.83 t C·hm⁻². The economic value of carbon storage was estimated at 202 million RMB. Mature forests had the highest carbon storage and economic value, young and middle-aged forests showed lower values, and over-mature forests exhibited a slight decline. (2) The spatial distribution of forest carbon storage followed a “core–transition zone–periphery” pattern. High-value areas were mainly located in protected zones with moderate terrain and a mature stand structure, while low-value areas were mainly concentrated in the scenic areas subject to frequent human activities. (3) The GWR model outperformed the OLS model in explaining spatial differentiation, with significantly improved model fitting accuracy and substantially reduced spatial autocorrelation in the residuals. (4) Forest carbon storage is co-regulated by multiple interacting factors, including stand volume, stand age, shrub layer height, soil depth, slope, and elevation, and each influencing factor exhibits significant spatial heterogeneity.

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