Application of a geographically-weighted regression analysis to estimate net primary production of Chinese forest ecosystems

Quan Wang\textsuperscript{1*}, Jian Ni\textsuperscript{2,3} and John Tenhunen\textsuperscript{1}

\textbf{ABSTRACT}

\textbf{Aim} The objective of this paper is to obtain a net primary production (NPP) regression model based on the geographically weighted regression (GWR) method, which includes spatial non-stationarity in the parameters estimated for forest ecosystems in China.

\textbf{Location} We used data across China.

\textbf{Methods} We examine the relationships between NPP of Chinese forest ecosystems and environmental variables, specifically altitude, temperature, precipitation and time-integrated normalized difference vegetation index (TINDVI) based on the ordinary least squares (OLS) regression, the \textit{spatial lag} model and GWR methods.

\textbf{Results} The GWR method made significantly better predictions of NPP in simulations than did OLS, as indicated both by corrected Akaike Information Criterion ($AIC_c$) and $R^2$. GWR provided a value of 4891 for $AIC_c$ and 0.66 for $R^2$, compared with 5036 and 0.58, respectively, by OLS. GWR has the potential to reveal local patterns in the spatial distribution of a parameter, which would be ignored by the OLS approach. Furthermore, OLS may provide a false general relationship between spatially non-stationary variables. Spatial autocorrelation violates a basic assumption of the OLS method. The \textit{spatial lag} model with the consideration of spatial autocorrelation had improved performance in the NPP simulation as compared with OLS (5001 for $AIC_c$ and 0.60 for $R^2$), but it was still not as good as that via the GWR method. Moreover, statistically significant positive spatial autocorrelation remained in the NPP residuals with the \textit{spatial lag} model at small spatial scales, while no positive spatial autocorrelation across spatial scales can be found in the GWR residuals.

\textbf{Conclusions} We conclude that the regression analysis for Chinese forest NPP with respect to environmental factors and based alternatively on OLS, the \textit{spatial lag} model, and GWR methods indicated that there was a significant improvement in model performance of GWR over OLS and the \textit{spatial lag} model.

\textbf{Keywords}
China, forests, GWR, NDVI, NPP, OLS, regression, spatial autocorrelation.

\textbf{INTRODUCTION}

Net primary production (NPP) is an important component of the carbon cycle and a key indicator of ecosystem performance (Lobell \textit{et al}., 2002). It represents the amount of carbon that is retained by plants after assimilation through photosynthesis and autotrophic respiration (Clark \textit{et al}., 2001). Forest ecosystems are important as major terrestrial carbon reservoirs in the global carbon cycle (Dixon \textit{et al}., 1994), for their commercial value, for their importance in maintaining regional biodiversity, and for maintenance of hydrological integrity of catchments. Thus, quantification of forest NPP in a spatial context remains an important challenge at landscape, regional and continental scales.

Several models have been proposed to predict spatial variation in NPP. As early as the 1960–70s, the International Biological Program (IBP) launched plot-based forest studies of biomass and NPP, which recently have been used to extrapolate to regional and national levels (e.g. Clark \textit{et al}., 2001; Jenkins \textit{et al}., 2001; Ni,
As a result, there has been significant progress in the development of regional- and global-scale models as well as estimates of forest biomass and NPP for large areas (e.g. Raich et al., 1991; Melillo et al., 1993; Woodward et al., 1995; Cramer et al., 1999, 2001). Establishment of the Global Primary Production Data Initiative of the Data and Information System, International Geosphere–Biosphere Programme (IGBP-DIS GPPDI) will help to further improve models and data bases used over a variety of spatial scales (Zheng et al., 2003).

Despite proposed advantages of process-based models for extrapolation in the context of changing climate inputs, they are inherently difficult to apply in carbon balance simulations at large scales due to the large information input required and difficulties confronted in their parameterization. Thus, empirical approaches are still used to derive important relationships in large-scale NPP simulations. The approaches typically relate vegetation attributes, including NPP to climate variables, such as temperature, precipitation, and evaporation (Holdrige, 1967; Lieth, 1975; Uchijima, 1985; Neilson & Marks, 1994). More recently, empirical relationships between NPP and remotely-sensed data have been widely investigated (e.g. Jiang et al., 1999; Zheng et al., 2003). Such data-based approaches have provided valuable insight into short-term vegetation dynamics, including changes in NPP and gross primary production (GPP), especially together with the use of remote sensing data (e.g. Tucker et al., 1981; Tucker & Sellers, 1986; Fung et al., 1987).

Regression techniques are empirical approaches that have been commonly applied in NPP simulations. The regression model parameters derived, such as from the ordinary least squares (OLS) method, are assumed to apply globally over the entire region from which measured data have been taken, based on the assumption of spatial stationarity in the relationship between the variables under study (Foody, 2003). However, in most cases, this assumption is invalid (e.g. Grist et al., 1997; Li et al., 2002; Foody, 2003; Zhang et al., 2004). This failure to account for spatial autocorrelation prevents an in-depth interpretation of almost all geographical analyses in ecology to date (Jetz et al., 2004).

Alternatively, one must account for spatial autocorrelation in the regression model (Fotheringham et al., 2002). Spatial auto-regressive models typically have an additional parameter as compared to the OLS method, as found for example in the spatial lag model (Anselin, 2002). Geographically weighted regression (GWR), a recent refinement to normal regression methods, explicitly deals with the spatial non-stationarity of empirical relationships (Fotheringham et al., 2002). The technique provides a weighting of information that is locally associated, and allows regression model parameters to vary in space. This can help reveal spatial variations in the empirical relationships between variables that would otherwise be ignored in the overall analysis.

The aim of this paper is to derive an NPP regression model, focusing on the spatial non-stationarity of estimated parameters as based on the GWR method. The dependent variable is Chinese forest NPP, derived from plot inventory data covering the entire country (Luo, 1996; Ni et al., 2001; Ni, 2003). The NPP database contains nearly all forest types found in the northern hemisphere, from boreal needle-leaved and broadleaved forests, through temperate deciduous broadleaved forest and warm-temperate (subtropical) evergreen broadleaved forest, to tropical rainforest (cf. Ni, 2003). The independent variables include temperature, precipitation, altitude, and yearly Time-Integrated Normalized Difference Vegetation Index (TINDVI). Temperature and precipitation are two main climate parameters controlling the carbon cycle and have been used in many models (e.g. Miami model from Lieth, 1972), while NDVI is the most commonly used remote sensing index, which has been regarded as a surrogate measure for primary production (Box et al., 1989).

Although many studies have suggested the positive relationship between NDVI and annual above-ground NPP for different geographical areas and ecosystems (Goward et al., 1985; Box et al., 1989; Burke et al., 1991; Hobbs, 1995; Paruelo et al., 1997), this relationship is not constant across biomes (Box et al., 1989; Paruelo et al., 1997) and is not always strong. It is worthwhile to examine further the relationship between NPP and NDVI, especially in the case of Chinese forest ecosystems, where a large number of plot data have been compiled.

**MATERIALS AND METHODS**

**Data preparation**

**NPP**

The NPP data of 17 Chinese forest types were compiled by Luo (1996) and have been utilized in NPP studies for China by Ni et al. (2001) and Ni (2003). These data were derived primarily from a 5-year national forest inventory conducted between 1989 and 1993 (China Ministry of Forestry, 1994), but also from previous forest inventories (1956–70) and published forest reports and journals up to 1994 (Luo, 1996). The data set includes forest NPP data from 1248 sites in 29 Provinces/Autonomous Regions of China. The variables included are site name, latitude, longitude, altitude, dominant species, stand age, tree height, diameter at breast height (d.b.h), leaf area index (LAI), biomass and NPP estimates for all plant components, i.e. stem, branch, leaf, root and total ecosystem. The LAI, biomass and NPP were estimated by common methods as described by Luo (1996).

**TINDVI**

The normalized difference vegetation index (NDVI), calculated from reflected red and near-infrared radiation, has been related to various vegetation properties, including leaf area index, light absorption capacity, and photosynthetic potential. Most NDVI time series data are currently obtained from satellite data sources, such as AVHRR (Advanced Very High Resolution Radiometer) GAC data source (James & Kalluri, 1994) or 1 km data source (Eidenshink & Faundeen, 1994); SPOT-4 VEGETATION data source (Duchemin et al., 2002); and MODIS data source (van Leeuwen et al., 1999). NDVI used in this study was from AVHRR Land Biosphere data archived by Goddard DAAC (http://daac.gsfc.nasa.gov/CAMPAIGN_DOCS/LAND_BIO/GLBDST_Data.html). This land data set (8 × 8 km resolution) was generated from the Global Area Coverage (GAC) data (4 × 4 km resolution) by the five-channel AVHRR instrument boarded on the NOAA.
satellite 7, 9, 11 and 14. A consistent processing algorithm was used for the entire data processing period (1981–present) and the GAC data have been carefully recalibrated and renavigated. Ten-day composite NDVI time-series with 8 km resolution were downloaded for the entire period that NPP was measured. The compositing method is the maximum value composite MVC (Holben, 1986).

Considerable noise remains in the NDVI time series from satellite-borne data sources, even after the compositing procedure. This is reflected in the sudden increase in NDVI values in temporal profiles, which is obviously due to cloudy conditions or missing data. To obtain reasonably smooth NDVI trends, further procedures must be applied to remove the spurious points. In this study, we applied the weighted least-squares approach from Swets et al. (1999) to smooth the 10-day composite NDVI time-series and remove the remaining noises.

Phenological metrics from the NDVI time series were obtained by methods of Reed et al. (1994). The start and end of the growing season was identified using a backward- or forward-looking, moving-mean technique (Reed et al., 1994). The duration of the growing season was thus estimated from the start and end date. Values of NDVI associated with dormant vegetation or soil were used as a baseline to detect phenological stages. Linear temporal interpolation was used to estimate the daily smoothed NDVI, while the TINDVI was calculated from the daily smoothed NDVI for the entire growing season.

Many studies have reported a high correlation between TIN-DVI and NPP for grassland and shrub biomes (e.g. Paruelo et al., 1997; Yang et al., 1998; Wylie et al., 2003), but few studies have reported results for forest ecosystems. This is primarily because NDVI may be decoupled from carbon assimilation for certain forest types, e.g. evergreen forests, and thus, the correlation is expected to be lower. However, estimates of the relationship between NDVI and NPP have been reported for Chinese forest ecosystems (Cheng & Zhao, 1990; Jiang et al., 1999) and such data have been included into IGBP-DIS GPPDI dataset (Zheng et al., 2003). Thus, we conclude that further study of these potentials is justified and necessary.

T, P

Two main climate parameters, temperature and precipitation, were obtained from the CRU TS 2.0 global climate database (Mitchell et al., 2003, unpublished data). This dataset comprises 1200 monthly grids of observed climate, for the period 1901–2000, and covering the global land surface at 0.5 degree resolution. Yearly mean temperature and annual total precipitation were calculated for the period from 1989 to 1993, corresponding to period of NPP measurements.

Regression models

Since OLS method has been well documented, we describe here only the theoretical background for the GWR method and the spatial lag model.

Theoretical background for the GWR method

Geographically weighted regression is a technique that expands standard regression for use with spatial data. The underlying assumption of the global regression method is that the relationship under study is spatially constant, and thus, the estimated parameters remain constant over space. However, in most cases, the relationship varies in space. A technique like GWR assesses local influences, allowing for a spatial shift in parameters and a more appropriate fit. Although the technique does not allow extrapolation beyond the region in which the model was established, it does allow the parameters to vary locally within the study area and may provide a more appropriate and accurate basis for descriptive and predictive purposes (Foody, 2003). A detailed description of GWR is given by Fotheringham et al. (2002). Here we provide only a simple illustration.

A global regression model can be presented as:

$$y = \beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p + \varepsilon$$

where $y$ is the dependent variable, $x_1$ to $x_p$ are independent variables, $\beta_0$ is the intercept, $\beta_1$ to $\beta_p$ are estimated coefficients, and $\varepsilon$ is the error term.

GWR allows local rather than global parameters to be estimated and the above model is rewritten as:

$$y = \tilde{\beta}(\mu, \nu) + \beta_1(\mu, \nu)x_1 + \ldots + \beta_p(\mu, \nu)x_p + \varepsilon$$

where $(\mu, \nu)$ denotes the coordinates of the samples in space.

In geographically weighted regression, the parameter estimates are made using an approach in which the contribution of a sample to the analysis is weighted based on its spatial proximity to the specific location under consideration. Thus the weighting of an observation is no longer constant in the calibration but varies with different locations. Data from observations close to the location under consideration are weighted more than data from observations far away. The parameters are estimated from:

$$\tilde{\beta}(\mu, \nu) = (X^TW(\mu, \nu)X)^{-1}X^TW(\mu, \nu)y$$

where $\tilde{\beta}(\mu, \nu)$ represents an estimate of $\beta$, $W(\mu, \nu)$ is the weighting matrix, which acts to ensure that observations near to the location at which the parameter estimates are to be made have more influence on the analysis than those far away. $X$ is a matrix of independent variables.

Several methods have been proposed to determine the weighting matrix (Fotheringham et al., 2002). For fixed kernel size with a Gaussian function, $W_j$ (the weight of the specific point $j$ in the space at which data are observed to any point $i$ in the space from which parameters are estimated) can be represented as a continuous function of $d_{ij}$, the distance between $i$ and $j$:

$$W_i = \exp \left[ -\frac{(d_{ij}/b)^2}{2} \right]$$

where $b$ is referred to as the bandwidth.

An alternative kernel that utilizes the bi-square function can have $W_i$ as:

$$W_i = \begin{cases} 1 - (d_{ij}/b)^2 & d_{ij} < b \\ 0 & \text{otherwise} \end{cases}$$
Fixed kernels in regions where data are dense may suffer from bias when the kernels are larger than needed. When the kernels are smaller than needed, they may not estimate the parameters reliably where data are scarce (Fotheringham et al., 2002), thus spatially varying kernels have also been proposed.

Parameter estimation in GWR is highly dependent on the weighting function of the bandwidth of the kernel used. As the bandwidth increases, the parameter estimates will tend to the estimate from a global model. The selection of the weighting function and bandwidth can be determined using a cross-validation (CV) approach (cf. Fotheringham et al., 2002) or the generalized cross-validation criterion (GCV) of Loader (1999); or Akaike Information Criterion (AIC) from Hurvich et al. (1998).

Criteria related to model performance

Different from the normal approaches such as stepwise regression, we applied corrected Akaike Information Criterion (AICc) for variable and model selection (Akaike, 1973; Fotheringham et al., 2002). AICc is defined according to Fotheringham et al. (2002):

\[
\text{AIC}_c = 2n \log(y) + n \log(2\pi) + n \left(\frac{n + \text{tr}(S)}{n - 2 - \text{tr}(S)}\right) + \frac{2k}{n} \tag{6}
\]

where \( n \) is the sample size, \( \hat{\sigma} \) is the estimated standard deviation of the error term, and \( \text{tr}(S) \) denotes the trace of the hat matrix \( S \). The \( c \) subscript denotes that this is ‘corrected’ AIC estimate (Fotheringham et al., 2002).

As a general rule, the lower the AIC\(_c\), the closer the approximation of the model to reality. Thus the best model is the one with the smallest AIC\(_c\). However, as a rule of thumb, a ‘serious’ difference between two models is generally regarded as one in which the difference in AIC\(_c\) values between the models is at least 3 (Fotheringham et al., 2002). Moreover, the different degrees of freedom in the GWR and OLS models may affect the assessment of the fit of data between models in two different groups, if it solely depends on AIC\(_c\).

An approximate likelihood ratio test, based on the F-test, can be used to compare the relative performance of the GWR and OLS models to replicate the observed data (Fotheringham et al., 2002). This test is based on the result that the distribution of residual sum of squares of the GWR model divided by the effective number of parameters may be reasonably approximated by a \( \chi^2 \) distribution with effective degrees of freedom equal to the effective number of parameters. Thus

\[
F = \frac{\text{RSS}_d/\hat{d}_b}{\text{RSS}_d/\hat{d}_t} \tag{7}
\]

where \( \text{RSS}_d \) and \( \text{RSS}_b \) are the residual sum of squares of the GWR model and OLS model, respectively, while \( \hat{d}_t \) and \( \hat{d}_b \) are the degree of freedoms for the GWR and OLS model, respectively.

Model candidates

Various models have been designed based on the different combination of the variables both for GWR and OLS methods in order to select the best one. The detail of independent variables information for each model is illustrated in Table 1.

### Spatial lag model

The spatial lag model is one type of spatial autoregressive models in which the spatial interaction is incorporated on the right hand side of the regression model (Anselin, 2002). Within the spatial lag model, Eq 1 is illustrated as

\[
y = \rho W y + X \beta + \epsilon \tag{8}
\]

where \( y \) is the same as in Eq 1, representing an \( n \times 1 \) vector of observations, \( W \) is an \( n \times n \) spatial weights matrix, \( \rho \) is the spatial autoregressive parameter, \( X \) is an \( n \times k \) matrix of observations on the exogenous variables, with an associated \( k \times 1 \) regression coefficient vector \( \beta \), and \( \epsilon \) is the random error terms.

Compared with Eq 1, a spatial reaction function \( \rho W y \) has been included in Eq 8. Eq 8 can be further rearranged as

\[
y = (1 - \rho W)^{-1} X \beta + (1 - \rho W)^{-1} \epsilon \tag{9}
\]

### Spatial autocorrelation

Spatial autocorrelation measures the similarity between samples for a given variable as a function of spatial distance (Legendre, 1993; Diniz-Filho et al., 2003). The Moran’s I coefficient is the most commonly used coefficient in univariate autocorrelation analyses and is given as:

\[
I = \left(\frac{n}{s}\right) \left[ \frac{\sum \sum (y_i - \bar{y})(y_j - \bar{y})w_{ij}}{\sum (y_i - \bar{y})^2} \right] \tag{10}
\]

where \( n \) is the number of samples, \( y_i \) and \( y_j \) are the data values in quadrats \( i \) and \( j \), \( \bar{y} \) is the average of \( y \) and \( w_{ij} \) is an element of the spatial weights matrix \( W \). Under the null hypothesis of no spatial autocorrelation, \( I \) has an expected value near zero for large \( n \), with positive and negative values indicating positive and negative autocorrelation, respectively.

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Table 1: The independent variables of each model candidates designed for both GWR and OLS methods

<table>
<thead>
<tr>
<th>Models</th>
<th>Independent variables</th>
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<tbody>
<tr>
<td>Model 1</td>
<td>Altitude, Temperature, Precipitation, and TINDVI</td>
</tr>
<tr>
<td>Model 2</td>
<td>Altitude, Temperature, and Precipitation</td>
</tr>
<tr>
<td>Model 3</td>
<td>Altitude, Temperature, and TINDVI</td>
</tr>
<tr>
<td>Model 4</td>
<td>Altitude, Precipitation, and TINDVI</td>
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<tr>
<td>Model 5</td>
<td>Altitude, Temperature, and TINDVI</td>
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<tr>
<td>Model 6</td>
<td>Temperature, and Precipitation</td>
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<tr>
<td>Model 7</td>
<td>Precipitation, and TINDVI</td>
</tr>
<tr>
<td>Model 8</td>
<td>Temperature, and TINDVI</td>
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<td>Model 9</td>
<td>Altitude</td>
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<td>Model 10</td>
<td>Temperature</td>
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<td>Model 11</td>
<td>Precipitation</td>
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<tr>
<td>Model 12</td>
<td>TINDVI</td>
</tr>
</tbody>
</table>
RESULTS

Conventional OLS, GWR methods, and the spatial lag model have been adapted to analyse NPP in relation to environmental variables. Correlation analysis of NPP with altitude, temperature, precipitation and TINDVI revealed that NPP had significant correlation (P < 0.01) with all the above variables, with the highest correlation coefficient of 0.74 with precipitation, followed by 0.65 with temperature, −0.37 with altitude and −0.29 with TINDVI. However, this does not mean that all the variables should be included in the regression analysis since some variables may strongly correlate with each other and provide no further explanation of final variation.

OLS

Table 2 shows the AICc and $R^2$ for each model using the OLS method. The dependent variable was NPP, while independent variables were individually listed in Table 1. The best model determined from AICc and $R^2$ was Model 1, which had AICc = 5036 and $R^2 = 0.58$. The model was thus expressed as:

$$NPP = 6.1387 - 0.0009*ALT + 0.0998*T + 0.0075*P - 0.0087*TINDVI \quad (R^2 = 0.58) \quad (11)$$

where ALT, T, P and TINDVI refer to altitude, temperature, precipitation and time-integrated Normalized Difference Vegetation Index, respectively.

The scatter diagram between measured NPP and predicted NPP based on Eq 11 is shown in Fig. 1. Eq 11 obviously underestimates when NPP is high and overestimates when NPP is low. The standard deviation of NPP residuals was 3.54 t ha$^{-1}$ or 30.1% of mean NPP value. The large deviation was found in the southern part of China (< 35°N), where NPP was also large, and decreased toward the north.

Spatial autocorrelation of NPP and environmental factors (altitude, temperature, precipitation and TINDVI) are evident from Fig. 2. All the spatial correlograms in Fig. 2 show positive autocorrelation over short distances and negative autocorrelation at large distances. This type of correlogram profile can be interpreted as a linear gradient at macro scales (Diniz-Filho et al., 2003). The significance tests of Moran’s $I$ was calculated following Legendre & Legendre (1998) using a Bonferroni correction. The spatial correlogram for NPP indicates that NPP is positively autocorrelated up to c. 3600 km. For the environmental variables, positive spatial autocorrelation is up to c. 4800 km for altitude and TINDVI, while up to c. 3600 km for temperature and precipitation.

GWR

The GWR method has also been applied for each model mentioned above. For each model, GWR analysis was undertaken using an adaptively defined kernel with a bi-square function in which the bandwidth was determined by minimization of the AICc (Fotheringham et al., 2002). Also, the spatial non-stationarity of the model parameters was tested using Monte Carlo significance testing approach (Fotheringham et al., 2002). Several models produced similar results, as shown in Table 2. Model 1, Model 2, and Model 6 all have AICc around 4893 with an $R^2$ of 0.66. Nevertheless, Model 1 was determined as the best model for this category, with the lowest AICc of 4891 and
Moreover, Model 1 has the least effective degrees of freedom among all GWR models. The improvement of model performance was evident from OLS to GWR, both from the values of AICc and $R^2$ and from the F-test. Figure 3 shows the scatter diagram between measured NPP and predicted NPP using the GWR (Model 1). Remarkable improvement for low NPP simulation can be noted, if we compare Fig. 3 with Fig. 1, although both methods underestimated NPP in the high range. The standard deviation of NPP residuals of the GWR method was $3.21 \text{ t ha}^{-1}$ or $27.3\%$ of mean NPP. The F-test result (Table 2, Model 1, $P < 0.005$) suggests that the GWR model significantly improved model fitting over the OLS model.

Table 3 clearly indicates that all of the interquartile ranges of parameter estimates from GWR were outside the range of ±1 standard deviation of the OLS equivalent parameters estimates. Specifically, for the intercept coefficient $\beta_0$, the interquartile range $-12.5593$ to $8.0914$ of the GWR local parameter estimates was far beyond the scope of $5.3428$ to $6.9346$ of ±1 standard deviation of the OLS parameter estimate. Furthermore, the 95% CI ($4.5767$ to $7.7007$) of the OLS $\beta_0$ was within the median and 75% quartile, indicating that a large portion of the local $\beta_0$ values were smaller than the OLS $\beta_0$ value. Similarly, the interquartile ranges of $\beta_1$ ($-0.0015$ to $0.0075$), $\beta_2$ ($0.0606$ to $0.9816$), $\beta_3$ ($-0.0003$ to $0.0063$), $\beta_4$ ($0.0035$ to $0.0337$) of the GWR local estimates for parameters were far outside of the corresponding ±1 standard deviation of the OLS estimates for parameters. The 95% CIs ($-0.0012$ to $-0.0007$ for $\beta_0$ and $0.0325$ to $0.1671$ for $\beta_3$) of the OLS $\beta_0$ and $\beta_3$ were approximately within the 25% quartile and the median, showing a large portion of local estimates for both parameters were higher than OLS values. On the other hand, the 95% CI ($-0.0018$ to $0.0014$) of the OLS $\beta_3$ was within the 75% quartile and the maximum, indicating that a large portion of the local $\beta_3$ values were smaller than the OLS $\beta_3$ value. By contrast, the 95% CI ($-0.0188$ to $0.0014$) of the OLS $\beta_3$ was within the minimum and 25% quartile, indicating that a large portion of the local $\beta_3$ values were higher than the OLS $\beta_3$ value.

The above result suggested that the relationships between NPP and variables were spatially non-stationary. This has also been

Figure 2 Spatial correlograms for NPP, altitude, temperature, precipitation, and TINDVI. Closed circles indicate Moran’s I values are significantly larger than the value expected under the null hypothesis of no positive autocorrelation ($P < 0.05$ after Bonferroni correction). Open circles represent no significant positive autocorrelation.

Figure 3 Scatter diagram between measured NPP and GWR simulated NPP.

$R^2 = 0.66$. Moreover, Model 1 has the least effective degrees of freedom among all GWR models.
Panel f indicates the spatial distribution of NPP residuals using the GWR method. Basically, positive and negative NPP residuals were mixed together and no obvious spatial pattern can be determined.

Statistical results for the intercept and each parameter based on climate zone are illustrated in Fig. 5. The classification of climate zone here is simply from the latitude ranges as in Ni (2003). The boreal zone (> 45°N) includes Larix forest, boreal and subalpine Abies-Picea forest, boreal Pinus sylvestris var. mongolica forest, cold-temperate mixed coniferous broadleaved deciduous forest, and montane Populus-Betula forest. The temperate zone (33–45°N) includes typical temperate deciduous broadleaved forest, temperate coniferous forest (Pinus tabulaeformis), montane Populus-Betula forest, and temperate Tugai forest. The tropical zone (23–33°N) includes typical subtropical evergreen broadleaved forest, subtropical mixed evergreen–deciduous broadleaved forest, subtropical sclerophyllous evergreen broadleaved forest, subtropical subalpine Abies-Picea forest, subtropical coniferous forest. The tropical zone (< 23°N) includes tropical rain forest and monsoon forest.

Except in the temperate zone, the intercept had positive mean values. The largest standard deviation was found in the temperate zone also. The parameter for altitude had a positive mean value in boreal and temperate zones. This contradicts the OLS result which indicates a negative relationship between NPP and altitude. The parameter for temperature had positive mean values for all climate zones except the tropical zone. This is consistent with the OLS result. The boreal zone had the lowest slope with temperature, but also the least variation. While the parameter reached highest values in the temperate zone, it also had the largest standard deviation. This suggests that the NPP in the temperate zone is very sensitive to temperature. The negative relationship found in the tropical zone indicates that the temperature in this zone was outside of the optimum range for NPP since vegetations must provide more energy to support respiration at high temperatures.

The parameter for TINDVI exhibited a decreasing trend from the boreal zone to the tropical zone. Compared with the negative value in Eq 11 from OLS, both boreal and temperate zone NPP showed positive relationships with TINDVI. The relationship

\begin{table}
\centering
\begin{tabular}{lccccc}
\hline
Methods & Statistics & $\hat{\beta}_0$ & $\hat{\beta}_1$ & $\hat{\beta}_2$ & $\hat{\beta}_3$ & $\hat{\beta}_4$ \\
\hline
OLS & Estimate & 6.1387 & −0.0009 & 0.9998 & 0.0075 & −0.0087 \\
 & Standard error & 0.7959 & 0.0001 & 0.0343 & 0.0004 & 0.0051 \\
 & Lower limit of 95% CI & 4.5767 & −0.0012 & 0.0325 & 0.0067 & −0.0188 \\
 & Upper limit of 95% CI & 7.7007 & −0.0007 & 0.1671 & 0.0083 & 0.0014 \\
 & $b - 1$ SD & 5.3428 & −0.0011 & 0.0655 & 0.0071 & −0.0139 \\
 & $b + 1$ SD & 6.9346 & −0.0008 & 0.1341 & 0.0079 & −0.0036 \\
GWR & Mean & −0.5225 & 0.0021 & 0.5160 & 0.0020 & 0.0143 \\
 & Minimum & −19.2328 & −0.0052 & −0.8503 & −0.152 & −0.0640 \\
 & 25% quartile & −12.5593 & −0.0015 & 0.0606 & −0.0004 & 0.0035 \\
 & Median & 3.4685 & 0.0004 & 0.4752 & 0.0023 & 0.0235 \\
 & 75% quartile & 8.0914 & 0.0075 & 0.9816 & 0.0063 & 0.0337 \\
 & Maximum & 20.4342 & 0.0142 & 1.8626 & 0.0114 & 0.0692 \\
\hline
\end{tabular}
\caption{Descriptive statistics of the parameter estimates for the Model 1 both by OLS and GWR methods}
\end{table}
Spatial lag model

The application of the spatial lag model is based on the best model determined through the OLS (Model 1). The spatial weights matrix was generated following Anselin (2002). After having tested for various distance classes, we decided on a lag distance of 600 km with the lowest AICc. Table 4 lists the regression results. Compared with OLS Model 1 output (Table 2), the spatial lag model had a lower AICc (5001) and a slightly higher $R^2$ (0.60). The standard error was 3.46 t ha$^{-1}$ or 29.4% of the mean NPP value. Although the spatial lag model performed better than that of the OLS Model 1, it was inferior to the Model 1 using the GWR method, both from the standpoint of AICc and also $R^2$.

Ecological interpretations of GWR estimates

Spatially non-stationary relationships between NPP and parameters (altitude, temperature, precipitation, and TINDVI) were clearly shown in the above results. It is important for us to attempt to interpret the spatially non-stationary relationships in the context of ecological principles. In order to avoid compensating effects from other independent variables, we have applied both OLS and GWR analysis on NPP only with each single parameter (Model 9–12).
NPP in Chinese Forests

NPP and altitude, temperature and precipitation

NPP normally shows a decreasing trend along altitudinal gradients due to the decrease of temperature and the change in other environmental factors. However, this is rather hard to predict because of the diverse combinations of environmental factors along the altitude gradient, e.g. precipitation may increase with altitude only to a certain level. Consequently, the relationship between NPP and altitude is locally and spatially non-stationary.

The statistical analysis of the parameter from Model 9 for altitude in each climate zone had the following result: 0.0018 (± 0.0023) for the boreal zone, 0.0023 (± 0.0031) for the temperate zone, -0.0007 (± 0.0024) for the subtropical zone, and 0.0022 (± 0.0029) for the tropical zone. The explanation for this could be the difference

Table 4 Parameter estimates for NPP in the spatial lag model

<table>
<thead>
<tr>
<th>Variables</th>
<th>Spatial Lag model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wy</td>
<td>0.4511****</td>
</tr>
<tr>
<td>Constant</td>
<td>2.5989**</td>
</tr>
<tr>
<td>Altitude</td>
<td>-0.0006****</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.0510</td>
</tr>
<tr>
<td>Precipitation</td>
<td>0.0047****</td>
</tr>
<tr>
<td>TINDVI</td>
<td>-0.0009</td>
</tr>
<tr>
<td>AICc</td>
<td>5001</td>
</tr>
<tr>
<td>R²</td>
<td>0.60</td>
</tr>
</tbody>
</table>
of altitude within each climate zone. For boreal, temperate, and tropical zones, all the samples (plots) were nearly at the same altitude, thus, the effect of altitude on NPP is rather vague. However, the altitude difference could reach 3000 m from the east coast to middle mountainous region in the subtropical zone. Thus, only this region showed a statistically decreasing trend of NPP with altitude.

NPP is determined jointly by two processes, photosynthesis and respiration, which are controlled by temperature. Generally photosynthetic temperature responses are bell-shaped with an optimum temperature. Photosynthesis decreases when below and over this optimum temperature. On the other hand, respiration tends to respond to temperature exponentially. The response of NPP to temperature is therefore determined by the response rate of two processes to temperature. NPP has a positive relationship with respect to temperature, if the increase in photosynthetic rate surpasses the increase of respiration. Only a positive relationship was determined via the OLS method. Although statistically positive relationships were found for most climate zones by the GWR method, the temperate zone had an average slope of $-0.36 \pm 0.59$. The interpretation could be that photosynthesis in this zone is mainly controlled by water supply rather than temperature. The increase of temperature on the one hand raises the respiration rate, and simultaneously may induce a shortage in water supply which in turn depresses photosynthesis.

Precipitation is the main source of water supply to Chinese forest ecosystems. It can be predicated that there is a positive relationship between NPP and precipitation. This has been

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*Figure 4* Continued
shown both in the positive estimate of the parameters from OLS and GWR methods across all climate zones. The statistically negative mean of GWR estimates for precipitation in the temperate zone in Model 1 has been replaced by a positive mean of 0.0151 (± 0.0156) in Model 11, suggesting that compensating effects from other factors may lead to incorrect estimation of the parameter.

**NPP and TINDVI**

TINDVI is a parameter indicating vegetation photosynthetic activity and is closely related with NPP (e.g. Hobbs, 1995; Paruelo et al., 1997). Correlation analysis of NPP and TINDVI in Chinese forest ecosystems revealed that there was not a strong statistically significant relationship. Moreover, this relationship was negative based on OLS analysis, which contradicts most previous studies reporting strong and positive relationships between them (Goward et al., 1985; Box et al., 1989; Burke et al., 1991; Hobbs, 1995; Paruelo et al., 1997).

The scatter diagram of NPP with TINDVI is shown in Fig. 6. Using the OLS method, a negative slope of −0.0577 was determined. However, the coefficient of determination ($R^2$) was only 0.09. Extremely large residuals remained if TINDVI was used as the sole independent variable. Significant improvement of the model performance using the GWR method was found ($F = 27.22, P < 0.001$). As presented in Table 2 (Model 12), the $R^2$ using GWR improved to 0.63 together with AICc from 5775 to 4985. The spatial distribution of the parameter for TINDVI in Model 12 was similar to Panel e in Fig. 4, but with a different range. The estimate of the parameter had a median of 0.0234 ranging from −0.2010 to 0.1261. The southern part of China had negative values, while middle and northern China had positive values. Statistical analysis of the parameter over climate zones provided the following result: 0.0491 (± 0.0066) for the boreal zone, 0.0407 (± 0.0367) for the temperate zone, −0.0173 (± 0.0686) for the subtropical zone, and −0.0022 (± 0.0686) for the tropical zone.
for the subtropical zone, and −0.0602 (± 0.1069) for the tropical zone. This result repeats the above findings that NPP in boreal and temperate zones has a positive relationship with TINDVI, while a negative relationship occurs in subtropical and tropical zones. The main reason for the poor relationship between NPP and NDVI in subtropical and tropical zones is that the NDVI is no longer associated with carbon assimilation in these regions which are dominated by evergreens.

The instability of Chinese forest NPP-TINDVI in the spatial dimension is indicated in the above results. This casts doubt on NPP calculated solely based on the global relationship of NDVI and NPP in Chinese forest ecosystems which was first reported by Cheng & Zhao (1990) and adopted by Jiang et al. (1999) and has been further included into the IGBP-DIS GPPDI dataset (Zheng et al., 2003).

DISCUSSION AND CONCLUSIONS

Autocorrelation is the lack of independence between pairs of observations at a given distance in time or space and is found commonly in ecological data (Legendre, 1993). To consider the spatial autocorrelation in NPP analysis is of ecological significance, for both exogenous (e.g. autocorrelated environment) and endogenous factors (e.g. canopy characteristics) can lead to nearby sites in space tending to have more similar NPP values than would be expected by chance. Spatial autocorrelation is problematic for classical statistical tests like OLS regression for violating the assumption of independently distributed errors (Haining, 1990; Legendre, 1993), and the standard errors are usually underestimated when positive autocorrelation is present and Type I errors may be strongly inflated (Legendre, 1993). The importance of considering spatial autocorrelation in geographical ecology has been addressed by a number of recent papers (e.g. Diniz-Filho et al., 2003; Legendre et al., 2002; Lichstein et al., 2002). Lennon (2000) called attention to the problems caused by spatial autocorrelation for the possibility of generating widespread ‘red herrings’ in the interpretation of ecological mechanisms besides the well-know inflation of Type I errors; and he argued that virtually all geographical analyses had to be redone by taking into account spatial autocorrelation.

The present paper has investigated the relationship between Chinese forest NPP with environmental factors based on the OLS (no consideration of spatial autocorrelation), the spatial lag model (with one extra parameter accounting for spatial autocorrelation), and the GWR method. Significant improvement in model performance in NPP simulation was found for GWR over OLS. Since there was significant spatial autocorrelation of NPP and environmental factors (altitude, temperature, precipitation and TINDVI), the spatial lag model with consideration of spatial autocorrelation performed better than the OLS approach but still inferior to the GWR method. This result, however, is somehow contradictory to the criticism of Jetz et al. (2004) with respect to the study of Foody (2004) on avian species richness in sub-Saharan Africa (using the GWR approach). Jetz et al. (2004) suggest that it would be more useful to fit global parameters by correcting for spatial autocorrelation than to allow the parameters to vary locally as described with the GWR method. Nevertheless, strong correlations between the local parameters were found in our GWR result. Thus, it may not be possible to exclude the problems mentioned by Jetz et al. (2004) that local variation in the parameters might simply reflect excessive flexibility of GWR. However, the spatially non-stationary relationships of NPP with each single parameter (altitude, temperature, precipitation, and TINDVI) as revealed in the above analysis (Model 9–12) suggest that the effects of these environmental variables do vary locally. We support this interpretation rather than the conjecture of Jetz et al. (2004) that the relationships are global but vary locally due to interaction terms.

It would be useful for us to check the remaining spatial autocorrelation in the NPP residuals to help to clarify the criticism. Figure 7 shows the spatial correlograms for OLS Model 1 residuals, residuals from the spatial lag model, and residuals from GWR Model 1. The OLS Model 1 residuals had significant spatial autocorrelation, and those from the spatial lag model, and residuals from GWR Model 1. The OLS Model 1 residuals had significant spatial autocorrelation up to c. 1200 km. Although there was no significant spatial autocorrelation for residuals from the spatial lag model at large spatial scales, they were strongly autocorrelated at small spatial scales (up to c. 360 km) as indicated in Fig. 7. In comparison, no positive spatial autocorrelation was found for the GWR Model 1 residuals in the context of spatial scale, suggesting the ability of GWR approach to deal with spatial non-stationary problems.

Figure 7 Spatial correlograms for OLS residuals, residuals from the spatial lag model, and GWR residuals. Closed circles indicate Moran’s I values are significantly larger than the value expected under the null hypothesis of no positive autocorrelation ($P < 0.05$ after Bonferroni correction). Open circles represent no significant positive autocorrelation.
It is interesting to see that spatial patterns in the spatial lag model residuals are still remaining even when an autoregressive term has been included in the model, which obviously does not remove the autocorrelation problem nearly as well as GWR. This is opposite to the claim of Jetz et al. (2004) that standard GWR models do not adequately address spatial autocorrelation. Similar results have also been presented by Fotheringham et al. (2002). The main reason, as pointed out by Fotheringham et al. (2002), is that GWR provides a more directly interpretable solution to the problem of spatially autocorrelated error terms in regression models applied to spatial data. In GWR, the spatial non-stationarity of the parameter is modelled directly, rather than allowing the non-stationarity to be reflected through the error terms in the global model. This seems a better solution to the spatial non-stationarity.

The superiority of GWR over other models is mainly due to the consideration of the actual spatial variation of the relationship of NPP with environmental variables. Global statistical methods like OLS sometimes may ignore the location information and even provide a false relationship. For example, the OLS method obtained a negative slope for the relationship between Chinese forest NPP and TINDVI, while the GWR method revealed that there are positive relationships between them in boreal and temperate zones. Although the GWR is a local statistical technique, unlike the global methods that have the potential to be applied in other regions (extrapolation), the adoption of GWR in future regression analyses on spatial non-stationary relationships seems to be necessary, especially when interpolation is more important, such as in a large region like China.

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REFERENCES


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