EXPLORING SPATIAL RELATIONSHIP BETWEEN BUTTERFLY RICHNESS AND ENVIRONMENTAL PREDICTORS AT A LOCAL SCALE IN NORTH-EASTERN TURKEY

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Abstract. Spatial distribution pattern of butterfly species richness were explored using geographically weighted regression (GWR) and ordinary least square (OLS) regression. These models were compared to assess their abilities in modelling butterfly species richness and, further the spatial variation in the relationship between butterfly species richness and environmental predictors was questioned. Data on the occurrence of butterflies from "Die Tagfalter der Türkei unter besonderer Berücksichtigung der angrenzenden Länder" (The Butterflies of Turkey with special attention to the adjacent countries) and three groups of environmental predictors (climatology, topology, and physical features) were incorporated in the analyses after eliminating highly correlated, redundant predictors. Furthermore, Monte Carlo permutation test was applied simultaneously to assess non-stationarity in the relationship between butterfly species richness and environmental predictors. The results indicated that GWR model predicted butterfly species richness better than the OLS model and also, demonstrated spatial non-stationarity in the relationship between butterfly species richness and environmental predictors. In addition, it was found that most of the variation in butterfly species richness was associated with minimum temperature in January, maximum temperature in July, diurnal range, and solar radiation. This result indicated that the distribution of butterfly species richness is mostly governed by climatic environmental predictors, particularly temperature related predictors, indicating that many butterfly species may respond to projected climate changes rapidly.

Keywords: butterfly richness, environmental predictors, geographically weighted regression, nonstationarity, ordinary least squares

Introduction

Understanding ecological requirements and impacts of environmental factors for distribution of species richness are among the key components of nature conservation (Osborne et. al, 2007). However, inventory data are scarce and limited logistics and funding opportunities impede data acquisition in many regions (Faith et al., 2001a, b; Newbold et al., 2009). Therefore, the spatial distribution of most of the species is still unknown in many parts of the world (Purvis and Hector, 2000). All these restrict understanding the relationships between environmental factors and species richness. Fortunately, Geographic Information System (GIS) in conjunction with multivariate statistics offers various techniques to model distribution of species richness (Pereira et al., 1991; Luoto et al., 2002; Elith et al., 2006) and evaluate the impact of environmental factors on this distribution. Thus, these techniques compensate our lack of knowledge on distribution of species richness and their ecological requirements (Scott, 1998). Moreover, such techniques are not only able to predict the distribution of species richness, richness, and determine the influence of environmental predictors on species richness, species richness and determine the influence of environmental predictors on species richness.

but can also indicate where the biodiversity conservation efforts should be concentrated (Myers et al., 2000; Maes et al., 2003). Thus, spatial models have become substantially important tools for biodiversity conservation (Luoto et al., 2002; Lobo and Martín-Piera, 2002), and may have been used to guide decision makers towards the impacts of environmental modifications (Fleishman et al., 2001b). However, most techniques or models, especially global models, have not included spatial effects, i.e. spatial autocorrelation and spatial non-stationarity, in modelling equation (Kupfer and Farris, 2007); whereas ecological relationships being modelled indicate spatial heterogeneity. In other words, they are spatially vary (non-stationarity) and if this variation is not incorporated in models, then biased parameter estimates and incorrect predictions will be obtained (Anselin and Griffith, 1988; Shi et al., 2006). On the other hand, geographically weighted regression (GWR) enables to explore local spatial variation in ecological relationships; hence, it provides to investigate spatial variation in the relationship between species richness and environmental factors. In short, GWR allows detecting impact of environmental factors on distribution of species richness for local scale.

Here, I analysed local GWR and global OLS regression models using environmental predictors for butterfly species richness in the Lesser Caucasus region of north-eastern Turkey. I chose to explore the spatial relationship between butterfly species and environmental predictors for various reasons. First, butterflies have often been proposed as effective surrogates to measure the overall species richness of an area (Holl, 1995; Blair and Launer, 1997; Nally et al., 2003). Therefore, understanding the spatial relationship between environmental predictors and butterfly species richness would provide an understanding for the spatial relationship between environmental predictors and overall biodiversity. Second, butterflies are extremely sensitive to variations in environmental predictors (Scoble, 1992; Simonson et al., 2001), and hence, their distribution can be successfully modelled as a function of environmental predictors (Nally et al., 2003). Furthermore, butterflies respond to environmental changes, such as climate and land use, quickly (Warren et al., 2001; Luoto et al., 2006). This enables to evaluate impacts of environmental changes in time for biodiversity conservation. Third, it has been documented that approximately 448 taxa of butterflies (including 369 species and 79 subspecies) exist in Turkey (Wagener, 2005). This number is not definitive because studies describing butterfly species have not been completed thus far. Nevertheless, this demonstrates that Turkey is an important region for butterfly diversity. This expression becomes more meaningful when it is stated that there are 576 taxa of butterflies in the whole of Europe (Stefanescu et al., 2004). However, butterfly studies in Turkey have mainly been restricted to taxonomic studies, and these are not sufficient for butterfly conservation. All these make significant the determination of influence of environmental predictor on butterfly richness not only for butterfly conservation, but also for biodiversity conservation. Therefore, I explored the spatial relationship between butterfly species richness and environmental predictors for a region of Turkey in the hope that this study will be considered a pioneer on giving a new perspective for butterfly studies in Turkey. In the study, I simultaneously applied geographically weighted regression (GWR) and ordinary least squares (OLS) regression by using environmental predictors and specifically aimed to: (i) determine the best predictive regression model for explaining patterns of butterfly species richness in the Lesser Caucasus region; (ii) identify significant non-stationary environmental predictors for the spatial distribution of butterflies; and (iii) investigate the relationship between environmental predictors and butterfly species richness and the spatial variation in this relationship.

Materials and methods

Study area

Study area is the continuation of the Caucasus ecoregion, and occupies approximately 35000 km² area in north-eastern Turkey (*Fig. 1a*). The region covers Ardahan, southern and eastern Artvin, north-eastern Erzurum, and parts of Kars but excludes the northern slopes of the Kaçkar Mountains, coastal Artvin, and the Aras valley (*Fig. 1b*).



Figure 1. a. Location of the study area; b. Study area, provinces and altitude; c. Number of butterfly species in each UTM grid cells

The area is mainly characterized by high mountains, plateaus, and deep valleys, like the Eastern Anatolia Mountains, Yalnizçam and Allahuekber Mountains, Kars-Erzurum Plateaus, and Çoruh valley and has an altitude ranging from 50 m to 3980 m (*Fig. 1b*). The mountains are the main refuges that divide the region into two main ecological subunits, humid temperate forests and dry high mountain steppe-alpine meadows. However, when the deep valleys are included, another ecological unit dominated by Mediterranean vegetation appears in the Çoruh and Tortum valleys. This diverse landscape in conjunction with the varying climate and evolutionary history of the area has led to high taxonomic diversity, high endemism rate, and various relict organisms and ecosystems. For example, 3650 plant taxa have been documented in the study area, of which 376 are endemic. The region also has a rich and diverse fauna, providing habitat for many animal species that are not found elsewhere in Turkey. Naturally, high species richness and significant endemism are also common among butterfly species. The area was projected using Universal Transverse Mercator (UTM) north zone 37 and divided into 336 mapping grids of 10×10 km for further analysis (*Fig. 1c*). All the available data, including species richness and environmental predictors, were arranged according to the scale of the mapping grids.

Butterfly Data

Butterfly species data were obtained from "Die Tagfalter der Türkei unter besonderer Berücksichtigung der angrenzenden Länder" (Hesselbarth et al., 1995) (The Butterflies of Turkey with special attention to the adjacent countries). Although studies on butterflies in Turkey have recently accelerating, the study by Hesselbarth et al. (1995) is the most detailed study on butterflies and their distribution in Turkey. The work was published as 3 monumental volumes in 1995. I used all the data related to the study area recorded by these authors. The data comprised 2833 presence records of 251 species and sub-species, which constituted 56.02 % of the described butterfly species of Turkey, thus highlighting the importance of the study area for butterflies. I constructed a presence map showing the number of butterflies in each mapping grid. The map indicated that the data covered 120 grids of the study area, with species richness ranging from 8 to 133 (*Fig. 1c*). Almost two-thirds of the grids remained empty, which were excluded from the analyses.

Environmental Predictors

Three groups of environmental predictors that are potentially affecting the distribution of butterfly species richness were collated: (1) climatology, (2) topography, and (3) physical features.

Climatology

I chose the following 9 climate predictors to represent the climate regime of the study area: (1) mean annual temperature (MAT), (2) mean maximum temperature in July (MaxT), (3) mean minimum temperature in January (MinT), (4) mean annual precipitation (MAP), (5) precipitation seasonality (PS), (6) relative humidity (RH), (7) solar radiation (SR), (8) isothermality (ITH), and (9) diurnal range (DR), (*Table 1*). Estimates of these predictors were obtained using co-kriging models for the 30-year (1975-2005) climatology data. All the data were derived from the 26 homogeneously distributed climatology stations of the Turkish State Meteorological Service (TSMS). The annual mean of each climatological predictor was interpolated using Arc-GIS 9.2 for the 30-year period. Kriged estimates of the predictors were built with a 90-m spatial resolution and an R² value of > 0.85 and the mean of these kriged predictors in each mapping grid were used for regression models.

Topography

Altitude (DEM), aspect (north and east facing; NA, EA), slope (SLP), and ruggedness (RGD) were determined as the topographical predictors. These predictors were extracted from a Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) with a 90-m spatial resolution (*Table 1*). Cos-sine and sine transformations were also applied to reorganize aspect as the north and east facing aspects. Topographic predictors were averaged to the grid size of 10×10 km before being used in the analyses.

Physical Features

Three different predictors – soil heterogeneity (SH), lake shore lines (LSL), and river intensity (RI) that were a measure of the physical features of the study area were used in the models of butterfly species richness. I derived lake shore lines and river intensity from a 1:250000 scale digital lake and river map by measuring the length for each mapping grid. Soil heterogeneity was calculated as the total heterogeneity for each grid by using a 6 class digital thematic soil map (*Table 1*).

| Name | Abbr | Definition | Source |
|---------------------------|------|-----------------------------------|--------------------------|
| Climatology data | | | |
| Mean annual temperature | MAT | Average annual temperature | |
| Mean maximum | MaxT | Average maximum temperature of | |
| temperature of July | | July | |
| Mean minimum | MinT | Average minimum temperature of | |
| temperature of January | | January | |
| Mean annual precipitation | MAP | Average annual precipitation | Intermediated maint data |
| Precipitation seasonality | PS | Coefficient of variation | interpolated point data |
| Relative humidity | RH | Average annual relative humidity | 01 1 51/15 |
| Total solar radiation | SR | Total solar radiation | |
| Isothermality | ITH | (Mean diurnal range / Temperature | |
| | | annual range)* 100 | |
| Diurnal range | DR | Mean of monthly (max temp - min | |
| | | temp) | |
| Topography data | | | |
| Altitude | DEM | Average Altitude | USGS |
| Ruggedness | RGD | Standard deviation of DEM | |
| Slope | SLP | Average Slope | Extracted from DEM |
| East aspect | EA | Average Eastness | Extracted Holli DEM |
| North aspect | NA | Average Northness | |
| Physical features | | | |
| Lake shore line | LSL | Total length | HAT CIS Company |
| River intensity | RI | Total intensity | TIAT GIS Company |
| Soil heterogeneity | SH | Total heterogeneity | Ministry of |
| - | | | Agriculture |

Table 1. Environmental predictor, their abbreviations, definitions and source of the data

TSMS, Turkish State Meteorological Service; USGS, U.S. Geological Service

Global correlation analysis

Before analysing the predictive regression models for butterfly species richness, a global correlation analysis was performed and variance influence factors (VIF) were calculated to determine the least correlated and redundant environmental predictors. Implementation of such preliminary eliminations prevents multicollinearity among predictors, which is one of the assumptions of the regression models used in this study. First, I normalised skewed dependent and predictor variables to 0 mean and unit variance and then employed correlation analysis and VIF to remove the redundant predictors. Environmental predictors were only incorporated in further analysis if the VIF values were < 10 and if the correlation coefficients between the predictors were < 0.65.

Regression analyses

I performed OLS regression and GWR using species richness as the dependent variable and environmental predictors as the independent variables.

Ordinary least square regression (OLS)

OLS is a global regression model, which assumes that the relationships that are modelled are the same throughout the study area (Kupfer et al., 2007), i.e. that the model is fitted to the entire study area. OLS is expressed using independent (predictor) variables and dependent (response) variable. This relationship is given by the formula:

$$yi = \beta o + \sum_{j=1}^{p} Xij \beta j + \varepsilon i$$
 (Eq.1.)

where yi is the dependent variable (butterfly species richness), Xij are the independent variables (environmental predictors) (i = 1, 2, 3, ..., n and j = 1, 2, 3, ..., p), $\beta_0, \beta_1,..., \alpha$ and β_p are the parameters to be estimated, and $\varepsilon_1, \varepsilon_{2,...}, \varepsilon_n$ are random error terms, assumed to be normally distributed with 0 mean and constant variance N($0,\sigma^2$).

Geographically weighted regression (GWR)

GWR is a statistical technique that concentrates on local spatial data analysis (Foody, 2004). In contrast to global OLS, this technique is a local model (Brunson et al., 1996; Shi et al., 2006), i.e. the model assumes that there is spatial variation within the relationships being modelled, known as spatial non-stationarity (Fotheringham et al., 2000; 2002). This allows local estimates to be made for parameters by incorporating geographical locations into the model (Shi et al., 2006). The model does this by including location information into the global OLS regression equation, and the above OLS formula is rewritten as:

$$yi = \beta_0(\mathbf{u}, \mathbf{v}) + \beta_1(\mathbf{u}, \mathbf{v})x_1 + \dots + \beta_n(\mathbf{u}, \mathbf{v})x_n + \varepsilon$$
(Eq.2)

where yi is the dependent variable (butterfly species richness), x_1 to x_n are independent variables (environmental predictors), β_0 is the intercept, β_1 to β_n are estimated parameter coefficients, ε is a random error term, and (u, v) are the locations where the data are collected. Determination of local parameter estimates is achieved by implementing the geographical weighting scheme. The weighting scheme is organised such that closer data (u, v) are given a heavier weight in the model than the data further away. This weighting procedure is performed using a kernel bandwidth (Foody, 2004; Miller et al., 2007). Kernel bandwidth determines the distance beyond which data points have no effects on local parameter estimates. In this study, I applied a Gaussian kernel function with adaptive bandwidth because data were not evenly distributed across the study area (Fotheringham et al., 2002; Miller et al., 2007). The Gaussian kernel function is given as follows:

$$Wij = \exp \left[-\frac{1}{2}(\frac{dij}{b})\right]^2$$
 (Eq.3)

where dij is the distance between regression location i and data point j and b is the bandwidth. The Gaussian function provides a continuous weighing function from regression point i to data point j and gives 0 weight to any data points beyond b.

Evaluation of OLS and GWR models

The goal was to identify whether local GWR or global OLS regression model was better at estimating butterfly species richness. Various diagnostic measures were obtained by running GWR 3.0 software. First, I underscored the major differences between the coefficient of determinations (\mathbb{R}^2) of local and global regressions. \mathbb{R}^2 indicates how well the regression line approximates the real data points. Although, it is the measure for the goodness of fit of models, it may be insufficient when there have been differences in degrees of freedom. GWR also produces locally varied R^2 values for each regression point. I visualised these values by using inverse distance weighting (IDW) in Arc-GIS 9.2 and evaluated the effectiveness of GWR at the local scale (e.g. Fotheringham et al., 1999; Fotheringham et al., 2000; Páez et al., 2002a). Second, I investigated the Akaike information criterion (AIC) (Fotheringham et al., 2002), which determines the relative information loss in estimated models. The aim is to minimize the AIC of a model, such that the model with the smallest AIC value is able to represent the reality of an area more accurately (Kupfer et al., 2007). Moreover, AIC can take into account different degree of freedoms while assessing model fit; hence, it is an appropriate measure for detecting more explanatory models for butterfly species richness. In addition, an approximate likelihood ratio test (F-test) was performed to compare the global OLS model and the local GWR model in the sense of hypothesis testing (Leung et al., 2000; Fotheringham et al., 2002). This test is based on the null hypothesis, which assumes that the local GWR model offers no improvement over the global OLS model. Moreover, predictions of OLS and GWR models for butterfly species richness were mapped applying IDW. This provides both to visually distinguish predictive abilities of global OLS and local GWR models and indicate butterfly-rich areas. Lastly, I explored residuals for OLS and GWR models using residual maps and a box-plot to assess how close the models predict reality and indicate distribution of residuals across the study area.

Test for spatial non-stationarity

I investigated the spatial non-stationarity of local parameter estimates of the model predictors because spatial heterogeneity influences the predicted distribution of species richness, i.e. the model fit. At the same time, significant non-stationarity for estimated parameters of environmental predictors was explored and non-stationary environmental predictors for butterfly species richness were obtained. A Monte Carlo permutation test was performed for these purposes (Brunsdon et al., 1996; Fotheringham et al., 2002). The test compares the observed values of a test statistic with n-1 simulated ones and calculates *p*-values for the predictors. In addition to spatial non-stationarity test, patterns of residuals for the OLS and GWR models were examined as a way to demonstrate non-stationarity by using spatially autocorrelated residuals (Diniz-Filho et al., 2003; Jetz et al., 2005). To evaluate the residuals, Moran's I autocorrelation coefficients were calculated. Moran's I coefficients can range from -1 (negative autocorrelation) to 1 (positive autocorrelation) indicating perfect dispersion and perfect correlation, respectively.

Exploring spatial relationship between butterfly richness and environmental predictors

After detecting significant non-stationary environmental predictors for butterfly species richness, local spatial relationships between butterfly richness and non-stationarity predictors were also examined. For this purpose, a set of parameter estimates, including coefficients and t-values, were obtained and mapped using IDW. This helps to visualize spatial variation in the relationship between butterfly species richness and non-stationary environmental predictors and determine where this variation is significant for butterfly species richness. It is also the way for indicating the impacts of non-stationary environmental predictors on butterfly species richness.



Figure 2. a. Distribution of butterfly species richness predicted by GWR model; b Distribution of butterfly species richness predicted by OLS regression model; c Residuals from GWR model; d Residuals from OLS regression model

Results

Environmental predictors

After removing redundant environmental predictors following the assessment of the correlation analysis and VIF, 12 predictor variables remained for regression analysis. These were ruggedness, northern and eastern aspect, minimum temperature in January, maximum temperature in July, diurnal range, isothermality, precipitation seasonality, solar radiation, lake shore line, river intensity, and soil heterogeneity (*Table 1*). *Comparisons between OLS model and GWR model*

The results showed that local GWR and global OLS regression models had differences with respect of their diagnostic measures. The coefficient of determination (\mathbf{R}^2) for OLS was 0.48; i.e. 48% of the variation in butterfly species richness was explained by the environmental predictors (*Table 2*). MaxT (p-value = 0.028) and MinT (p-value = 0.034) were significant environmental predictors in OLS regression model according to the 95% confidence level, and they both had negative coefficients (MaxT =-0.76; MinT = -0.43). This implied that butterfly species richness decreased with MaxT and MinT. In contrast, the R^2 for GWR increased to 0.74, and its local range was between 0.57 and 0.90 (Table 2, Fig. 4a). Although there is an increase in R² values, which demonstrates the effectiveness of GWR over OLS, this increase may be due to the difference in the degrees of freedom. However, a reduction in AIC values from 1162.95 (OLS) to 1040.11 (GWR), lower residual sum of squares (RSS), and lower standard errors (SE) indicated that GWR was more explanatory than OLS regression for modelling distribution of butterfly species richness (Table 2). In addition, the results of the approximate F-test (ANOVA) demonstrated that GWR model had significant improvement over OLS model (*p-value* = 0.0194; *Table 3*). Thus, GWR is a better predictive regression model for explaining the variation in butterfly species richness.

Table 2. Diagnostic Measure for OLS and GWR-(RSS; residual sum of square; AIC: akaike information criterion; Std-error: standard error; $R^2 = coefficient$ of determination)

| Models | RSS | AIC | Std-error | \mathbf{R}^2 |
|--------|----------|---------|-----------|----------------|
| OLS | 87587.13 | 1162.95 | 27.87 | 0.48 |
| GWR | 52362.37 | 1040.11 | 24.03 | 0.74 |

Table 3. An approximate F-test (ANOVA)-(SS: sum of squares; DF: degree of freedom; MS: mean square; F: F statistic; P value: probability of F-distribution)

| Source | SS | DF | MS | F | Р |
|-----------------|---------|-------|----------|------|--------|
| OLS residuals | 87587.1 | 13.00 | | | |
| GWR improvement | 35224.7 | 21.13 | 1667.046 | | |
| GWR residuals | 52362.4 | 84.87 | 617.0061 | 2.70 | 0.0194 |

Predicted butterfly species richness and residuals

Predictions of GWR model for butterfly species richness were range from 8 to 333, whereas these were between 0.14 and 57.38 in OLS regression (*Figs. 2a and b*). This result indicated that predictions of global OLS regression are well below the observed species richness (*Fig. 1c, Fig. 2b*). In addition, predicted distribution pattern of species richness in OLS model are not congruent with observed distribution of butterfly species richness (*Fig. 1c, Fig. 2b*). This means that predicted species richness is low in areas where observed species richness is high or vice versa; i.e. observed species richness is high in north east and south east parts of the study area (70-133) while predicted species richness are very low for these parts (generally 0.14-9.56 and from place to place 9.56-26.63, *Fig. 1c, Fig. 2b*). Moreover, prediction map of OLS model for butterfly species richness mostly exhibited spotty pattern that is not in accordance with actual species richness pattern (*Fig. 2b*). However, local GWR model produced more homogeneous prediction pattern for butterfly species richness (*Fig. 2a*). Similarly, residual range and

pattern indicated the strength of GWR model (*Figs. 2c, d and Fig. 3*). Residual range was -35.13-33.12 (mean, 0.28) in GWR model, whereas that for the OLS regression was -6.91-75.61 (mean, 11.48). Also, residuals were mostly between -1.94 and -5.28 in GWR model (*Fig.2c*). These results demonstrated that local GWR model achieve better predictions resulting in low variability of residuals than the global OLS regression model (*Figs. 2c, d and Fig. 3*).



Figure 3. Box-plot for residuals of local GWR and global OLS models

Spatial non-stationarity and spatial relationship of butterfly richness and environmental predictors

The estimated parameter coefficients of GWR model indicated significant nonstationarity in 4 of the 12 environmental predictors, according to the Monte Carlo test. These predictors were MinT, MaxT, DR, and SR (*p-values* < 0.001, *Table 4*). The intercept of the GWR model also displayed significant non-stationarity (*p-value* < 0.001, *Table 4*). Non-stationarity of predictors means that they were not constant across the study area, indicating that spatial variation exists in the relationship between butterfly species richness and these environmental predictors. However, patterns of coefficients (in combination with the *p-values*) indicated that non-stationarity could not be always significant across the entire study area (*Fig. 4*).

| Table 4. | Spatial | non-stationarity | , of e | estimated | parameters |
|----------|---------|------------------|--------|-----------|------------|
|----------|---------|------------------|--------|-----------|------------|

| Parameter | P-value |
|-----------|-------------|
| Intercept | 0.00000 *** |
| RGD | 0.33000 n/s |
| EA | 0.26000 n/s |
| NA | 0.70000 n/s |
| MinT | 0.00000 *** |
| MaxT | 0.00000 *** |
| DR | 0.00000 *** |
| ITH | 0.51000 n/s |
| PS | 0.20000 n/s |
| SR | 0.00000 *** |
| LSL | 0.34000 n/s |
| RI | 0.70000 n/s |
| SH | 0.90000 n/s |



Figure 4. a. Locally variable R-square for GWR; estimated coefficients and t-values for significant predictors of GWR model including b. Intercept of the model; c. Maximum temperature of July (MaxT); d. Minimum temperature of January (MinT); e. Diurnal Range (DR); f. Solar Radiation (SR)

The regression coefficients for MaxT and MinT were mostly negative throughout the study area, whereas those for DR and SR were positive (Figs. 4c, d, e, and f). This means that butterfly species richness decreased with MinT and MaxT in majority of the area, similar to the predictions of OLS model; however, estimated coefficients of these predictors had the greatest and significant effect on the distribution of butterfly species richness only in the south-west part of the area (Figs. 4c, d). In addition, MaxT and MinT environmental predictors indicated non-significant positive effects on the butterfly species richness in a part of north and south. In contrast to MaxT and MinT, DR and SR increased the species richness of butterflies across the entire study area (Figs. 4e, f). However, these positive effects on species richness were not significant in all parts of the area. SR only indicated significant spatial variation in the south-west of the study area whereas DR had significant non-stationarity in the south-west and northwest parts of the area (Figs. 4e, f). Coefficients for the intercept showed significant variation only in the north-west of the study area (Fig. 4b). Spatial non-stationarity in environmental predictors was also observed with autocorrelated residuals. Analyses of spatial autocorrelation of residuals indicated that the OLS model had significantly correlated residuals at a lag distance of 0–50 km (Moran's I = 0.681, 0.422; *p-value* = 0.027, 0.038; *Fig.* 5). However, GWR residuals did not show a significant autocorrelation for the same lag distance (Moran's I = 0.134, -0.036; *p-value* = 0.062, 0.069; *Fig.* 5).



Figure 5. Spatial autocorrelation of model residuals for the GWR and OLS regression models, (* P values; 0.01 < P < 0.05)

Discussion

Results supported that GWR model is a better predictor of butterfly species richness than OLS regression model. GWR model not only has more explanatory power but also investigates the spatial variation in the relationship between butterfly species richness and environmental predictors. This enabled us to determine the local impacts of environmental predictors on species richness. OLS model only achieved an average global estimate and missed local scale variations in the relationship between butterfly species richness and environmental predictors. The results of OLS regression model suggested that MaxT and MinT were significant (p < 0.05) and negatively affected species richness across the entire study area with coefficients of -0.76 and -0.43, respectively. However, although the estimates of MaxT and MinT were mostly negative in GWR model as well, they also indicated positive effects on species richness for almost one-third of the study area (Figs. 4c, d; MaxT coefficients ranged between -4.74 and 0.22 and MinT coefficients ranged between -0.76 and 0.27). This is because of GWR model's ability to take into account local variation or non-stationarity of the environmental predictors. Furthermore, although SR and DR were not among the significant environmental predictors of OLS regression, they had significant positive effects on species richness in GWR model, suggesting that spatial scale is an important factor for determining significant predictors. The GWR model provides fine scale estimates, which enables it to identify significant predictors for the model that cannot be distinguished using global OLS regression.

On the other hand, the application of different spatial scales could be useful for observing the responses of environmental predictors at each scale because it has been experienced that environmental predictors can act differently at varying spatial scales (Osborne et al., 2007), which may affect the success of the models. It can be achieved applying different kernel size with fixed kernel bandwidth. In that way, an optimum

kernel size can be detected as well. Optimum kernel is the spatial scale at which the best model fit is achieved and the most explanatory predictors could be obtained. However, I did not obtain an optimum kernel bandwidth nor did I investigate the effect of scale on the significance of predictors. The distribution of data used in the study was not homogenous across the study area, particularly around the border; therefore, using an adaptive kernel was the best choice for examining the relationship between environmental predictors and species richness in the current study. Using an adaptive kernel does not restrict bandwidth size, like that observed while using a constant kernel; in contrast, an adaptive adjusts the kernel size according to the distribution of the data. Thus, it provides a best model fit for irregularly distributed data.

In addition, it was noticed that including spatial non-stationarity in regression model increased the model fit as well. It was observed that R² of GWR model was 0.74 with the local range between 0.73 and 0.90; whereas it was 0.48 for OLS regression model. Similarly, significant local variation in local parameter estimates of environmental predictors increases the success of the model as well. I have seen that local R² values from the GWR model ranged from 0.73 to 0.90 for the western part of the study area; however, they were less (0.57-0.72) for the rest of the area (Fig. 4a). Significant nonstationarity was also observed in the western part of the area for MaxT, MinT, SR, and DR (Figs. 4c, d, e, and f), highlighting that significant variation of estimated coefficients enhances the fit of the model in related parts. On the other hand, although non-stationarity of predictors increases the model fit, it leads to significant autocorrelation in model residuals if not modelled as in the OLS regression. This situation was observed in patterns of OLS regression residuals (Fig. 5). In substance, autocorrelation in model residuals is another way to indicate the spatial variation in the relationship between butterfly species richness and environmental predictor. All these indicated that spatial variation in ecological relationships should be modelled; otherwise suboptimal predictions, autocorrelated residuals and biased parameter estimates are obtained as observed in OLS regression model. This situation makes the OLS regression model inappropriate for exploring the spatial relationship between butterfly species richness and environmental predictors.

As stated previously; MaxT, MinT, DR, and SR were the significant non-stationary environmental predictors for the distribution of butterfly species richness. This finding indicates the importance of temperature-related environmental predictors on the spatial distribution of butterfly species. The result is compatible with results of earlier studies that show a strong relationship between the geographic pattern of butterfly species richness and the current climate (Virtanen and Neuvonen, 1999; Kerr, 2001; Hill et al., 2003; Stefanescu et al., 2004; Luoto et al., 2006; Newbold et al., 2009), suggesting that butterfly species richness may easily respond to climate change (Luoto et al., 2006). Therefore, it can be concluded that changes in these environmental predictors may affect the distribution of butterfly richness, or even reduce the species richness. This study indicated the importance of exploring local impacts of environmental predictors on the distribution of butterfly species richness. Determination of significant environmental predictors and their effects on butterfly richness provides their management for sustainable butterfly conservation. It should be noted that butterflies are effective surrogates for representing entire biodiversity of an area. Therefore, conservation of butterfly species richness in the area provides to sustain biodiversity conservation for the area as well.

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