Factors explaining the patterns of benthic chlorophyll-a distribution in a large agricultural Iberian watershed (Guadiana river)

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A B S T R A C T

Benthic algal biomass depends on a number of variables, including local factors such as the ionic water composition, nutrient availability, light, or water velocity, and large-scale factors such as the drainage area and land uses in the watershed. The relative roles of local and large-scale factors affecting benthic chlorophyll variation were analyzed in the Guadiana watershed by means of variation partitioning and partial least squares regression. The potential relevance of 20 physical, chemical and physiographical variables was analyzed throughout the watershed, and separately in three distinct geological units: upper watershed calcareous streams, streams with siliceous bedrocks, and the main river reaches. Our results suggest that many predictors of algal biomass are intercorrelated but have independent effects, and that their importance varies between geological units. Nutrient content and land uses exerted the largest influence on the pattern of chlorophyll-a variation in the three ecoregions studied.

1. Introduction

The occurrence of algal biomass in river systems depends on a number of chemical variables, including nutrient availability (Welch and Patmont, 1989; Veraart et al., 2008) and other geochemical properties of the water, such as pH (Soininen, 2002). Physical and habitat variables such as canopy cover (Mosisch et al., 2001), turbidity (Munn et al., 1989), water temperature (Morin et al., 1999) and hydrologic disturbances (Powers, 1992; Biggs, 1995; Bertrand et al., 2001; Riseng et al., 2004) can also affect algal production and biomass. The action of biological agents through herbivory, parasitism, allelopathy or competition can cause major effects on algal biomass, though mostly at a local, patchy scale (Lamberti and Resch, 1983; Powers, 1992; Biggs and Gerbeaux, 1993; Stevenson, 1997; Hillebrand et al., 2002; Artmann et al., 2003). In stream headwaters, algae can become abundant under open canopies, but generally nutrients limit their occurrence (Hill and Fanta, 2008; Sabater et al., 2011). In middle and lower courses, nutrients become progressively more abundant, and benthic algal biomass progresses according to local hydrological conditions and nutrient and light availability (Sabater and Sabater, 1988; Munn et al., 1989; Biggs, 2000; Frankforter et al., 2010). In heavily modified situations, algae can grow in excess and become a nuisance in rivers, especially under conditions of nutrient enrichment or riparian simplification. Altogether, the complexity of these algal-environment interactions is evidenced through multiple ecological processes operating at different spatial and temporal scales in stream ecosystems (Stevenson, 1997). Large-scale regional factors, such as climate, geology and land use, which play an important role at the watershed scale, should also be considered along with local processes to define the algal-nutrient interactions (Biggs, 1995; Leland et al., 2000). New approaches that recognize scale-dependent constraints are therefore required in order to identify the patterns occurring in river watersheds.

Several statistical approaches aiming to predict the effects of eutrophication on primary producers of biomass (usually estimated as the chlorophyll-a content) have been extensively applied to lotic systems (Nogueira et al., 1998; Tufford and McKeller, 1999; Hakanson et al., 2003; Çamdeviren et al., 2005), but less commonly to lotic systems (Biggs, 2000). The major difficulties in the application of statistical models in lotic systems are due to the variable hydrological patterns as well as to the patchy nature of benthic algal communities, features that have an adverse effect on their predictive power (Sellers and Bukaveckas, 2003; Carr et al., 2005; Sabater et al., 2008) but also to the strong collinearity among factors along the longitudinal river gradient. Nutrients often explain a small proportion of the variation of algal biomass in many of these models (Lohman et al., 1992; Biggs, 2000; Dodds et al., 2002), and their relevance decreases in large-scale studies (Leland, 1995). Including as many as possible of the different factors involved in the distribution of benthic chlorophyll-a while using methods that properly account
for collinearity increases the reliability of chlorophyll explanation and may potentially improve management strategies.

Agricultural catchments include several of the disturbances that a priori can promote algal development. Nutrient concentrations in agricultural streams are generally higher than in better-preserved basins (Munn et al., 2010), resulting in a variety of ecological problems, including increased biomass of aquatic plants and algae, hypoxia, and biodiversity loss (O’Brien and Wehr, 2009; Frankforter et al., 2010). Bentic chlorophyll-a concentration tends to increase with increasing agricultural land use (Busse et al., 2006; O’Brien and Wehr, 2009).

The Guadiana (SW of the Iberian Peninsula) is a good example of an agricultural watershed with complex hydrology. The hydrological patterns in this watershed are a combination of the characteristic variability of Mediterranean regimes and severe human pressure in the form of extensive agriculture in much of the watershed which has resulted in huge water abstraction of superficial and groundwater resources and sizeable nutrient inputs (Sabater et al., 2009). This variability makes the prediction of chlorophyll biomass patterns very difficult, and requires a consideration of the environmental factors operating at different levels. These should include variables directly relevant to algae at the habitat scale as well as others operating at the watershed scale, which define the climatic and physical framework of the river segments.

In this study, we analyze the key physicochemical and physiographical factors affecting the distribution of chlorophyll-a concentration in the Guadiana watershed, with two main aims: (1) to assess the importance of the proximate (physical and chemical) and large-scale factors (land use, geological setting, time of year) in influencing chlorophyll-a distribution, and (2) to describe how much the patterns of chlorophyll-a distribution differ between the different ecotypes of the Guadiana watershed. We assess the patterns of bentic chlorophyll-a throughout the watershed and in the main geophysical units: upper calcareous subcatchment, mid-low calcareous subcatchment, and the main river reaches (Urrea and Sabater, 2009). To achieve our first goal, we analyze the potential dependence of chlorophyll-a on proximate and large-scale factors by using a partial least squares regression approach, and we examine patterns of chlorophyll-a distribution in different ecotypes by means of variation partitioning. We hypothesize that chlorophyll-a distribution is best predicted by considering physical and chemical factors as well as landscape factors. To test this possibility, we determine how much of chlorophyll-a variation is explained by each set of factors.

2. Materials and methods

2.1. Chlorophyll sampling, preparation and analysis

A total of 223 localities scattered throughout the Spanish part of the Guadiana watershed were sampled during winter (November 2005–February 2006) and spring (March–April 2006) (Fig. 1). The summer period could not be included in the previously defined scheme because many tributaries had dried out by this time. The sampling sites were selected according to the previously defined water bodies in the watershed (CHG, 2005). Fifty-nine of the sampling sites were situated in the upper Guadiana calcareous catchment, with low slope and slow-moving waters; 136 sites were situated in the siliceous middle and lower parts, where the drainage network is of high density and low permeability. The remaining 28 sites were situated in the main course of the Guadiana and Zújar (the Guadiana’s main tributary). Three hundred samples of epilithic algae were collected and analyzed for chlorophyll-a concentration during both winter and spring. However, some spring samples could not be collected because the river section was temporarily dry. Algal samples were pooled from rocks or cobbles collected from a 10 m river reach in a well-lit part of the river, avoiding shaded areas and pools. At least six rocks or cobbles were collected from a variety of locations within the sample site. A surface area of 1–2 cm² from each rock was scraped with a knife to obtain a mixed sampling area of 10 cm² (CEN, 2002). Up to three replicates were collected at each sampling point for chlorophyll analysis. The samples were then preserved in dark and cold conditions and taken to the laboratory for pigment analysis.

Bentic algal chlorophyll-a concentration was measured spectrophotometrically (at 430, 665 and 750 nm) after extraction with 90% acetone. Estimation of algal biomass was derived from these measurements following a revised equation of Jeffrey and Humphrey (1975) described in Elosegui and Sabater (2009).

2.2. Environmental variables

Conductivity, pH, dissolved oxygen concentration and temperature were measured in the field with a WTW MultiLine F/SET-3 P4 probe. The river section in each sampling site was obtained after measuring the total width and partial depth across one transect every 10–50 cm. In each partial section, current velocity was measured with a portable current–metre (Neyrflux 80, Neyrtec). Total flow was later calculated as the sum of the partial flows of each section (Elosegui and Sabater, 2009).
and maximum depth were also determined from these measurements.

Water samples for chemical analyses were filtered (Whatman nylon filters, 0.2 μm pore) preserved with chloroform (0.7 mL of chloroform per 100 mL of water) and stored in polyethylene bottles (Murphy and Riley, 1956; Fishman et al., 1986; Kotlash and Chesman, 1998). The chemical elements and parameters analyzed included those characterizing the geochemistry of the waters (alkalinity, Ca\(^{2+}\), Cl\(^{-}\), SO\(_4^{2-}\)) as well as those directly affecting the primary producers (NH\(_4^{+}\), N, PO\(_4^{3-}\), P, NO\(_3^{-}\), N). The chemical analyses followed standard procedures (APHA, 1989).

Specific watershed characteristics were GIS-derived from the 1993 CORINE Land Cover data. Land use was expressed as the percentage of three principal land-use types (natural, agricultural and artificial). Drainage area, distance to the source, and geospatial measures (latitude, longitude and altitude) were also obtained from this database.

2.3. Data analysis

Most variables were transformed prior to analysis (Table 1) to satisfy the assumptions of the statistical methods used. Pearson correlation analysis was initially used to identify pair-wise relationships between all the variables measured and test for the existence of collinearity.

Partial least squares regression (PLSR) was used to assess the factors influencing chlorophyll-\(a\) concentration, including physical, chemical and physiographical variables, geological type, and sampling period. PLSR is a technique that combines features from principal component analysis and multiple regression by extracting latent factors from a set of predictors that maximize the explained variance of one or more dependent variables (Mevik and Wehrens, 2007). PLSR generally outperforms multiple linear regression and principal component regression – particularly in cases with high collinearity, a large number of predictors and small sample size, which are often the rule in ecology (Mevik and Wehrens, 2007; Carrascal et al., 2009). PLSR was computed using package “pls” (Mevik et al., 2011) from the R statistical environment (R Development Core Team, 2012). We used cross-validation to estimate the PLSR and jack-knife estimation to test for significance of regression coefficients. Plots of the coefficient of multiple determination \((R^2)\) and the root mean squared error of prediction (RMSEP) with the number of components (Mevik and Wehrens, 2007) both showed that five components were necessary and sufficient for the PLSR model estimate.

The respective relevance of the physical, chemical and physiographical variables in the spatial distribution of chlorophyll was analyzed by variation partitioning, using the “varpart” function of the “vegan” package (Oksanen et al., 2012) from the R software environment. Variation partitioning uses a series of partial regression analyses to decompose the variation of the dependent variable (chlorophyll-\(a\) in our case) into unique and shared effects of a set of predictors (Legendre and Legendre, 1998). Three sets of predictors were considered: physicochemical variables (variables 2–11 in Table 1), physiographical variables (variables 12–20 in Table 1), and geological type. This allowed decomposition of the variation into pure unique effects attributed to one of these sets, and effects shared between two or more of the sets of predictors. We first ran a variation partitioning analysis with the three sets in the whole watershed, and then separate analyses for the three geological types (calcareous, siliceous, and main river reaches), to assess whether the effects depended on the specific ecotype. The significance of the different components was evaluated by permutation tests with function “anova.rda” of the “vegan” package; note that

| Table 1 | Summary of chlorophyll-\(a\) and the 21 predictors measured (range and mean) for all 300 samples and for calcareous, siliceous and main river reaches ecotypes in the Guadiana river. The transformation used in the analyses, if any, is also given. |
|---------|------------------|------------------|------------------|
| Chlorophyll-\(a\) | Conductivity | NH\(_3\) | NO\(_3\) | XR | COMPANY | COMPANY | COMPANY |
| µg cm\(^{-2}\) | mS cm\(^{-1}\) | mg L\(^{-1}\) | mg L\(^{-1}\) | | | | |
| 0.32–410 | 102–120 | 0.01–100 | 0.01–150 | 0.01–150 | 0.01–150 | 0.01–150 | 0.01–150 |
| 169.6 | 9.0 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 |
| Transformation: Mean | Range | Mean | Range | Mean | Range | Mean | Range |
| Log10 x | 100–1200 | Log10 x | 1 Log10 | Log10 x | 1 Log10 | Log10 x | 1 Log10 |
| 3.2 Log10 | 2.5–1000 | 1 Log10 | 0.6 | 1 Log10 | 0.6 | 1 Log10 | 0.6 |

Note: The table above provides a summary of chlorophyll-\(a\) and 21 predictors measured (range and mean) for all 300 samples and for calcareous, siliceous, and main river reaches ecotypes in the Guadiana river. The transformation used in the analyses, if any, is also given.
only unique effects and not shared effects can be tested in variation partitioning (Oksanen et al., 2012).

3. Results

3.1. Environmental variables and benthic algal biomass

Physicochemical and physiographical variables are summarized in Table 1. Water flow increased from the tributaries in the calcareous and siliceous watershed to the main river reaches. Flows averaged 1.2 m$^3$/s in the main river reaches, and accordingly the wetted widths were also the highest (average of 20.2 m) (Table 1). Sulfate, calcium and alkalinity were higher in the calcareous ecotype (average values of 287.8 mg/L, 133.1 mg/L, and 209.3 mg/L, respectively) because of the nature of the bedrock type. Accordingly, conductivity was higher in that part of the watershed (average of 1114.5 µS/cm, but 117.8 µS/cm in the siliceous ecotype and 215.9 µS/cm in the main river reaches) (Table 1). Nitrates were the only nutrients showing higher values in the calcareous part (average of 10.2 mg/L; values of 3.4 mg/L in the siliceous and 5.0 mg/L in the main river reaches). Benthic algal biomass had the highest value in the calcareous ecotype (average of 260.2 mg/m$^2$), and averaged 117.8 mg/m$^2$ in the siliceous part, and 215.9 mg/m$^2$ in the main river reaches (Table 1 and Fig. 2).

3.2. Algal biomass models

Most of the physical, chemical and physiographical variables were significantly correlated with each other and with benthic algal biomass (chlorophyll-a) (Table 2). The latter variable was significantly correlated with 13 out of 17 predictors (Table 2), but most strongly to nitrate, calcium, conductivity, alkalinity (positive correlations) and temperature (negative). These pervasive, sizeable correlations favour the use of a method that is less sensitive to collinearity, such as PLSR.

Results of the PLSR analysis with the 20 environmental predictors provided five significant latent vectors explaining 39.0% (cross-validation estimate) of the total variance of chlorophyll-a concentration. The main significant variables were both proximate (e.g., temperature) and large-scale factors (e.g., sampling period and ecotype), chlorophyll-a increased in the main river reaches, but its values were negatively associated with the siliceous sites and water temperature (Table 3). Nutrients (nitrate, ammonia and

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**Table 2** Pearson correlation coefficients between chlorophyll-a and all measured variables. Significant correlations ($p < 0.05$) are given in bold. See Table for the transformations used for certain variables.

<table>
<thead>
<tr>
<th></th>
<th>Chlorophyll-a</th>
<th>Conductivity</th>
<th>pH</th>
<th>Oxygen</th>
<th>Ammonia</th>
<th>Nitrite</th>
<th>SRP</th>
<th>Sulfate</th>
<th>Chloride</th>
<th>Calcium</th>
<th>Alkalinity</th>
<th>Temperature</th>
<th>Flow</th>
<th>Wet width</th>
<th>Depth to source</th>
<th>Natural area</th>
<th>Drainage area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll-a</td>
<td>0.41</td>
<td>0.13</td>
<td>0.03</td>
<td>0.35</td>
<td>0.26</td>
<td>0.24</td>
<td>0.46</td>
<td>0.41</td>
<td>0.22</td>
<td>0.10</td>
<td>-0.02</td>
<td>-0.04</td>
<td>0.34</td>
<td>-0.01</td>
<td>-0.28</td>
<td>-0.35</td>
<td>0.26</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.13</td>
<td>0.35</td>
<td>0.26</td>
<td>0.26</td>
<td>0.24</td>
<td>0.46</td>
<td>0.13</td>
<td>0.10</td>
<td>0.35</td>
<td>0.26</td>
<td>0.22</td>
<td>-0.04</td>
<td>0.24</td>
<td>0.26</td>
<td>-0.35</td>
<td>0.24</td>
<td>0.34</td>
</tr>
</tbody>
</table>

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**Fig. 2.** Map of the Guadiana watershed with indication of the average values of chlorophyll-a in the studied sites. Values are the means of the concentrations, and 4 categories were determined following Dodd et al. (1998). Green squares correspond to oligotrophic sites, yellow diamonds to mesotrophic sites, orange triangles to eutrophic sites and finally red circles to hiperutrophic sites. (For interpretation of the references to color in this text, the reader is referred to the web version of the article.)
SRP) played a key role in the variation of benthic algal biomass (Table 3). Large-scale factors such as increasing water flow (the associated drainage area and the distance to source) also had a positive influence on benthic algal variation.

Variance partitioning with the three sets of variables revealed that both physicochemical effects and physiographical effects were significantly related to benthic chlorophyll-α distribution and that geology played a less important role, mostly shared together with physicochemical and physiographical variables (Fig. 3).

The effects of physicochemical and physiographical factors on chlorophyll-α concentration were always significant but varied according to the ecotype studied (Fig. 4). Within the calcareous ecotype, the variance of chlorophyll-α was mostly influenced by the shared effects of physicochemical and physiographical factors (25%), but this influence was smaller in the other two ecotypes. In the siliceous ecotype, the overall explained variance was smaller, and in the main river reaches water chlorophyll-α was mostly influenced by physiographical factors (Fig. 4).

### 4. Discussion

Chlorophyll concentration provides critical information regarding trophic state of rivers and is of functional importance to stream ecosystems as the base of primary production (Smucker et al., 2013). Chlorophyll-α values higher than 100 mg/m², and peaking up to 1000 mg/m², have been reported in rivers with high pollution levels (Odum, 1957; McConnell and Sigler, 1959; Bombowina, 1972; Munn et al., 2010). About 30% of the samples in the Guadiana watershed presented low chlorophyll concentration (<20 mg/m²), all of which corresponded to headwater streams, and another 25% had chlorophyll concentrations between 20 and 70 mg/m². These values were constrained to stream tributaries with relatively undisturbed conditions. Concentrations of benthic chlorophyll were higher (70–600 mg/m²) in areas of high population density and intensive agriculture. Most of these sites were located in the middle sections of the siliceous ecotype as well as in sampling localities of the calcareous ecotype, regardless of the stream order. The highest chlorophyll concentrations (values higher than 600 mg/m²) occurred mainly in the main watercourse of the Guadiana and its larger tributaries, irrespective of the geological substrata (Fig. 2). This pattern could be attributed to the longitudinal accumulation of nutrients, as predicted by the River Continuum Concept (Vannote et al., 1980). The high chlorophyll values result from the combination of high nutrient concentrations (phosphates and inorganic nitrogen), steady hydrological conditions (common to the two sampling periods), and shallow waters receiving high light irradiances. We cannot rule out light availability as a possible explanation for the increase in productivity between the sites (Dubinsky et al., 1984; Glover et al., 1987). In the middle and lower Guadiana watershed the riparian cover is practically absent, and light is never limiting. The sampling periods were characterized by extremely low water flows (MMA, 2006) derived from the absence of notable rain episodes. This hydrological situation probably reinforced the high nutrient concentrations during the winter period, which, despite the low water temperatures, allowed high algal mass growth (428.2 mg/m² on average).

Human activity and land use changes have long been known to influence the physical, chemical, and biological characteristics of streams (e.g., Peierls et al., 1991; Carpenter et al., 1998). In many watersheds where intensive agriculture occupies the largest fraction of land area, high nutrient concentrations may be a consequence of the extensive use of nitrate-rich fertilizers (Moreno et al., 2006).

The various field-based studies of the factors accounting for the benthic algal biomass coincide in the role that nutrients play in accounting for most of the benthic chlorophyll-α concentration in rivers (Sabater and Admiraal, 2005). However, while some models find no relationship between nutrients and benthic algal biomass (Munn et al., 1989; Kjeldsen, 1994) others link nutrient inputs with increasing periphyton biomass. Among these latter studies, the proportion of explained variance ranged from 0.05 to 0.6 (Biggs and Close, 1989; Lohman et al., 1992; Dodds et al., 1998, 2002; Sabater and Sabater, 2000; Flinders et al., 2009), encompassing a high variability in these empirical expressions. The predictive value of these models, usually assessed with single or multiple linear regressions, is impaired by co-occurring biotic interactions, abiotic stressors, hydrodynamics, water turbidity, riparian shading and human impact (Stevenson, 1997). Other studies comparing relationships between land use, nutrient concentrations, and algal biomass in streams have found closer relationships between land use and chlorophyll concentrations than between nutrients and chlorophyll (Taylor et al., 2004; Carr et al., 2005).

The model we used in this paper included factors operating at different spatial scales, from local to basin-wide. The PLSR models

### Table 3

Results of partial least squares regression of chlorophyll-α with 17 quantitative predictors and geology as season as categorical factors. The statistics are based on jack-knife estimates. See Table 1 for the transformations used for certain variables.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>t value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conductivity</td>
<td>9.04E−05</td>
<td>2.21</td>
</tr>
<tr>
<td>pH</td>
<td>2.83E−02</td>
<td>0.70</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>3.05E−01</td>
<td>0.48</td>
</tr>
<tr>
<td>Ammonia</td>
<td>1.02E−03</td>
<td>2.71</td>
</tr>
<tr>
<td>Nitrate</td>
<td>1.36E−03</td>
<td>4.06</td>
</tr>
<tr>
<td>SRP</td>
<td>1.09E−03</td>
<td>2.38</td>
</tr>
<tr>
<td>Sulfate</td>
<td>2.08E−02</td>
<td>0.85</td>
</tr>
<tr>
<td>Chloride</td>
<td>2.00E−02</td>
<td>1.43</td>
</tr>
<tr>
<td>Calcium</td>
<td>2.40E−02</td>
<td>1.54</td>
</tr>
<tr>
<td>Alkalinity</td>
<td>7.06E−01</td>
<td>1.44</td>
</tr>
<tr>
<td>Temperature</td>
<td>−4.45E−02</td>
<td>−6.04</td>
</tr>
<tr>
<td>Flow</td>
<td>1.93E−02</td>
<td>2.65</td>
</tr>
<tr>
<td>Wet width</td>
<td>3.06E−02</td>
<td>1.84</td>
</tr>
<tr>
<td>Maximum depth</td>
<td>1.05E−01</td>
<td>0.06</td>
</tr>
<tr>
<td>% Natural</td>
<td>−1.40E−02</td>
<td>−1.17</td>
</tr>
<tr>
<td>Drainage area</td>
<td>9.52E−02</td>
<td>3.18</td>
</tr>
<tr>
<td>Distance to source</td>
<td>5.13E−02</td>
<td>3.20</td>
</tr>
<tr>
<td>Siliceous sampling sites</td>
<td>−6.79E−02</td>
<td>−3.17</td>
</tr>
<tr>
<td>Mainstream sampling sites</td>
<td>5.44E−02</td>
<td>4.97</td>
</tr>
<tr>
<td>Spring season</td>
<td>−5.62E−02</td>
<td>−6.43</td>
</tr>
<tr>
<td>Winter season</td>
<td>8.94E−01</td>
<td>0.71</td>
</tr>
</tbody>
</table>

![Fig. 3. Variation partitioning of chlorophyll-α among the three explanatory data sets: physiographical variables, physicochemical variables and geology. See Section 2.3 in methods for the variables used in each set. Values are adjusted R² coefficients. Bold figures indicate significant unique effects (permutation tests, p < 0.05); note that shared effects cannot be tested.](image-url)
Fig. 4. Variation partitioning of chlorophyll-a with the physiographical and physicochemical variables in the three ecotypes (calcareaous, siliceous and main river reaches). Dominant effects are highlighted with arrows. Values are adjusted R² coefficients. Bold figures indicate significant proportions of variance explained (permutation tests, p < 0.05).

obtained here confirm that nutrients are key factors in explaining chlorophyll-a variation, but also large-scale factors such as the drainage area or specific land uses play an important role in driving chlorophyll-a distribution both at the scale of the whole watershed and in the different geophysical units of the Guadiana watershed. Variation partitioning showed that chlorophyll concentration was strongly related to the shared effects of physicochemical and physiographical factors. This result linked land uses, mostly influenced by anthropogenic practices to stream chemical and ecological condition. Chlorophyll concentration in the main river reaches was mainly affected by physiographical factors, as it is indicated by the variation partitioning analysis. PLSR results highlighted that drainage area was the most important physiographical factor accounting for the chlorophyll-a variation. Runoff and subsurface flow are directly related to drainage area, and are the main drivers in elevating nutrient loading to streams through the transport of fertilizers. All these results show that chlorophyll concentration provides critical information to the ecological status of large basins, which should be considered in focusing the management efforts.

5. Conclusions

Our analyses showed that patterns of chlorophyll distribution can be attributed not only to water quality variation, but that a considerable proportion of variation in chlorophyll-a concentration can be explained by physiographical factors. Therefore models predicting algal biomass in a watershed require the use of multiple scales including physical and chemical-local factors that directly provoke algal responses, and also of physical large-scale factors that exert indirect effects on algae.

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