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Article

# Phytoplankton Diversity Relates Negatively with Productivity in Tropical High-Altitude Lakes from Southern Ecuador

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**Abstract:** Tropical high-altitude lakes are vital freshwater reservoirs in the Andean regions. They are heavily threatened by human activities that may alter their functioning and hamper the provisioning of key ecosystem services such as water supply. Despite their ecological and social relevance, we know little about these waterbodies, especially regarding the factors influencing their functioning. Here, we explored the links between several environmental variables and phytoplankton productivity, measured as chlorophyll-a concentration and total phytoplankton biovolume. For this, we sampled twenty-four tropical high-altitude lakes located over three-thousand meters above sea level in Southern Ecuador. We found that four abiotic factors combined explained 76% of the variation in chlorophyll-a concentration amongst lakes. Contrary to what studies from temperate regions suggest, taxa richness was not related to either chlorophyll-a concentrations or total phytoplankton biovolume. Moreover, phytoplankton biovolume diversity was negatively correlated to both chlorophyll-a concentrations and total phytoplankton biovolume. This was due to a very uneven distribution of productivity amongst taxa in the more productive lakes. To the best of our knowledge, this is the first attempt to explore the determinants of phytoplankton functioning in tropical high-altitude lakes. We hope that this study will help to establish a baseline for evaluating the consequences of human activities in the ecology and functioning of this vital but fragile ecosystem. Our results suggest that by modifying the abiotic and biotic parameters of tropical high-altitude lakes, human activities can indirectly impact their functioning and their capacity to provide vital ecosystem services.

**Keywords:** biodiversity; Ecuador; páramo; phytoplankton; productivity; tropical high-altitude lakes

## 1. Introduction

High-altitude lakes, also called high-mountain lakes, are important natural freshwater reservoirs for human consumption, irrigation and hydropower production purposes in Andean regions [1–4]. Like high-altitude temperate lakes, tropical high-altitude lakes (hereafter TRHALs) have low average water temperatures. The latter are negatively related to altitude and cloud cover as a determinant of solar incidence. TRHALs also can have extreme diel water temperature variations. They are submitted to strong winds and receive intense solar UV radiations. Generally, but not always, they are low in nutrients [5–8]. Due to their low latitudes, TRHALs have some specific features not shared by high-altitude temperate lakes. This includes moderate or no seasonality, no ice cover, polymictic mixing regimes that often have a complex thermal structure, intense UV radiation through the year, high dissolved organic carbon and low UV transparency [2–5,9–13]. All these features make TRHALs unique extreme freshwater ecosystems. One type of TRHALs are the *páramo* lakes, located above

the tree line between approximately from 3200 to 4500 meters above sea level (m.a.s.l.) and filled almost exclusively by rain and groundwater. Another type are the *glacial* lakes, located at even higher altitudes and are fed directly by glacier melting waters. These two types of lakes can show important differences in both abiotic and biotic characteristics [13]. This study focuses on *páramo* lakes, located between 3288 and 3362 meters above sea level without a direct connection to glaciers.

TRHALs show a wide range of phytoplankton productivity levels, with chlorophyll-a concentrations ranging from below  $1 \mu\text{g L}^{-1}$  to values over  $8 \text{mg L}^{-1}$  [4,6,14–17]. Their phytoplanktonic productivity has been negatively related to depth [4], UV radiation [18] and positively to pH [16], total phosphate [4] and total nitrogen [13]. Productivity in TRHALs has often been described as nutrient limited [4,6,14]. Studies of phytoplankton diversity in TRHALs reported over a hundred different genera in different regions of Ecuador [4,13,17]. Regarding the phytoplankton diversity per lake, previous studies counted from 5 to 45 genera per lake in Southern Ecuador [4,13], with taxonomic richness decreasing with altitude and increasing with conductivity [13].

Despite their ecological and social relevance, we still know little about the abiotic or biotic factors influencing the functioning of tropical high-altitude lakes (TRHALs). It is well established that under controlled experimental conditions, phytoplankton communities with multiple species produce more biomass than monocultures [19–21] and that species richness and biomass are positively related [22]. A recent meta-analysis on the importance of species richness for productivity suggests that the above-mentioned effects are even stronger in natural conditions [23]. However, this synthesis only included information from two studies based on phytoplankton communities from temperate regions. To date, observational studies on the relationship between phytoplankton diversity and functioning in freshwater lakes have completely ignored TRHALs (Table 1, [24–51]).

**Table 1.** Exhaustive list of studies about the relationship between phytoplankton diversity and functioning in freshwater lentic ecosystems around the world. Latitudes in bold represent studies including tropical lakes (i.e., below  $23^\circ$  either South or North). Altitudes in bold represent studies in lakes above 2500 m above sea level. Notice that no previous study has considered tropical high-altitude lakes. \* refers to “lakes” but some studies include other type of waterbodies such as ponds and reservoirs. (n.a) means not available in the original publication.

Study	Country	Lake(s) *	Latitude °	Altitude (m.a.s.l)
Interlandi & Kilham 2001	USA	Jackson, Lewis & Yellowstone	43N–44N	2064–2372
Grover & Chrzanowski 2004	USA	Joe Pool & Eagle Mountain	32N–33N	162–198
Passy & Legendre 2006	USA	>50 lakes	<b>21S</b> , 25N–68N	n.a.
Ptacnik et al. 2008	Finland, Norway, Sweden	ca. 500 lakes	55N–65N	n.a.
Das et al. 2008	Canada	Elk, Shawnigan & Sooke	48N	60–183
Striebel et al. 2009	Germany	46 lakes	n.a.	n.a.
Hogsden et al. 2009	USA	Little Rock	46N	500
Cardinale et al. 2009	Norway	492 lakes	58N–70N	n.a.
Kruk et al. 2009	Uruguay	18 lakes	33S–35S	0–5
Vogt et al. 2010	Canada	65 lakes	48N	n.a.
Korneva 2010	Russia	9 reservoirs & 7 lakes	49N–59N	10–120
Korhonen et al. 2011	Finland	100 lakes	59N–66N	n.a.
Stomp et al. 2011	USA	540 lakes & reservoirs	27N–49N	1–2753
Pomati et al. 2012	Switzerland	Zurich	47N	406

Table 1. Cont.

Study	Country	Lake(s) *	Latitude °	Altitude (m.a.s.l)
Borics et al. 2012	Hungary	26 lakes	n.a.	n.a.
Fornarelli et al. 2013	Australia	Fitzroy falls reservoir	34S	60–822
Weyhenmeyer et al. 2013	Sweden	205 lakes	56N–69N	n.a.
Palfy et al. 2013	Hungary	Balaton	46N	105
Skacelova & Leps 2014	Czech Republic	>400 lakes *	48N–50N	160–720
Filstrup et al. 2014	USA	131 lakes	40N–43N	<500
Fernandez et al. 2014	Argentina	Paso de las Piedras reservoir	38S–39S	155
Santos et al. 2014	Brazil	19 reservoirs	<b>13S–18S</b>	300–820
Zimmerman & Cardinale 2014	USA	1033 lakes	26N–49N	<b>0–3403</b>
Beyter et al. 2016	USA	Las Cruces pond	32N	1190
Tian et al. 2016	China	Nansihu	34N–35N	28
Costa et al. 2016	Brazil	7 reservoirs	6S–8S	413–560
Fontana et al. 2017	Switzerland, Romania	28 lakes	44N–47N	0, 406, 435
Abonyi et al. 2018	Finland, Norway, Sweden	n.a.	55N–65N	<300
This study	Ecuador	24 lakes	<b>3.56S–3.62S</b>	<b>&gt;3280</b>

The uniqueness of tropical high-altitude lakes suggests that previous findings from temperate lakes about the relationship between phytoplankton diversity and functioning might not be extrapolated. The main purpose of the current study is to depict potential links between phytoplankton biodiversity and productivity, quantified as chlorophyll-a concentration and total phytoplankton biovolume. In addition, we aimed to explore if other abiotic variables, independently or in addition to biodiversity, relate to phytoplankton productivity. For this, we examined a set of twenty-four tropical high-altitude shallow lakes located over 3280 meters above sea level in Southern Ecuador.

## 2. Materials and Methods

### 2.1. Study System

*Tres Lagunas* belongs to a tropical high-altitude wetland ecosystem called *páramo* [1]. It is located at the eastern range of the southern Ecuadorian Andes, at approximately 20 km from Saraguro and 95 km from Loja, at the border of the Oña and Zamora-Chinchi provinces (Figure 1).

This ecosystem harbors hundreds of small shallow freshwater lakes where rivers in the Amazon mountain range (heading to the Pacific Ocean) and the Andean mountain range (heading to the Atlantic Ocean) begin. The lake system *Tres Lagunas* consists of around 75 shallow lakes, including three larger ones: *Condorshillu* (6.3 ha), *Tres Lagunas* (8.5 ha) and *Laguna Grande* (12 ha). For the present study, we included the three larger lakes (as major freshwater reservoirs) and another 21 smaller lakes that were randomly selected in the map. The 24 lakes had areas ranging from 0.5 to 12 ha, maximum depths from 1 to 9 m and altitudes above sea level ranging from 3288 to 3362 m. Eleven of these lakes are in the Amazon (eastern) mountain range and thirteen in the Andes (western) range. The GPS coordinates of the center of the *Tres Lagunas* system are 3°35'50" S and 79°3'46" W.

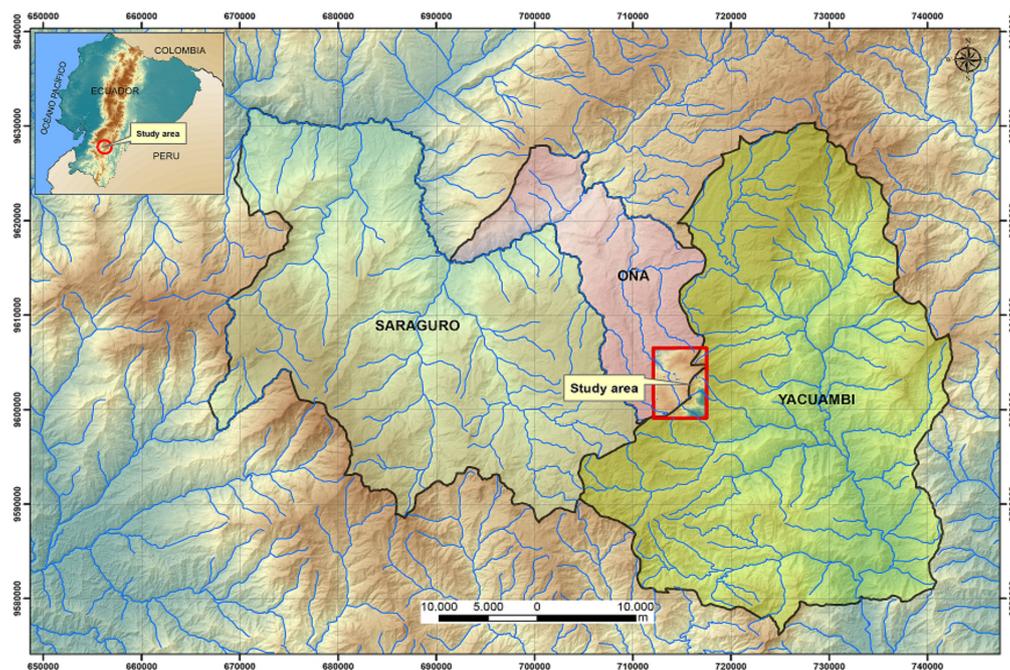


Figure 1. Location of the *Tres Lagunas* wetland system in southern Ecuador.

## 2.2. In Situ Analyses and Sampling

The field work described in this study was performed in November 2016. *In situ*, we collected data on total chlorophyll-*a* concentration ( $\mu\text{g L}^{-1}$ ) with a bbe Moldaenke fluoroprobe. Dissolved oxygen ( $\text{mg L}^{-1}$ ), redox potential (mV), conductivity ( $\mu\text{S/cm}$ ), pH and water temperature ( $^{\circ}\text{C}$ ) were measured at the same locations with a HQ40D HACH® portable multiprobe. All the mentioned variables were measured once for each lake near its center. Water samples for nutrient analyses were collected in 10 mL plastic acid-washed tubes at 0.5 m subsurface depth near the center of the lakes on the same days as the *in situ* measurements. We preserved the water samples with 98% sulfuric acid for further chemical analyses. For phytoplankton analyses, we collected samples in 100 mL acid-washed plastic bottles at 0.5 m subsurface depth near the center of the lakes. We preserved them with 1% final concentration glutaraldehyde, neutralized to pH 7 with NaOH. All samples were immediately stored in the dark, under cold conditions and sent by plane to the laboratory to be analyzed. Due to the harsh access conditions of the wetland and to the remoteness of some lakes, the *in situ* measurements and water samplings of the 24 lakes took four complete days (from November 8th to 11th, 2016). All measurements and water samplings were performed from 10 AM to 3 PM.

## 2.3. Ex Situ Laboratory Analyses

Total phosphate ( $\mu\text{g L}^{-1}$ ) and dissolved nitrite/nitrate ( $\mu\text{g L}^{-1}$ ) quantifications were performed in the laboratory on an AQ2 discrete analyzer, based on EPA (United States Environmental Protection Agency) 365.1 version 2 and EPA 353.2 version 2 methods respectively. Phytoplankton abundances were determined using an inverted microscope with 40x magnification. Phytoplankton from water samples was first concentrated via sedimentation in 50 mL Falcon tubes for 24 h. For cell counting, we used the Sedgwick-Rafter camera cell counter and included 100 fields of vision for each sample/lake. A field of vision measured  $0.38 \text{ mm}^2$ . We took digital pictures of each field of vision for further phytoplankton identification and counting. For each taxon, we estimated the average cell biovolume (in  $\mu\text{m}^3$ ) using at least fifty individuals (see Table S1 for some examples on the estimations of average cell biovolumes). In each sample, the biovolume of each taxon was calculated as the product of the average cell biovolume by its cell density (in cells per ml). Total phytoplankton biovolume (biovolume of algae per volume of water,  $\mu\text{m}^3 \text{ mL}^{-1}$ ) was calculated as the sum of the biovolumes of all the taxa

present in the sample. Phytoplankton richness in each sample was calculated by counting the number of different taxa at the genus level. As another measure of phytoplankton diversity, we estimated the Shannon's diversity index ( $H'$ ) based on the biovolumes of each genus in each lake/sample. The Shannon's diversity index was calculated with the following formula:

$$H' = - \sum_{i=1}^S p_i * \ln(p_i)$$

where  $S$  is the number of genera in the sample and  $p_i$  is the relative biovolume of each taxon to total phytoplankton biovolume. Thus, we refer to this variable as phytoplankton biovolume diversity. The value of the phytoplankton biovolume diversity increases with the number of genera and with the evenness in the contribution of each genus to total phytoplankton biovolume. Thus, samples with only a few taxa contributing in large proportion to total biovolume would have a low phytoplankton biovolume diversity (low Shannon's index based on biovolumes). On the contrary, samples with most taxa contributing in similar proportions to total biovolume would have a high phytoplankton biovolume diversity (high Shannon's index based on biovolumes). Professor Miriam Steinitz-Kannan (Northern Kentucky University) and Doctor Kalina Manoylov (Georgia College and State University) supervised and validated the taxonomic identification of the taxa.

### 3. Data Analyses

Our dataset included four geographic variables: lake surface (in hectares, ha), altitude (in meters above sea level, m.a.s.l.), latitude (in degrees), longitude (in degrees); seven physico-chemical variables: water temperature (in °Celsius), pH, redox potential (in mV), conductivity (in S/m), oxygen concentration (in mg L<sup>-1</sup>), total phosphate (in µg L<sup>-1</sup>), dissolved nitrites/nitrates (in µg L<sup>-1</sup>) and four biological variables: taxonomic richness (number of genera), phytoplankton biovolume diversity (no units), chlorophyll-a (in µg L<sup>-1</sup>) and total phytoplankton biovolume (in µm<sup>3</sup> mL<sup>-1</sup>, which represents the biovolume of phytoplankton in µm<sup>3</sup> per mL of lake water). We used chlorophyll-a concentrations and total phytoplankton biovolume as two proxies of phytoplankton productivity. We ran linear-models linking single or multiple of the above-mentioned variables to phytoplankton productivity (i.e., chlorophyll-a and total biovolume separately). We then used the AIC (Akaike information criterion) to determine the abiotic (chemical, physical, geographic) or biotic variables that better described chlorophyll-a and total phytoplankton biovolume. We used JMP (SAS, version 14.0.0) for all statistical analyses. Total phytoplankton biovolume and surface of lakes were log transformed to improve the normality of the data.

### 4. Results

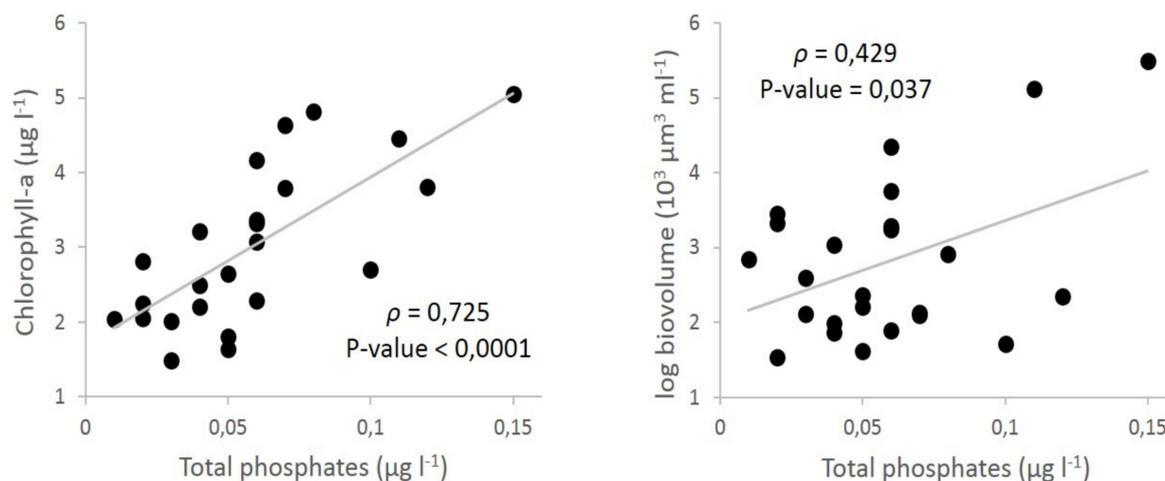
Chlorophyll-a concentrations in the lakes from *Tres Lagunas* ranged from 1.49 to 5.05 µg L<sup>-1</sup>, with an average concentration of 3.01 µg L<sup>-1</sup>. Total phytoplankton biovolume spanned over four orders of magnitude, from 34.08.10<sup>3</sup> to 31.02.10<sup>7</sup> µm<sup>3</sup> mL<sup>-1</sup>, with an average value of 20.1.10<sup>7</sup> µm<sup>3</sup> mL<sup>-1</sup>. Chlorophyll-a concentration and total phytoplankton biovolume (log transformed) were positively correlated across the lakes (*correlation coefficient* = 0.514,  $P$  = 0.01,  $N$  = 24). Genera richness ranged from 15 to 43 per lake with an average richness of 26.75 genera per lake. The less diverse lake in terms of phytoplankton biovolume diversity had a Shannon's index of 0.057 whereas the more diverse one had a Shannon's index of 0.939. The average phytoplankton biovolume diversity (Shannon's) index of the lakes was 0.521. These two measures of phytoplankton diversity (genera richness and phytoplankton biovolume diversity) were positively related (*correlation coefficient* = 0.343,  $P$  = 0.1,  $N$  = 24), but would still encompass different aspects of phytoplankton's diversity.

Four abiotic variables correlated well to chlorophyll-a concentration (Table 2). This included total phosphate concentration (Figure 2), oxygen concentration and altitude, that related all positively to chlorophyll-a concentrations. This means that lakes with higher phosphate concentrations, more

dissolved oxygen levels and located at higher altitudes showed higher chlorophyll-a concentrations. The percentages of variance in chlorophyll-a concentrations explained by total phosphate, oxygen and altitude were 53%, 31% and 19% respectively. The surface of the lakes (log transformed) correlated negatively to chlorophyll-a, meaning that smaller lakes had higher chlorophyll-a concentrations than larger lakes. Only total phosphate concentrations related well and positively to total phytoplankton biovolumes (i.e., log biovolume, Figure 2, Table 2).

**Table 2.** List of abiotic and biotic variables (related variables) that correlated significantly with either chlorophyll-a or total biovolume (response variable). Variables are ranked from more positive to more negative correlation coefficients and includes only variables with  $p$ -values below 0.1.

Response Variable	Related Variable	Correlation Coefficient	$p$ -Value
Chlorophyll-a	Total Phosphate	0.725	<0.0001
Chlorophyll-a	Oxygen	0.559	0.004
Chlorophyll-a	Altitude	0.436	0.033
Log biovolume	Total Phosphate	0.429	0.037
Chlorophyll-a	Shannon (Biovolume)	−0.393	0.058
Chlorophyll-a	Log Surface	−0.504	0.012
Log biovolume	Shannon (Biovolume)	−0.658	<0.001

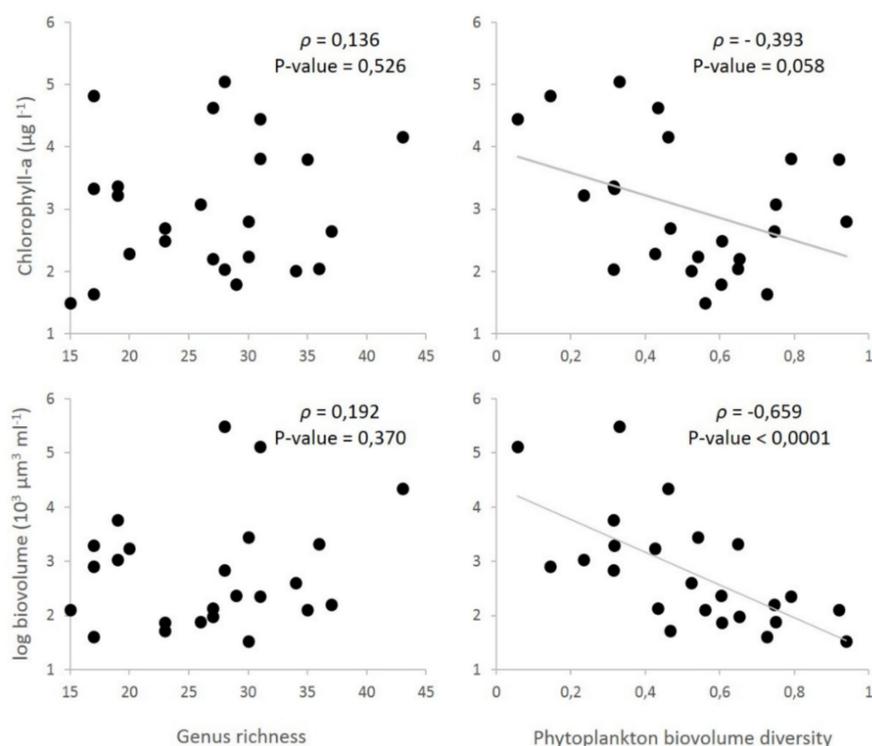


**Figure 2.** Correlations between total phosphates (phosphates, in  $\mu\text{g L}^{-1}$ ) and chlorophyll-a concentrations ( $\mu\text{g L}^{-1}$ , left panel) and between total phosphates and total phytoplankton biovolume (log biovolume in  $10^3 \mu\text{m}^3 \text{mL}^{-1}$ , right panel). Indicated statistics are the correlation coefficients ( $\rho$ ) and  $p$ -values. Grey lines represent linear fits.

In other words, lakes with higher phosphate concentrations had also higher total phytoplankton biovolumes. Together, the correlation analyses suggest that phytoplankton production in the *Tres Lagunas* system, quantified as chlorophyll-a and total biovolume, might be partially phosphorous limited.

The two measures of phytoplankton biodiversity, genera richness (taxa richness) and Shannon's diversity index (phytoplankton biovolume diversity), showed different relationships with chlorophyll-a concentrations and total phytoplankton biovolumes (Table 2, Figure 3). Taxa richness was not related to either chlorophyll-a concentrations or total phytoplankton biovolumes. On the contrary, phytoplankton biovolume diversity (measured as Shannon's diversity index based on biovolumes) was negatively correlated to both chlorophyll-a concentrations and total phytoplankton biovolumes (Figure 3). This suggests that lakes dominated by fewer genera had higher chlorophyll-a concentrations and total biovolume levels than lakes with more even distributions of biovolume amongst different taxa.

Regarding the negative relationship between phytoplankton biovolume diversity and total biovolume (Figure 3, low right hand panel), a closer look at data allowed us to observe some interesting trends. We noticed the presence of three groups of lakes based on their total phytoplankton biovolumes. The first group includes three lakes with values of total phytoplankton biovolume above  $1.10^6 \mu\text{m}^3 \text{mL}^{-1}$  and Shannon's diversity index values spanning from very low to intermediate. The analysis of the taxonomic composition of each lake showed that the communities of the two lakes with highest total biovolumes were largely dominated by *Mougeotia*, a filamentous alga (family: Zygnemataceae). This genus represented up to 96% of the total biovolume and 61% of the cell counts. The lake with the third highest total biovolume was largely dominated by *Peridinium*, a dinoflagellate representing 72% of the total biovolume and 74% of cell counts. This information is clearly showing that an extremely uneven distribution of biovolume amongst the different taxa explains the combined high total biovolume and low biovolume diversity values of these three lakes. The second group of lakes includes nine waterbodies with total phytoplankton biovolumes ranging from  $0.5.10^4$  to  $1.10^6 \mu\text{m}^3 \text{mL}^{-1}$  and with Shannon indexes varying from low to intermediate/high. Overall, these lakes also reported a large dominance of biovolume production (up to 95%) by the dinoflagellate *Peridinium*, or by colonial diatoms such as *Synedra*, *Fragilaria* or *Asterionella*. However, these taxa did not over-dominate cell counts, with percentages of total abundance ranging from 25 to 40%. Finally, a group of twelve lakes had biovolume values below  $0.5.10^4 \mu\text{m}^3 \text{mL}^{-1}$  and phytoplankton biovolume diversities spanning from intermediate to high. In these lakes, the above-mentioned genera represented less than 70% of the total biovolume and less than 38% of the cell counts. In lakes from groups 2 and 3, the genus *Mougeotia* was not recorded at all.



**Figure 3.** Correlations between genus richness (left panels), phytoplankton biovolume diversity (Shannon's diversity based on biovolume, right panels), chlorophyll-a (in  $\mu\text{g L}^{-1}$ , upper panels) and total phytoplankton biovolume (log biovolume in  $10^3 \mu\text{m}^3 \text{mL}^{-1}$ , lower panels). Indicated statistics are the correlation coefficients ( $\rho$ ) and  $p$ -values of the correlation. Grey lines represent linear fits for  $P$  values below 0.1.

Overall, the analysis of the composition of phytoplankton communities suggests that the observed negative relationship between total biovolume and phytoplankton biovolume diversity (Figure 3) can

be largely explained by a very uneven distribution of biovolume amongst taxa. Total phytoplankton biovolume in the samples from *Tres Lagunas* decreased as the dominance, both in biovolume and cell counts, of some taxa such as *Mougeotia* and *Peridinium* decreased. As the contribution of each taxa to total chlorophyll-a could not be determined, we can only speculate about the reasons why chlorophyll-a decreases as phytoplankton biovolume diversity increases. Based on the distribution of the data from the positive correlation between total phytoplankton biovolume and chlorophyll-a concentration, it is quite possible that the uneven contribution of taxa to total biovolume is at the origin of a negative correlation between biovolume diversity and chlorophyll-a concentration. Five lakes were characterized with low biovolume diversity but very high chlorophyll-a values, three of which also showed the highest biovolume levels that resulted from the dominance of one single taxon.

After fitting linear models with all possible combinations of single and multiple factors (both abiotic and biotic) to chlorophyll-a concentrations and total phytoplankton biovolumes, we ranked these models according to the Akaike criteria (AICc, Table 3).

**Table 3.** Summary table of the different linear models (single and multiple factor) linking abiotic and biotic variables to chlorophyll-a. Models are ranked by increasing AICc (Akaike information criterion) values. *Oxygen* stands for oxygen concentration, *altitude* is for altitude above sea level.

Factors Included in Model	R <sup>2</sup>	p-Value	AICc
Total phosphate, oxygen, altitude, log surface	0.777	<0.0001	50.764
Total phosphate, oxygen, log Surface	0.724	<0.0001	52.249
Total phosphate, altitude	0.684	<0.0001	52.322
Total phosphate, oxygen, altitude	0.719	<0.0001	52.707
Total phosphate, altitude, log Surface	0.717	<0.0001	52.877
Total phosphate, oxygen	0.628	<0.0001	56.198
Total phosphate, log Surface	0.586	<0.0001	58.776
Total phosphate	0.525	<0.0001	59.166
Oxygen, log Surface	0.578	0.0001	59.244
Oxygen, altitude, log Surface	0.602	0.0003	61.099
Oxygen	0.312	0.0045	68.062
Altitude, log Surface	0.379	0.0067	68.52
Oxygen, altitude	0.375	0.0071	68.659
Log Surface	0.254	0.012	70.011
Altitude	0.190	0.0331	71.984

For chlorophyll-a concentration, the linear model that better described variation in the data (77.7%, with the lowest AICc value) included four abiotic factors: total phosphate, oxygen, altitude and log surface. As shown previously with the correlations, the best single abiotic predictor of chlorophyll-a concentration was total phosphate, explaining 52.5% of the variation amongst lakes. None of the biotic variables included in our study appeared in the models that better predicted chlorophyll-a concentrations. For total phytoplankton biovolume, the model that better described variation in the data (50.3%, with lowest AICc, Table 4) included total phosphate concentration and phytoplankton biovolume diversity (Shannon's index based on biovolumes). The best single predictor of total phytoplankton biovolume was phytoplankton biovolume diversity (Shannon's diversity), explaining 43.3% of the variation in total biovolume among lakes.

**Table 4.** Summary table of the different linear models (single and multiple factor) linking abiotic and biotic variables to total phytoplankton biovolume. Models are ranked by increasing AICc (Akaike information criterion) values. Only models with  $p$ -values below 0.05 are presented.

Factors Included in the Model	R <sup>2</sup>	$p$ -value	AICc
Total phosphate, Shannon's diversity	0.503	<0.001	63.223
Shannon's diversity	0.433	<0.001	63.466
Total phosphate	0.184	0.0367	72.226

## 5. Discussion

The levels of chlorophyll-a measured in this group of lakes from *Tres Lagunas* are comparable to most previous studies in tropical high-altitude lakes (TRHALs) from Mexico, Bolivia and other parts of Ecuador [6,13,15–17]. Like in a recent study in the Cajas National Park in Southern Ecuador [4], chlorophyll-a values correlated positively with total phosphate concentrations. However, another study with similar levels of phytoplankton production involving TRHALs in Ecuador found that total nitrogen concentration was the only variable that explained some variation in chlorophyll-a amongst lakes [13]. Other abiotic variables such as pH [16] and UV radiation [18] have been related to chlorophyll-a concentrations in TRHALs as well. Such discrepancies amongst studies in terms of the abiotic variables that relate with phytoplankton's productivity (with chlorophyll-a as a proxy) suggest that the large geographic variation in the productivity of TRHALs can hardly be predicted by one single abiotic factor. In line with this hypothesis, our analysis showed that chlorophyll-a concentrations had simultaneous positive and negative links with several abiotic variables, including phosphate concentration, oxygen concentration, altitude and lake surface. According to the results of the linear models, these four abiotic variables together explained 78% of the variation in chlorophyll-a levels amongst the lakes from *Tres Lagunas*. In brief, our results showed smaller lakes located at higher altitudes, with higher concentrations of oxygen and total phosphates tend to be more productive in terms of chlorophyll-a concentrations.

Despite the positive correlation of chlorophyll-a with total phytoplankton biovolume observed in our dataset, the links between the different abiotic variables and total biovolume were weak. Among all the abiotic variables included in this study, only total phosphate concentration related to total phytoplankton biovolume, explaining just 18% of its variation (versus 52% for chlorophyll-a). This result suggests that other variables not included in our study (abiotic or biotic) might be more relevant as determinants of total phytoplankton biovolume. Previous studies about the determinants of phytoplankton production in tropical high-altitude lakes using total biovolume as proxy are very rare. This can be explained because acquiring total biovolume information requires more sophisticated equipment (e.g., particle counter, cytometer) or time demanding techniques (e.g., microscopy). In a recent study, total phytoplankton biomass was measured along sixteen lakes in the Ecuadorian Andes, but none of the abiotic variables included related to phytoplankton biomass [13]. In our study, only phytoplankton biovolume diversity index strongly improved the capacity of the linear models to predict total biovolume variation among lakes. Alone, it was the best single predictor of total biovolume (43.3% of the variation) and together with total phosphate explained up to 50.3% of the variation.

So far, studies on the relationship between phytoplankton diversity and ecosystem functioning in freshwater lakes have overlooked tropical high-altitude lakes. To be best of our knowledge, this study represents the first attempt to link phytoplankton diversity to productivity in these extreme aquatic ecosystems. Our results revealed no relation between taxonomic richness and either chlorophyll-a or total phytoplankton biovolume. A similar null pattern between taxonomic richness and functioning was described before in temperate lakes from Finland [27] but contradicts most studies from temperate lakes that show a positive impact of taxonomic richness on phytoplankton productivity [27,29,35]. Moreover, phytoplankton biovolume diversity, measured as the Shannon's diversity index based on biovolumes, correlated negatively with both chlorophyll-a and total phytoplankton biovolume.

As explained earlier, the Shannon's diversity index used here was based on the contribution of each genera's biovolume to total biovolume. In other words, it is a measure of the evenness in the distribution of total biovolume across the different genera in a sample or lake. Total biovolume can relate to biovolume diversity via two non-exclusive mechanisms: firstly, via a more even distribution of biovolumes across taxa (higher Shannon's index). This would result in a positive correlation between phytoplankton biovolume diversity and total biovolume. Secondly, by having only a few taxa contributing largely to total biovolume, which results in lower Shannon's index values. This would result in a negative relationship between total biovolume and biovolume diversity, as observed in our dataset.

Although not included as one of the factors explaining much variation in chlorophyll-a amongst lakes, phytoplankton biovolume diversity turned out to be the best single predictor of total phytoplankton biovolume. The analysis of community composition revealed that this pattern was mainly due to changes in the dominance of a few taxa amongst lakes, both in terms of abundance and biovolume. A reduction in the prevalence of taxa such as *Mougeotia* (a filamentous algae) and *Peridinium* (a dinoflagellate) resulted in a concomitant increase of biovolume diversity and a decrease of total phytoplankton biovolume. Such negative links between diversity and productivity, due to the dominance of some taxa, are not very frequent but have been reported in temperate lakes [34,41,43,50]. Previous observational studies about the importance of biodiversity for ecosystem functioning in freshwater ecosystems have led to the belief that phytoplankton diversity has a general positive impact on productivity [23]. This means that in order to be more productive, freshwater bodies must contain more species of phytoplankton. However, this conclusion was based on a large dataset that included over 1150 sites from Scandinavia [27] and North America [46] but containing no single data from high-altitude tropical lakes. Our results offer original empirical evidence suggesting that such effects are not universal. In our set of lakes, the most productive lakes were not necessarily the more diverse ones, suggesting that some conclusions driven from temperate lakes should not be extrapolated to other ecosystems such as *páramo* lakes. To confirm our findings, we advocate for additional studies testing the influence of phytoplankton diversity on functioning from a wider variety of freshwater ecosystems.

Phytoplankton productivity in the *Tres Lagunas* lakes showed large geographic variation, due largely to variation in abiotic and biotic factors, as reported in previous studies from temperate regions [27,31,35,36,46]. Overall, chlorophyll-a was strongly related to four abiotic factors whereas total biovolume was linked to phytoplankton biovolume diversity. However, the scope of these findings has at least two limitations. Firstly, lakes were sampled only once, thus ignoring the spatial and temporal variability in the abiotic and biotic parameters considered. It is possible that the relationships among variables described in this study might vary when considering other spatiotemporal scales [24,35]. Secondly, the patterns described here are purely correlational because no causal relationships amongst variables can be established using only observational data [27,31]. Our study addresses diversity as a possible determinant of phytoplankton productivity, but it is well known that the alternate perspective, with productivity as a determinant of diversity can be considered too [24,31,36].

Tropical high-altitude lakes (TRHALs) are the major freshwater reservoirs in Andean regions. They are very vulnerable to human activities, putting their own functioning and the provisioning of key ecosystem services such as water supply at risk [1–4,52,53]. As in other South American high-altitude ecosystems, road construction, controlled fires, agriculture, livestock and extreme sports are modifying the *Tres Lagunas* ecosystem. To our best knowledge, no environmental impact studies have ever been made in this region and no actions to mitigate their potential impacts have been considered. We hope this study will help to establish a baseline for evaluating some of the future consequences of human activities in the ecology and functioning of this vital but fragile ecosystem. Our results suggest that by impacting abiotic and biotic parameters of these lakes, human driven activities can also have either positive or negative impacts on the functioning of tropical high-altitude lakes and the provisioning of ecosystem services.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/2071-1050/11/19/5235/s1>.

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**Data Availability:** Data included in this study will be available in the Dryad Digital Repository upon acceptance.

**Conflicts of Interest:** The authors declare no conflict of interest.

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