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RESEARCH ARTICLE

Effects of temporal and spatial variability in energy fluxes on phytoplankton

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Abstract

Climate change has significantly altered the energy dynamics of lakes; however, little is known of how the temporal and spatial variation in energy fluxes impacts the structure and function of lake ecosystems. This study combined long-term (2011–2018) measurements of lake energy fluxes with environmental, nutrient, and phytoplankton data at five stations to investigate the effects of variably energy fluxes on phytoplankton production and composition in a large, shallow, eutrophic lake (Lake Taihu, China). Overall, atmospheric warming increased heat storage and water temperatures, with energy fluxes exhibiting significant spatial heterogeneity. Specifically, faster rates of energy input and higher energy budgets increases were observed in the clear macrophyte-rich regions of the lake compared to turbid hypereutrophic habitats. Temporal variation in energy fluxes was a strong predictor of primary production (as chlorophyll *a*), the spatial extent of cyanobacterial blooms, and phytoplankton biodiversity at the whole-lake level, whereas 42.4% of the variation in phytoplankton community composition was explained by a combination of energy fluxes, nutrients, and other environmental factors. Cyanobacterial taxa were significantly correlated with nutrients (total nitrogen and phosphorus), while green algal abundance was associated mainly with variations in the energy budget. These findings highlight the spatial variability of energy fluxes driven by local environmental conditions, underscoring the need for climate adaptation and mitigation strategies to account for heterogeneous energy effects on lake production and structure.

Global surface temperatures have risen by ~1.1°C since the pre-industrial era (1850–1900), leading to widespread environmental and societal impacts (IPCC 2023). Lakes are sensitive indicators of this climate change due to their shallow nature, high surface area to volume ratios, and distinct seasonality of energy fluxes (Adrian et al. 2009). Lakes also play a vital role in energy fluxes, water budgets, and regional meteorological conditions due to their high heat storage, thermal inertia, and evaporation characteristics (Ala-Konni et al. 2022; Woolway et al. 2020). However, most research has focused on temperature and evaporation effects (W. Wang et al. 2018; X. Wang et al. 2024), with limited comprehensive analysis of how energy fluxes may regulate lake respond to climate change (Tong et al. 2023; J. Zhou et al. 2023). Therefore, quantification of patterns and consequences of variation in energy fluxes will provide insights into the processes controlling changes in production, structure, and function of lake ecosystems, as well as lentic response to future climate warming.

Climate variability regulates lake structure and function over diverse temporal and spatial scales by altering influxes of energy and matter both directly into the basin as well as into adjacent ecosystems (Leavitt et al. 2009; Dröscher et al. 2009). While solar irradiance is the main source of energy to most lakes (Juday 1940), these short-wavelength fluxes are comparatively stable among years (Kopp 2016) and are responsible mainly for broad intra-annual patterns within lakes (i.e., seasonality). In contrast, atmospheric characteristics

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(temperature, transparency, humidity, kinetic energy of wind, etc.) introduce variation in energy exchanges on shorter timescales by modifying the processes that regulate instantaneous energy transfer between water and the atmosphere (e.g., evaporation, long wavelength thermal transmission) (W. Wang et al. 2018; Zhao et al. 2022). As a result, variation in atmospheric features such as air temperature (AT) are closely correlated to changes in key physical events in lakes such rates of water warming, incidence of thermal stratification, deoxygenation, and timing of ice formation or loss (Leppäranta et al. 2017; Woolway et al. 2020; Jane et al. 2021). Effects of these atmospheric features are further modified by characteristics of the lake (e.g., morphometry, transparency, mixing regime) and surrounding environment (J. Zhou et al. 2023). However, despite the clear role of energy fluxes in regulating the physical processes within lakes, there remains uncertainty as to how spatial and temporal variability in energy fluxes may influence biological features such as lake production and plankton composition (Feng et al. 2016; J. Zhou et al. 2023), thereby complicating generalized predictions about lake responses to future climate change (Friedrich et al. 2018).

Here, we conducted a long-term (2011–2018) analysis of the eddy covariance (EC) measurements at five stations within a large shallow eutrophic lake (Lake Taihu, China) to quantify how the spatial and temporal variability in atmospheric energy exchange affects the production and composition of phytoplankton assemblages. We expected that atmospheric warming should increase energy influx to Lake Taihu, leading to a higher heat content and a warmer water column. However, we predicted that the effects of increased energy flux may be different in turbid eutrophic waters and clear macrophyte-rich habitats, resulting in spatial variability in planktonic responses. Finally, this study aimed to advance our understanding of how variation in lake energy fluxes may interact with other environmental variables, such as nutrient status, to influence phytoplankton assemblages. These analyses were designed to better understand how future atmospheric warming will affect energy fluxes and influence the spatial and temporal variability of lake ecology.

Materials and methods

Study site

Lake Taihu is China's 3rd largest freshwater lake, with an area of 2338 km^2, a mean depth of 2 m, and a maximum depth of 3 m (Qin et al. 2007). The lake remains ice-free year-round, serving as a critical water source for over 9 million people and irrigating millions of hectares of farmland (Qin et al. 2019). Since the 1990s, the northwestern regions of the lake have experienced accelerated eutrophication accompanied by harmful cyanobacteria blooms of *Microcystis* spp. In contrast, the southeastern regions of Lake Taihu exhibit abundant submerged aquatic vegetation and have relatively good (mesotrophic) water quality (Qin et al. 2007). Thus, like other large lakes (e.g., Lake Winnipeg [Canada], Lake Erie [USA]), Lake Taihu exhibits significant spatial variation in its water quality and ecological conditions.

Lake Taihu has a long history of research by national and international scientists (L. Guo 2007; Stone 2011). The basin has one of the longest records of limnological observation in China (since 1989), is currently one of the major components of the Global Terrestrial Observing System, and is an international location for long-term ecological research. In addition to conventional limnological monitoring, energy fluxes into and out of the lake have been measured at five stations during 2011–2018. Consequently, Lake Taihu represents a unique opportunity to explore how the spatial and temporal variability in energy fluxes affects the production and composition of phytoplankton assemblages in a natural freshwater ecosystem.

Eddy flux network and data processing

Eddy covariance analysis is widely used to study energy fluxes in freshwater systems. An in situ EC network was established in Lake Taihu during 2011–2018 (Zhang et al. 2020), consisting of five freshwater sites that represent different biological attributes (e.g., phytoplankton abundance, submerged macrophyte cover), trophic status, and wind-induced mixing regimes, including Meiliangwan (MLW), Dapukou (DPK), Pingtaishan (PTS), Bifenggang (BFG), and Xiaoleishan (XLS) stations (Fig. 1). The MLW and DPK sites are located in the eutrophic or hypereutrophic northern and western regions of Lake Taihu (Secchi depth [SD] = 0.27 ± 0.05 m), respectively, where cyanobacterial blooms are common. Site PTS is situated in the middle of the lake, where blooms are more occasional and strong wind-wave induced turbulence restricts the growth of aquatic vegetation (Secchi = 0.35 ± 0.04 m). Station BFG is located in the relatively clear and shallow eastern region of the lake (Secchi = 0.43 ± 0.08 m), where submerged macrophytes (mainly *Potamogeton malaianus* and *Hydrilla verticillata*) are common, but algal blooms are rare. Station XLS is located in the moderately clear (Secchi = 0.34 ± 0.03 m) but vegetation-free southern region of the lake.

Each EC site was equipped with a system consisting of a sonic anemometer/thermometer, an open-path H_2O/CO_2 infrared gas analyzer, a four-way net radiometer, an anemometer and wind vane, and an AT and humidity probe. The EC stations were installed at a height of 3.5–9.4 m above the water surface. In addition, water temperature (WT) was measured at 30-min intervals at depths of 0.2, 0.5, 1.0, and 1.5 m, as well as in the sediment at about 5 cm below the water–sediment interface. The EC data were recorded at 10 Hz and block-averaged to 30-min intervals for analysis. All variables, including microclimate parameters (air pressure [AP], AT, relative humidity, wind speed [WS], rainfall [R]), radiation fluxes (upward and downward shortwave and longwave radiation), and WT at various depths, were reported as 30-min averages over the period from January 2011 to December 2018.

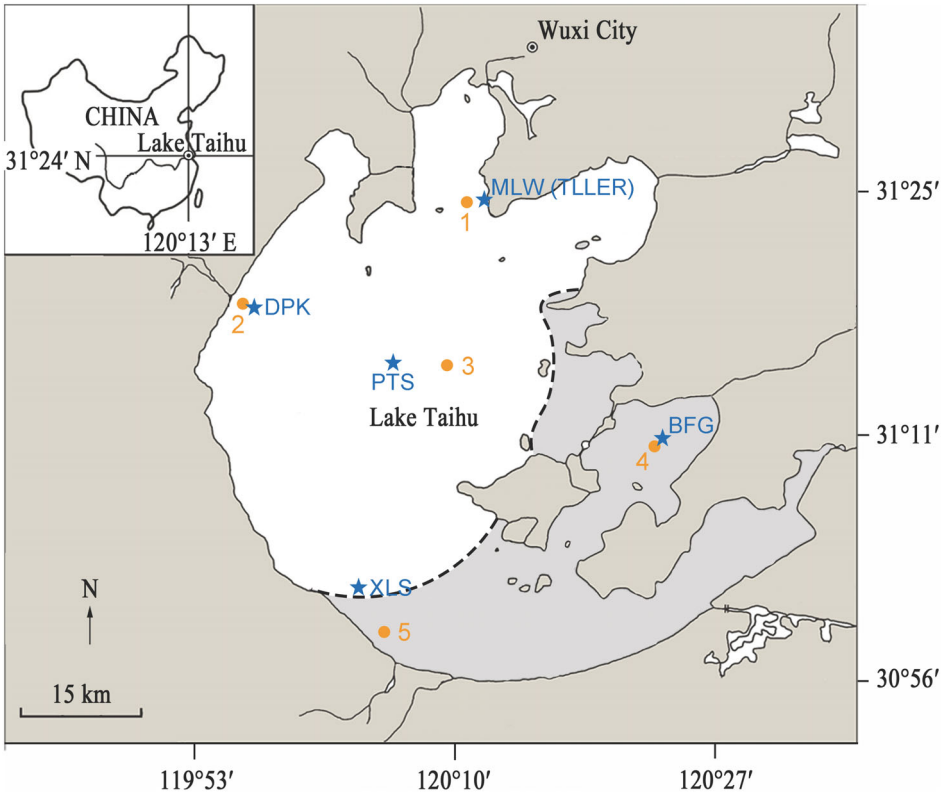

Fig. 1. Monitoring and sampling sites in Lake Taihu, China. Five eddy covariance systems (blue stars) were deployed in Lake Taihu: Meiliangwan (MLW), Dapukou (DPK), Pingtaishan (PTS), Bifenggang (BFG), and Xiaoleishan (XLS). Based on the locations of the eddy covariance systems, five additional sites (orange circles) were selected from the Taihu Laboratory for Lake Ecosystem Research (co-location with the MLW) for monthly (Sites 1–3) or quarterly (Sites 4–6) sampling of limnological parameters. The white area indicates the cyanobacteria-dominated region, while the gray area indicates the macrophyte-rich region.

Data quality control and gap-filling procedures

Given the challenges of EC measurements over lakes, including frequent data gaps caused by unsuitable environmental conditions and variable wind directions affecting fetch at shoreline towers, rigorous data quality control and gap-filling procedures were implemented (Zhang et al. 2020).

Data quality was ensured through weekly examination of 30-min time series to identify abnormal values, with site visits every 1–2 months for instrument maintenance and 10 Hz data downloads. Outlier data were screened using a five-point moving average filter, and data points deviating by more than two standard deviations from the moving average were discarded. Radiometers were field-calibrated against laboratory standards, showing mean bias errors less than 1 W m^{-2} across radiation components.

Gap-filling was essential to maintain data continuity and comparability across sites and time. Short gaps (30 min to 1 h) were filled by linear interpolation. For longer gaps in meteorological variables, radiation components, and WT, a spatial interpolation method was used, involving linear regression with data from the most correlated nearby site for the corresponding month. Large data gaps in EC flux variables (sensible heat flux, latent heat flux, and friction velocity) were filled using a hybrid approach. When relevant state variables were available, gaps were filled using bulk transfer relationships with locally tuned transfer coefficients specific to each site (Xiao et al. 2013).

To harmonize transitions between original and gap-filled data, a five-point moving average was applied to the gap-filled-time series, with further smoothing by linear interpolation if deviations exceeded twice the standard deviation.

Lake energy fluxes

Lake energy budgets were calculated following Henderson-Sellers (1986);

$$\Delta Q = \mathrm{DR} + \mathrm{DLR} - \mathrm{UR} - \mathrm{ULR} - H - \lambda E + \Delta Q_B + \Delta Q_F + \Delta Q_P \quad (1)$$

where ΔQ is the energy budget, DR is the downward shortwave radiation, DLR is the downward longwave radiation, UR is the upward shortwave radiation, ULR is the upward longwave radiation, H is the sensible heat, and λE is the latent heat, ΔQ_B is the net energy flux between sediment and water, ΔQ_F is the net energy flux carried by the inflow and outflow of the lake, and ΔQ_P is the energy flux resulting from precipitation.

According to J. Wang and Bras (1999), ΔQ_B can be estimated using the time series of the observed water and sediment temperatures, based on thermal conductivity for saturated soils. In addition, considering an annual inflow of 9.3×10^9 m^3 and a 1°C temperature difference between the inflows and the lake water, ΔQ_F was estimated to be no more than 0.5 W m^{-2} (W. Wang et al. 2014), less than 2% of the annual energy budget. Assuming an annual precipitation rate of 1100 mm and that the rainwater was at a wet-bulb temperature, ΔQ_P was estimated to be -0.5 W m^{-2} (Shoemaker et al. 2005). Therefore, considering the minor contributions of ΔQ_F and ΔQ_P, the energy balance equation was simplified to:

$$\Delta Q = \mathrm{DR} + \mathrm{DLR} - \mathrm{UR} - \mathrm{ULR} - H - \lambda E + \Delta Q_B \quad (2)$$

Accordingly, the lake's energy input and output were described by the following equation:

$$Q_{IN} = \mathrm{DR} + \mathrm{DLR} + Q_{BI} \quad (3)$$

where Q_{IN} is the lake energy input, and Q_{BI} is the energy flux from the sediment to water, whereas

$$Q_{OUT} = \mathrm{UR} + \mathrm{ULR} + H + \lambda E + Q_{BO} \quad (4)$$

where Q_{OUT} are the lake energy output, and Q_{BO} is the energy flux from water to the sediment.

The Bowen ratio (β), which is the ratio of sensible heat (H) to latent heat (λE), is calculated as:

$$\beta = \frac{H}{\lambda E} \quad (5)$$

Lake environmental and phytoplankton characteristics

To document the spatial and temporal dynamics of Lake Taihu in response to its energy fluxes, long-term in situ monitoring of limnological parameters and phytoplankton assemblages was obtained from the Taihu Laboratory for Lake Ecosystem Research. The Taihu Laboratory for Lake Ecosystem Research is located on the shore of Meiliang Bay in northern Lake Taihu (co-location with the site MLW, Fig. 1) and is a long-term site-specific observation station of the Chinese Ecosystem Research Network and Global Lake Ecological Observatory Network.

Five monitoring sites were selected to correspond most closely with EC observation stations (Fig. 1). Sites 1, 2, and 3 were sampled monthly, while Sites 4 and 5 were sampled quarterly (February, May, August, November). At each site, in situ dissolved oxygen and pH measurements were taken using a multi-parameter water quality sonde (YSI 6600, Yellow Spring Instruments), while SD was measured using a 20-cm diameter Secchi disk. Samples for water chemistry were collected by pooling discrete samples from the surface (0.5 m), middle, and bottom (0.5 m above the bottom) layers of the water column. These samples were analyzed for total nitrogen (TN), total dissolved nitrogen, ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), total phosphorus (TP), total dissolved phosphorus, phosphate (PO_4^{3-}), permanganate index (COD_{Mn}), and chlorophyll *a* (Chl *a*) following the methods described by the American Public Health Association (APHA 1995).

To quantify the phytoplankton community composition, 1 L of each depth-integrated water sample was fixed with Lugol's iodine solution (2% final concentration). After settling for at least 48 h, phytoplankton were identified to species or genus and enumerated using a Sedgwick–Rafter counting chamber under 200–400× microscopic magnifications (Olympus Corporation) (Hu et al. 1980). Based on the abundance of the phytoplankton community, the Shannon index was calculated using the vegan package in R 4.3.2 to assess the richness of the phytoplankton community in Lake Taihu.

The intensity of cyanobacterial blooms

Consistent with EC's monitoring period, the intensity of cyanobacterial blooms was estimated for the period from January 2011 to December 2018 based on MODIS-Aqua satellite imagery following our standard methods (Shi et al. 2017). Briefly, we downloaded the Moderate Resolution Imaging Spectroradiometer (MODIS) M-Aqua Level 0 (raw) images from National Aeronautics and Space Adminstration's (NASA) Goddard Space Flight Center Web site (http://oceancolor.gsfc.nasa.gov/), selected high-quality cloud-free scenes, and processed them to Level 1 (calibrated spectral radiance) data using the SeaDAS software package. We then derived the atmospherically Rayleigh-corrected MODIS-Aqua data. To retrieve Chl *a* concentrations from images of Lake Taihu, we used a validated statistical model relating measured in situ Chl *a* to remotely sensed spectral characteristics, which we then applied to the selected MODIS-Aqua images (Shi et al. 2017). This procedure allowed us to derive Chl *a* concentrations and the physical area of surface blooms to estimate the intensity of cyanobacterial outbreaks.

Statistical analyses

Sen's slope was calculated to analyze long-term trends in AT, WT, and energy fluxes of Lake Taihu at all five EC stations. Sen's slopes and their significance ($\alpha = 0.05$) were calculated using the trend package in R 4.3.2 (Sen 1968).

Mantel's test was performed to identify the relationships among energy fluxes (energy input, energy output, energy budget, H, λE, and β), environmental variables (WS, R, WT, SD, and dissolved oxygen), water chemistry (TN, total dissolved nitrogen, NO_2^-, NO_3^-, NH_4^+, TP, total dissolved phosphorus, PO_4^{3-}, and COD_{Mn}), and phytoplankton community composition based on Spearman's correlation (Somers and Jackson 2022). Euclidean distances were used to calculate the phenotypic distance.

Variation partition analysis was conducted to identify the relative contributions of energy fluxes, environmental

variables, and nutrients to the phytoplankton community composition using the "varpart" function of the *vegan* package (Oksanen et al. 2022). Variation partition analysis was performed to evaluate the direct and interactive correlations between the energy, environmental, and nutrient predictors of phytoplankton community composition. All partitioned fractions of variation were significant in an ANOVA permutation test using the *vegan* package in R 4.3.2 (Oksanen et al. 2022). Moreover, redundancy analysis (RDA) was employed to examine the contributions of the environmental and energetic parameters to changes in the dynamics of the 30 most abundant phytoplankton species or genera (Ter Braak 1991).

The distributions of WT, energy, and phytoplankton variables as a function of year and energy net fluxes were estimated using a generalized additive model in the *gam* package (Hastie and Tibshirani 1990). The significance of differences was examined with a one-way ANOVA using Tukey's Honestly Significant Difference test. Relationships among energy fluxes, environmental variables, nutrients, and phytoplankton communities were explored using Spearman's correlation coefficient in the *stats* package. All analyses were performed in R 4.3.2, and the level of significance used for all tests was $p < 0.05$ (R Core Team 2021).

Results

Variations in AT, WT, and lake energy fluxes

Water temperature (defined as the average values at various depths) in Lake Taihu exhibited a slightly higher value and a marginally more rapid rate of increase compared to AT between 2011 and 2018 (Fig. 2). Over the monitoring period, the average WT was 17.79°C ± 0.35°C, whereas the average AT was 17.07°C ± 0.42°C ($p > 0.05$, Fig. 2a). Notably, both AT and WT were higher in mesotrophic BFG and XLS than in eutrophic regions (MLW and DPK) of the lake ($p > 0.05$, Fig. 2b). Utilizing Sen's slope for trend analysis, we found that WT increased at a rate of 0.143°C ± 0.04°C per decade in Lake Taihu, whereas AT increased at a marginally, but not significantly, slower rate of 0.137°C ± 0.08°C per decade ($p > 0.05$, Fig. 2c).

Water temperatures in Lake Taihu were continuously fueled by energy inputs, resulting in a substantial amount of energy being stored within the lake during summer (Fig. 3). Energy influx into the lake exceeded losses at all five monitoring sites during spring, summer and fall, but not in individual winter months (Fig. 3a–e). In general, energy inputs were slightly higher in the less eutrophic sites of PTS, BFG, and XLS compared to the eutrophic MLW and DPK stations ($p > 0.05$), while energy output tended to be significantly higher at the DPK station than at the XLS site ($p < 0.05$, Fig. 3f).

The mean energy budget for Lake Taihu was 26.0 ± 6.6 W m^{-2} during 2011–2018 (Fig. 4a). Energy budgets were consistently lower in the eutrophic MLW and DPK compared to the less eutrophic sites of PTS, BFG, and XLS, although differences among sites were not always statistically significant (Fig. 4a). Pairwise correlation analysis revealed a strong positive relationship between the energy budget and WT (Spearman's $r = 0.698$, $p < 0.001$, Fig. 4b), indicating the key role of downwelling short- and longwave radiation on lake WT.

Marked spatial variations in the rates of change of energy fluxes were observed across Lake Taihu (Fig. 5). Specifically, the rate of change in energy inputs was greater in the central (PTS), southern (XLS), and eastern (BFG) regions when compared to the northwestern lake sites (MLW and DPK) (Fig. 5a). Notably, the rate of change of energy outputs was lowest in the southern and eastern regions of Lake Taihu (Fig. 5b). Taken together, temporal changes in the lake energy budget were geographically variable, with markedly lower rates of change in the northern region compared to the southern and eastern regions (Fig. 5c). For instance, energy budgets changed at 0.85 W m^{-2} decade^{-1} in the hypereutrophic site of DPK, while it was 1.23 W m^{-2} decade^{-1} in the mesotrophic XLS station (Fig. 5c). These findings highlight significant spatial heterogeneity in energy fluxes, with higher values and faster rates

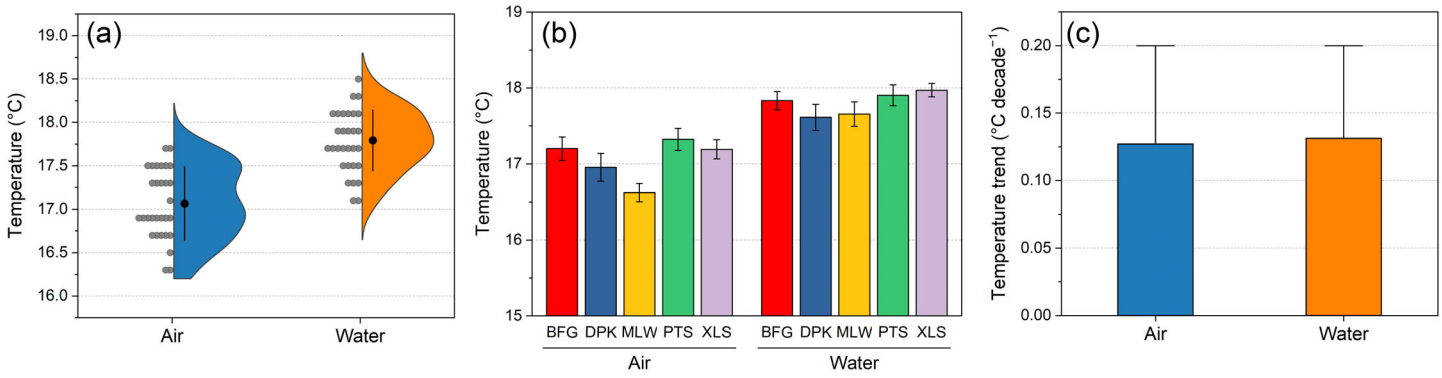

Fig. 2. Variations in air and water temperatures in Lake Taihu, 2011–2018. (**a**) Distributions of annual mean air and water temperatures during 2011–2018. (**b**) Average of air and water temperatures at five monitoring sites in Lake Taihu. (**c**) Rates of change in air and water temperatures in Lake Taihu.

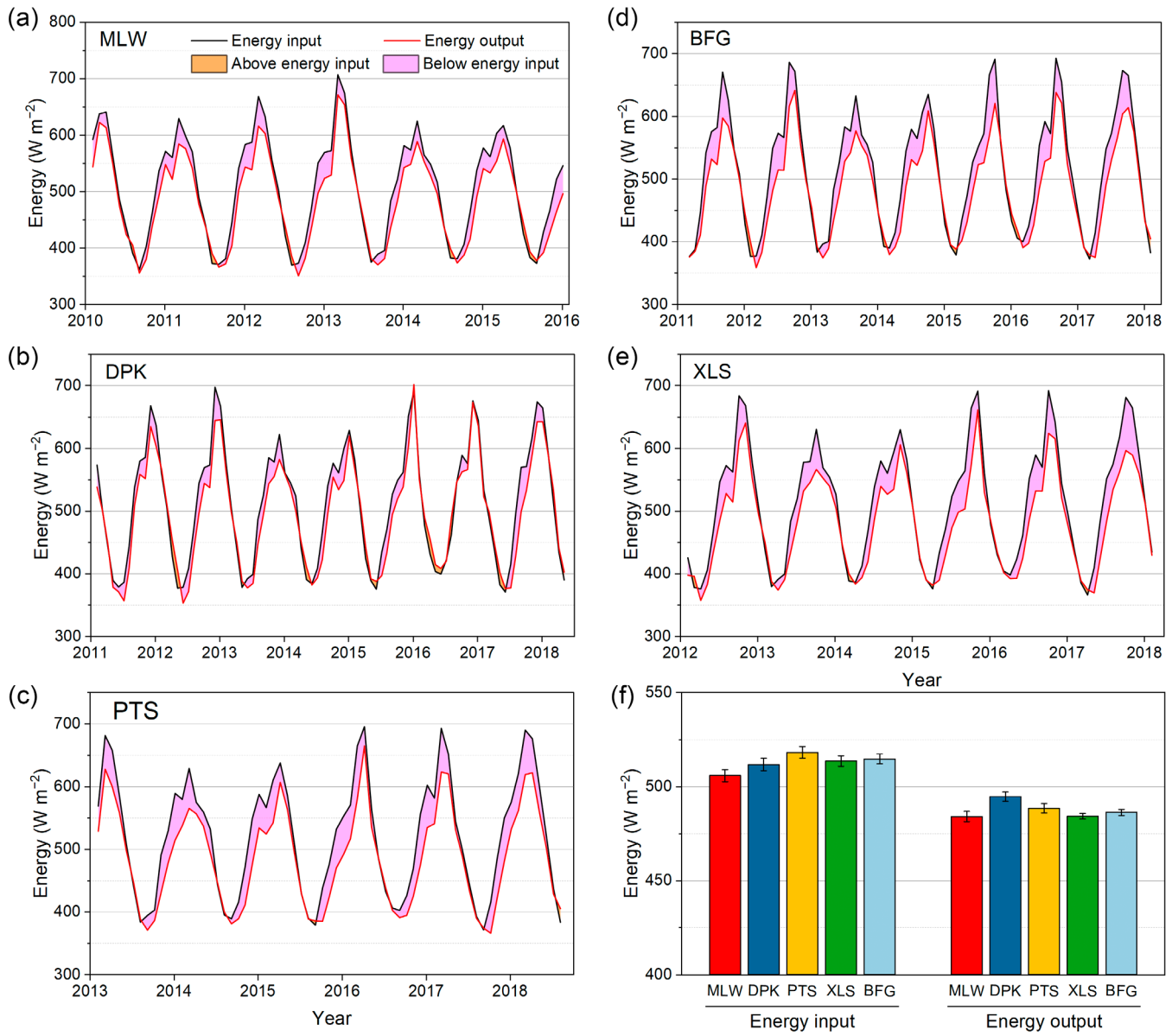

Fig. 3. Changes in the energy fluxes of Lake Taihu during 2011–2018. Variations in monthly averages of energy input and output at five monitoring sites (**a**, Meiliangwan [MLW]; **b**, Pingtaishan [PTS]; **c**, Dapukou [DPK]; **d**, Xiaoleishan [XLS]; **e**, Bifenggang [BFG]) during 2011–2018. (**f**) Distributions of the energy input and output at five monitoring sites in Lake Taihu.

of change observed in the clear and less productive regions of Lake Taihu (Fig. 5).

Relationships between phytoplankton and energy fluxes

Cyanobacterial blooms in Lake Taihu have become increasingly severe from 2011 to 2018. Specifically, analysis of in situ monitoring data revealed a significant increase in the annual mean of Chl *a* concentration by 2.7 μg L^{-1} decade^{-1} from 2011 to 2018 ($p < 0.05$, Fig. 6a). Satellite remote sensing data also suggested an increased physical extent (km^2) of cyanobacterial blooms, although the trend was not statistically significant ($p > 0.05$) during this period (Fig. 6b). Instead, phytoplankton diversity (Shannon index) declined significantly during 2011–2018 ($p < 0.05$, Fig. 6c).

The characteristics of cyanobacterial blooms and phytoplankton diversity were often significantly correlated with the energy fluxes in Lake Taihu (Fig. 6d–f). Analysis using generalized additive models showed that the annual mean of Chl *a* concentration and cyanobacterial blooms increased significantly ($p < 0.05$) with increasing energy budgets (Fig. 6d,e).

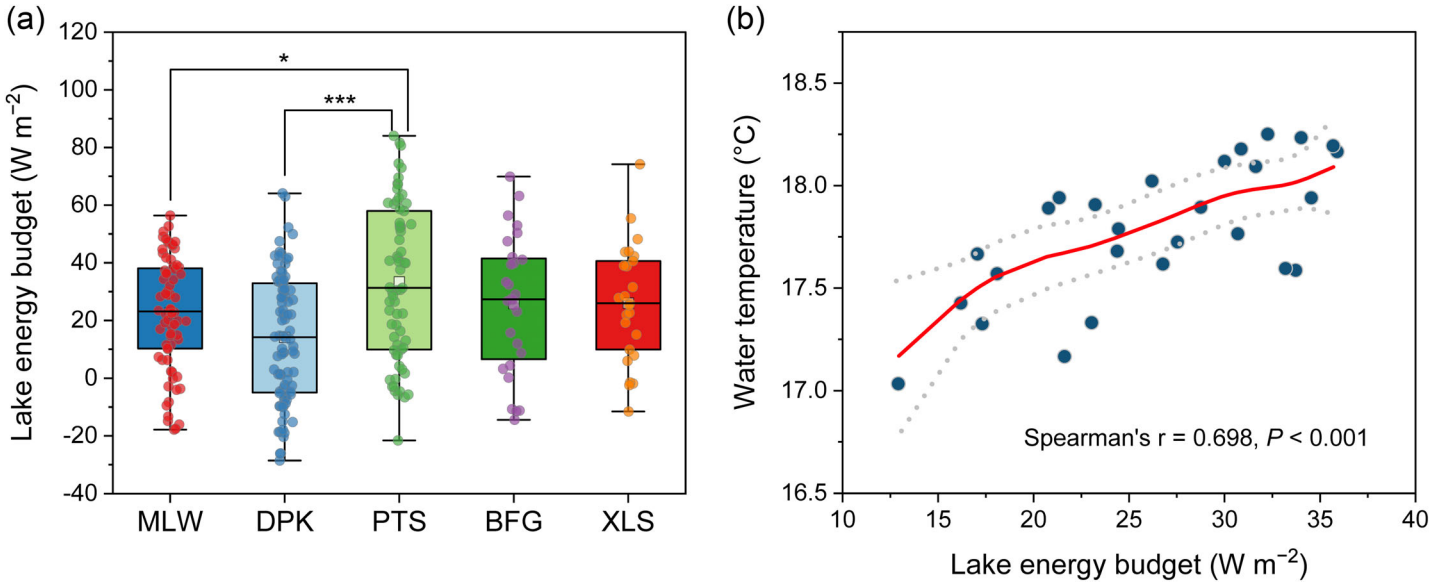

Fig. 4. Distributions of energy budget in Lake Taihu (**a**) and its relationship with water temperature (**b**) during 2011–2018. The relationship between the annual mean of energy budget and water temperature (WT) at five monitoring sites during 2011–2018 was analyzed using generalized additive models, with the red line representing the fitted values and the gray dotted line indicating the pointwise 95% credible interval. Pairwise correlations between WT and lake energy budget were examined using Spearman's correlation coefficient. Statistical significance indicated by *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ (ANOVA).

Notably, phytoplankton biodiversity decreased significantly with increasing energy budget in Lake Taihu ($p < 0.05$, Fig. 6f).

Variations in phytoplankton community composition with environmental characteristics

Correlation analysis showed that lake energy fluxes were correlated negatively with trophic status and positively with climatic factors (WT, WS, precipitation) (Fig. 7a). Mantel's test further showed that the taxonomic groups varied across the lake in response to local environmental factors. Specifically, Cyanophyta and Bacillariophyta were correlated significantly with nutrients (TN, TP, COD_{Mn}), while Chlorophyta were correlated only with the energy budget in Lake Taihu (Fig. 7a). Furthermore, RDA of the 30 most abundant genera or species showed that the abundances of *Microcystis* (Cyanophyta), *Spirulina* (Cyanophyta), *Merismopedia* (Cyanophyta), and *Crucigenia quadrata* (Bacillariophyta) were all significantly correlated with nutrients, while *Chlorella* (Chlorophyta) was correlated with the energy budget (Fig. 7b).

According to the variance partitioning analysis, 42.4% of variation in the phytoplankton community composition was explained by differences in spatial and temporal variation in energy, environmental, and nutrient characteristics of Lake Taihu (Fig. 7c). Specifically, energy, environment, and nutrients significantly explained 1.8%, 2.2%, and 13.8% of the

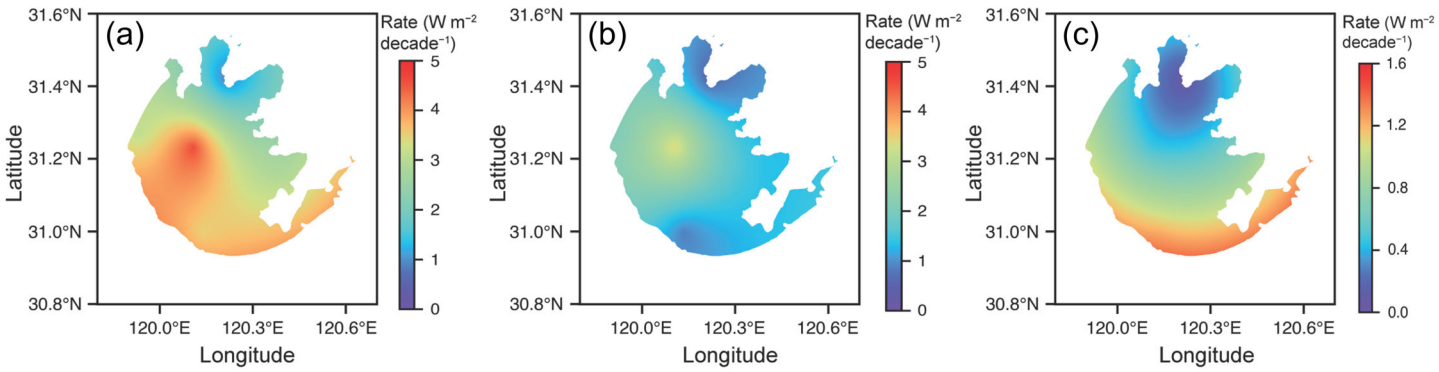

Fig. 5. Spatial distributions of the change rates of energy fluxes across Lake Taihu during 2011–2018. The change rates (W m^{-2} decade^{-1}) of the energy input (**a**), energy output (**b**), and energy budget (**c**) were examined using Sen's slope.

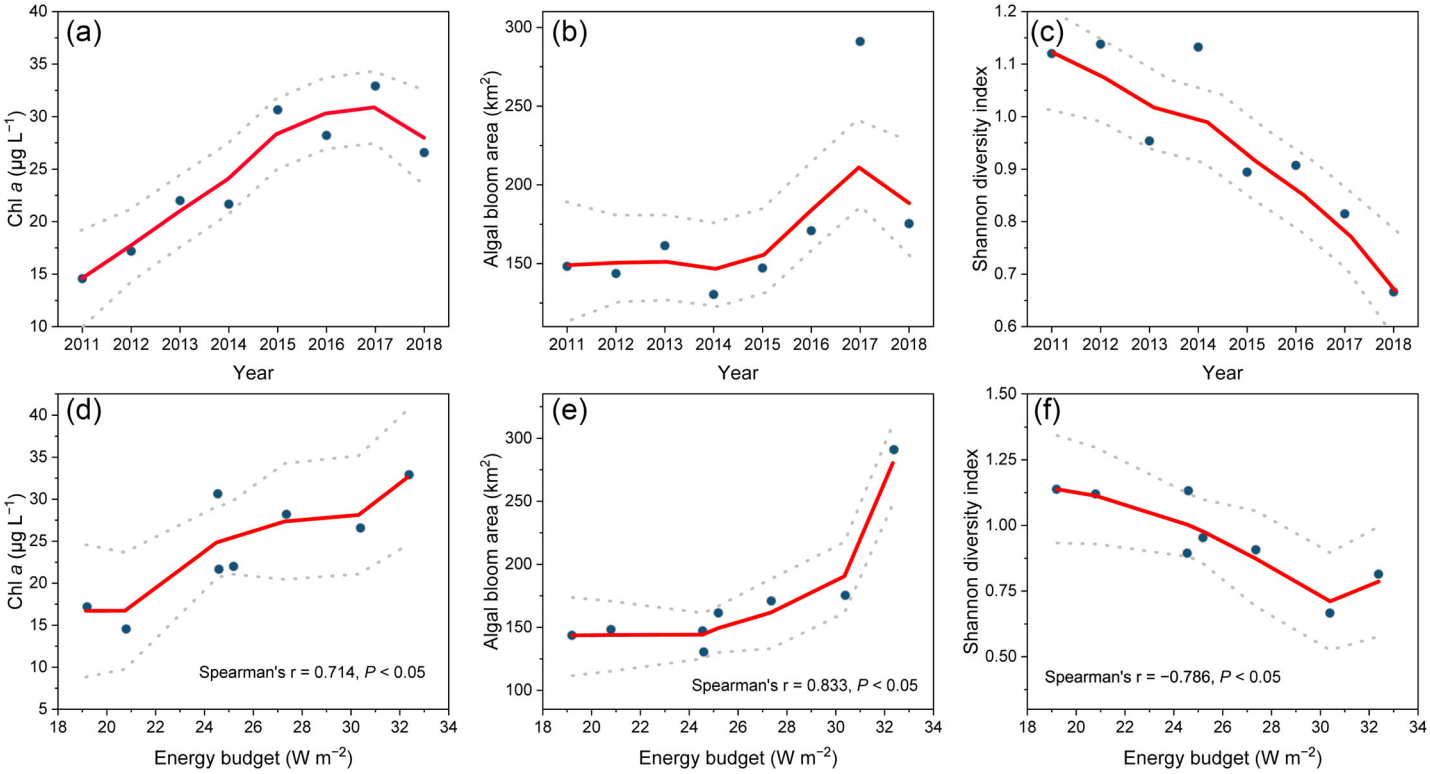

Fig. 6. Variations in phytoplankton (**a**, Chl *a* concentrations; **b**, cyanobacterial bloom extent; **c**, phytoplankton diversity) and their associations with energy budgets of Lake Taihu during 2011–2018. The red curve denotes the generalized additive model smoothing fit, bounded by gray dashed lines representing the 95% pointwise credible intervals. Statistical associations were quantified using Spearman's rank correlation analysis.

phytoplankton community structure ($p < 0.05$), respectively, while their combined effects explained an additional 11.4% of phytoplankton variance (Fig. 7c). Overall, these results suggest that while total lake production and phytoplankton diversity are regulated strongly by energy fluxes, the precise community structure in Lake Taihu is primarily influenced by nutrients and their interactions with energetic and environmental variables.

Discussion

Characterization of changes in energy fluxes

In Lake Taihu, AT and WT increased by 0.137°C decade^{-1} and 0.143°C decade^{-1} during 2011–2018, respectively, a pattern which is consistent with the mean global increase in surface temperature of 0.19°C (0.16–0.22°C) during 2011–2020 (IPCC 2023). Lake warming was primarily driven by an imbalance of the energy budget, resulting in a net heat accumulation in surface waters such as seen elsewhere (B. Wang, Ma, et al. 2017). Our findings showed that the annual energy budget increased across multiple regions of Lake Taihu, consistent with the observed warming of AT and WT (Figs. 2–4). However, energy influxes and overall budgets were greater and increased more rapidly in the clear and unproductive regions of Lake Taihu than in more eutrophic regions (Figs. 3–5), showing that the rate of lake heating is itself a function of the water-column characteristics of the basin (Huang et al. 2023).

Local variations of energy fluxes may result from spatial heterogeneity of the biophysical properties of Lake Taihu. The basin consists of different local ecotypes with varying trophic conditions, ranging from mesotrophic to hypertrophic status (Qin et al. 2007). Water transparency is significantly lower in the northern (MLW; 0.28 ± 0.09 m) and western (DPK; 0.26 ± 0.05 m) regions of Lake Taihu than in the eastern region (BFG; 0.43 ± 0.08 m) ($p < 0.05$, Supporting Information Fig. S1a), due to low macrophyte biomass, elevated phytoplankton densities, and frequent wind-induced suspension of sediment (Qin et al. 2007, 2019). These conditions favor energy losses via scattering and reflection, as well as rapid surface heating that enhances heat loss at night (W. Wang et al. 2018; J. Zhou et al. 2023). In contrast, the eastern regions of the lake are shallower ($p < 0.05$, Supporting Information Fig. S1b), host abundant submerged macrophytes, and are characterized by relatively higher light penetration (higher ratio of SD and water column depth; $p < 0.05$) with many locally clear locations (Supporting Information Fig. S1c). These features allow for greater penetration of solar radiation, potentially increased sediment heating, and increased local heat storage (Heiskanen et al. 2015; Xiao et al. 2013). Indeed, the annual net energy flux between the sediment and lake water

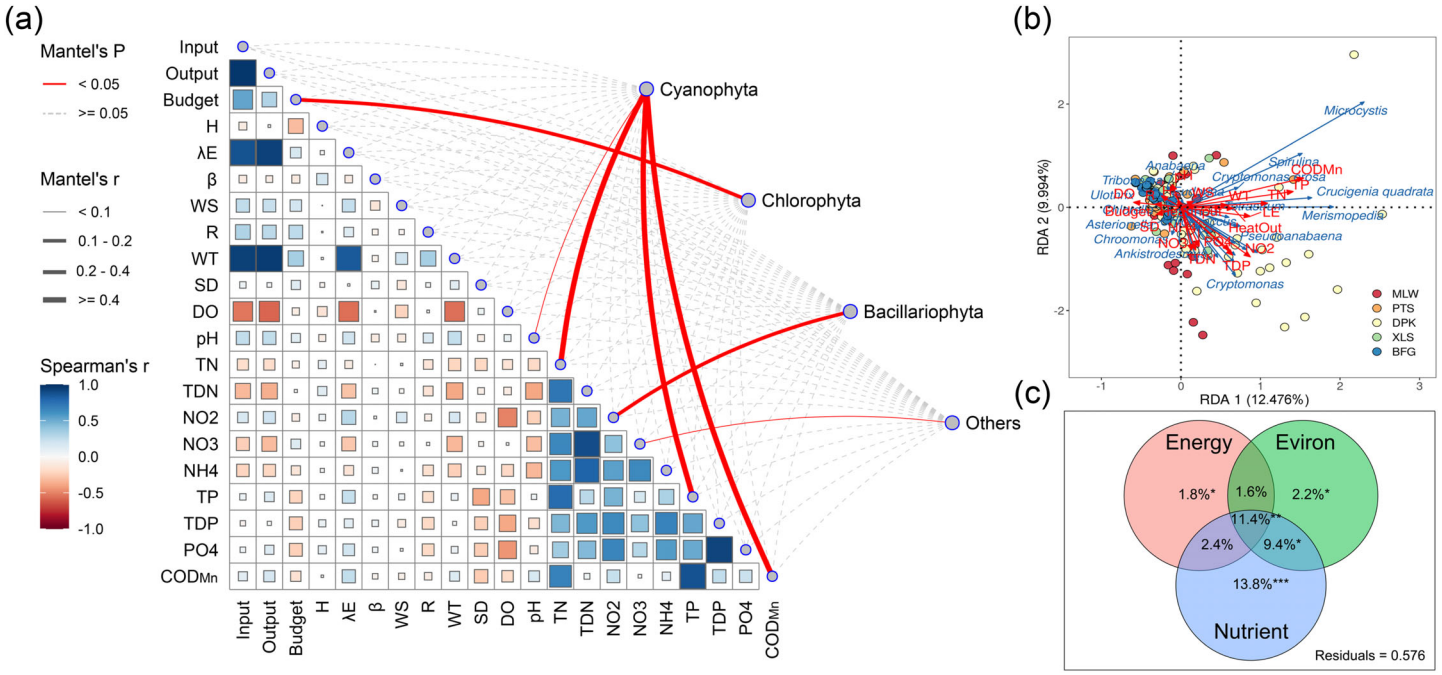

Fig. 7. Variations in phytoplankton community composition with environmental characteristics of Lake Taihu. (**a**) Correlations among energy fluxes (energy input [input], energy output [output], energy budget [budget], sensible heat flux [*H*], latent heat flux [λE], and Bowen ratio [β]), environmental factors (wind speed [WS], precipitation [R], water temperature [WT], Secchi depth [SD], dissolved oxygen [DO]), permanganate index (COD_{Mn}) and nutrients (total nitrogen [TN], total dissolved nitrogen [TDN], nitrite nitrogen [NO_2^-], nitrate [NO_3^-], ammonia [NH_4^+], total phosphorus [TP], total dissolved phosphorus [TDP], and phosphate [PO4]) with the phytoplankton community composition were examined using Mantel's test. The color gradient indicates the Spearman correlation coefficients, and the line thickness corresponds to Mantel's r statistic for the corresponding distance correlation. The line type denotes the statistical significance. (**b**) Redundancy analysis (RDA) was used to explore the ordination of the 30 most abundant phytoplankton species or genera in relation to environmental variables at the five monitoring sites. (**c**) Variation partitioning analysis of the relative contributions of energy fluxes (energy), environment (environ), and nutrients (nutrient) to the phytoplankton community composition. Statistical significance indicated by *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ (ANOVA).

is significantly higher ($p < 0.05$) in the eastern regions of Lake Taihu than in the northwestern regions (Supporting Information Fig. S2). Further, this divergence is likely amplified by horizontal heat transport processes, where advective energy redistribution via water currents modifies local energy budgets and drives basin-scale spatial variability (MacIntyre et al. 2014; Sugita et al. 2020). Although further research is required to evaluate the relative importance of these processes, the southeastern regions of Lake Taihu appear to store more energy than other habitats, resulting in higher values and faster rates of increase in energy input and budget (Fig. 5c).

Latent (λE) and sensible heat fluxes (*H*) from lakes are controlled primarily by gradients of water vapor and temperature, as well as the intensity of turbulent mixing induced by wind-related features such as surface roughness, fetch, WS, and atmospheric stability. Wind speed plays a crucial role in lake-atmosphere water and heat flux transport (B. Wang et al. 2015; Xiao et al. 2013) as higher bulk heat transfer (free convection) occurs under an unstable atmosphere (Goldbach and Kuttler 2015). Wind speed and wind-induced mixing tend to be higher in the middle and northwestern parts of Lake Taihu, due to longer fetches and the absence of submerged vegetation which otherwise increases drag and reduces water movement (Goldbach and Kuttler 2015; Jalil et al. 2019). Here, both λE and *H* values were significantly higher in the northwestern regions (MLW and DPK) of Lake Taihu than in the center (PTS) and southeastern (BFG and XLS) regions of the lake ($p < 0.05$, Supporting Information Fig. S3), consistent with the expected differences in properties controlling atmospheric energy exchange and the observation that clear and unproductive lakes are more sensitive to atmospheric warming (J. Zhou et al. 2023). Therefore, we conclude that energy fluxes can exhibit significant spatial variation within individual lakes, and presumably among lakes, even when ecosystems experience the same climatic conditions.

Our analysis confirms an annual average net energy budget of approximately 26 W m^{-2} across five monitoring stations in Lake Taihu, consistent with prior studies utilizing the same EC monitoring platform (Lee et al. 2014; W. Wang et al. 2014; Xiao et al. 2020). This value also aligns well with EC observations reported in global lake studies (W. Wang et al. 2014), underscoring the robustness of our measurements. The sediment-water heat flux contributes less than 5% of the total energy budget, affirming that the primary energy exchange

occurs at the air–water interface. The apparent discrepancy between this energy budget and the relatively modest observed lake warming rate (~ 0.14°C per decade) can be attributed to several factors. First, only a portion of the energy budget directly heats the water column; the remainder is redistributed via horizontal heat transport, biological processes such as photosynthesis and respiration, and anthropogenic influences including water diversion and fisheries. Second, technical limitations in temperature profiling, particularly turbulence-induced measurement noise, may lead to a 10–15% underestimation of heat storage changes in dynamic lake systems (Nordbo et al. 2011). Furthermore, differences between energy estimates derived from EC measurements and those from temperature-based calculations have long been recognized within the micrometeorological community (Foken 2008; Leuning et al. 2012; K. Wang and Dickinson 2012). In addition, consistency of the energy flux variables was further evaluated by examining the energy balance closure. Using observations from a subset of sites in the earlier years of the flux network, W. Wang, Shen, et al. (2017) reported annually closure rates of 73%, indicating that the sum of the measured sensible and latent heat fluxes ($H + \lambda E$) accounted for 73% of the annually available energy. These closure rates reflect the inherent challenges in fully capturing all energy flux components and contribute to the observed residual in the energy budget. Such systematic residuals are a recognized aspect of EC-based lake energy studies and highlight ongoing needs for methodological improvements and careful interpretation of energy budgets in complex lacustrine environments.

Roles of lake energy fluxes in controlling phytoplankton community structure

Atmospheric warming affects lake ecosystems by modifying the temporal and spatial characteristics of energy fluxes. To date, most research has focused on the effects that warming AT and WT have on lake production and community composition (Elliott 2012; Woolway et al. 2020), without specifically linking these features to changes in energy fluxes. For example, warmer water favors the growth of cyanobacteria (Freeman et al. 2020; Paerl and Huisman 2008), leading to more frequent and prolonged blooms of potentially toxic phytoplankton (Ho et al. 2019; Hou et al. 2022; Shi et al. 2019). In this study, algal biomass (as Chl *a*), cyanobacterial bloom extent, and phytoplankton species diversity were all strongly influenced by the variation of Lake Taihu's energy fluxes (Fig. 6), while phytoplankton composition was additionally affected by nutrients and their interactions with energy and other environmental parameters (Fig. 7). Increased heat content of lakes may enhance surface blooms by producing transient thermal stratification of surface waters that favor positively buoyant taxa such as colonial cyanobacteria (Huisman et al. 2018; Paerl and Huisman 2008), while warmer waters are regularly associated with elevated primary production (Woolway et al. 2020). Both stratification and eutrophication are also associated with reduced phytoplankton diversity in lakes (C. X. Guo et al. 2022). Further, variations in energy influx affect the phenology of annual species replacement, particularly leading to differences in the relative proportion of prokaryotic and eukaryotic phytoplankton (Elliott 2012; Huisman et al. 2018). Although speculative, we infer that the positive correlation between annual energy fluxes and the abundance of select chlorophytes may indicate this taxon exhibits particularly strong phenological changes in response to changing energy inputs.

Nutrient conditions (TN, TP, COD_{Mn}) significantly affected the species composition of Lake Taihu phytoplankton (cyanobacteria, diatoms), both uniquely and in association with energy fluxes and other factors (Fig. 7). Despite significant investments in lake restoration, nutrient influxes to Lake Taihu have exhibited an increasing trend (except station DPK) during 2011–2018 (Supporting Information Fig. S4). Strong effects of N and P on cyanobacteria are expected, as changes in elemental ratios of macronutrients are critical regulators of the presence of diazotrophic taxa in freshwaters (Elser et al. 2000). Similarly, nutrient status interacts with energy-regulated variations in mixing regimes to influence the abundance and composition of phytoplankton assemblages (Fernández-González et al. 2022). Negative correlations between COD_{Mn} and cyanobacteria are also consistent with the widespread deoxygenation of lake ecosystems that occurs due to a combination of warming waters and excess nutrient pollution (Jane et al. 2021). Indeed, in contrast to some other Chinese lakes, the concentrations of dissolved oxygen widely declined in Lake Taihu from 2011 to 2018 (Supporting Information Fig. S5) and, potentially, increasing nutrient release from sediment (North et al. 2014). Additionally, given the short timescale of horizontal transport (1–2 d for a 20 km distance at maximum 0.2 m/s current velocities; Xue et al. 2024) compared to phytoplankton community succession (weeks to months), local energy fluxes seem to the primary drivers of long-term biological trends. Finally, our findings are consistent with prior research suggesting that nutrient enrichment and climate warming jointly exacerbate the cyanobacterial blooms in Lake Taihu from 2011 to 2018, and helps explain why Lake Taihu continues to experience substantial blooms despite significant mitigation and restoration efforts (Qin et al. 2019).

Water depth and WS are additional environmental factors regulating phytoplankton community structure and Chl *a* concentrations in Lake Taihu. Studies have shown that rising water levels typically reduce water column mixing intensity, favoring cyanobacterial aggregation and bloom formation, whereas lower water levels promote the growth of submerged macrophytes (Wu et al. 2013). Additionally, lower WSs decrease vertical mixing, leading to elevated surface WTs and the development of hypoxic conditions, which enhance nutrient release from sediments and subsequently stimulate algal growth (Jalil et al. 2019). Therefore, when interpreting the influence of energy budgets on phytoplankton abundance,

it is essential to also consider the modifying effects of water depth fluctuations and WS variability on lake thermal dynamics and nutrient cycling. Integrating these factors provides a more comprehensive understanding of the spatiotemporal evolution of algal blooms in Lake Taihu.

Implications for understanding the impact of energy fluxes on lake ecosystems

Analysis of Lake Taihu limnological conditions revealed that spatial and temporal variation in energy fluxes underlay changes in lake production (as Chl *a*) and the physical extent of cyanobacterial blooms (surface area), while energy-nutrient interactions affect species composition (Fig. 8). The high spatial variation in energy fluxes demonstrates clearly that it cannot be assumed that energy fluxes are the same in all regions of a lake, as site-specific characteristics (e.g., aquatic plants, wind mixing, waves, transparency, water depth) appear to affect local energy storage, as well as its surface exchange with the atmosphere (Liu et al. 2012; W. Wang et al. 2014). Our results show that such heterogeneity is closely tied to differences in the physical, chemical, and biological features of distinct lake areas, with clear and non-eutrophic waters exhibiting the greatest temporal variation in energy budget, which may render these habitats more vulnerable to ecosystem shifts under future warming.

Given the importance of lake features in setting discrete energy fluxes, it seems unlikely that different lakes in a given geographic region will exhibit the same response to variations in AT or transmission of solar irradiance (e.g., cloudiness), in part due to variation in trophic status among and within lakes. Here we demonstrate that nutrients interact with local energy and environmental variables to influence phytoplankton community composition, linking vertical energy processes with ecological structure (Leavitt et al. 2009). These relationships highlight the need to integrate knowledge of energy–nutrient interactions into predictions of phytoplankton dynamics if we are to accurately project ecosystem responses and associated risks under climate change. In particular, spatial variation in lake energy budgets must be explicitly accounted for when designing adaptation and mitigation strategies.

In addition to their effects on the lakes themselves, disparities in energy flux characteristics among lakes may lead to regional differences in meteorological regimes (Feng et al. 2016; Long et al. 2007). For example, by the year 2100, lake evaporation is projected to increase by 16% under a high-emission scenario (RCP 8.5) (W. Wang et al. 2018; Zhao et al. 2022). An expected increase in lake water surface and evaporation rates will rise humidity levels in the surrounding atmosphere, leading to increased cloud formation and, consequently, greater precipitation (Zhao et al. 2022). This influx of moisture may create wetter conditions, potentially exacerbating local floods (W. Y. Zhou et al. 2021). While this study focused on vertical energy processes due to limited lateral

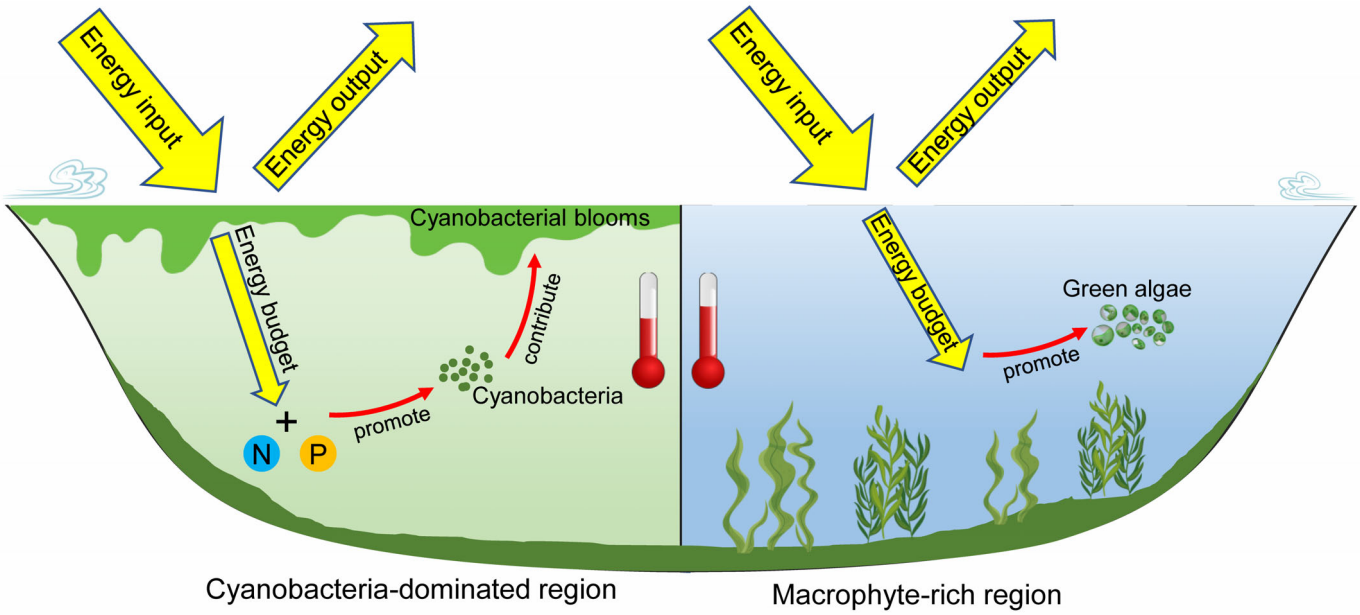

Fig. 8. Conceptual model illustrating the spatial heterogeneity of energy fluxes and their influence on phytoplankton dynamics in Lake Taihu. In the nutrient-enriched, cyanobacteria-dominated region (right), strong wind-driven mixing and low water transparency result in a relatively limited net energy budget. This energy, combined with elevated nitrogen (N) and phosphorus (P) availability, facilitates cyanobacterial proliferation and bloom formation. Conversely, in the clearer, macrophyte-rich region (left), reduced wind-induced mixing and higher energy retention lead to increased water temperature, which promotes the growth of green algae. These contrasting energy and nutrient regimes drive the distinct phytoplankton community structures observed across the lake.

energy fluxes, we note that horizontal advection during extreme wind events (e.g., typhoons) may transiently redistribute heat, warranting future integration of 3D hydrodynamic models to resolve sub-daily to seasonal dynamics (W. Zhou et al. 2024). In view of these findings, a robust understanding of the spatial and temporal variability of energy fluxes is indispensable for anticipating ecosystem trajectories and implementing effective management over coming decades.

Author Contributions

Jian Zhou: Conceptualization, data curation, funding acquisition, formal analysis, investigation, methodology, resources, software, validation, visualization, writing – original draft, writing – review and editing. Changchun Huang and Guonian Lü: Validation, visualization, writing – review and editing. Kun Shi: Methodology, resources, funding acquisition, validation, writing – review and editing. Peter R. Leavitt: Conceptualization, funding acquisition, methodology, formal analysis, visualization, resources, validation, supervision, writing – review and editing.

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Conflicts of Interest

Authors declare no conflicts of interest.

Data Availability Statement

The data of energy fluxes in this study are openly accessible online (Zhang et al. 2020) (https://doi.org/10.6084/m9.figshare.30472481), and the data of limnological parameters and phytoplankton assemblages are sourced from the Taihu Laboratory for Lake Ecosystem Research, Chinese Academy of Sciences.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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