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# Succession and Driving Factors of Macrophytes During the Past 60 Years in Lake Erhai, China

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**Abstract:** Macrophytes play a crucial role in maintaining the health of lake ecosystems. A thorough understanding of their long-term evolutionary processes and patterns is of great theoretical and practical significance for ecosystem restoration and mitigation of lake eutrophication. The succession process and driving factors of macrophytes in the Lake Erhai aquatic ecosystem were systematically analyzed using the investigation of macrophytes, literature research, and classification. A survey conducted in July 2022 showed that the macrophyte community in Lake Erhai is seriously degraded, with species numbers notably lower than historical levels from a decade ago (2011). The distribution area declined by over 70% compared to its peak in the 1980s. Over the past 60 years, the macrophyte community of Lake Erhai has undergone successive processes, including expansion, peak, decline, and stabilization. The dominant populations gradually transitioned from being indicative of clean water to pollution-tolerant species. The driving factors of the macrophytes succession of Lake Erhai were the development of cascade hydropower projects on the Xi'er River and the increased outflow capacity of Lake Erhai; these have resulted in substantial fluctuations in water levels, the eutrophication of the lake, pollutant discharge exceeding Lake Erhai's environmental capacity, and substantial climate change in the Lake Erhai basin. Our research provides important theoretical references for ecological restoration and management of early eutrophic lakes in China.

**Keywords:** Lake Erhai; macrophytes; succession; eutrophication; climate change; water-level fluctuation

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## 1. Introduction

As primary producers, macrophytes are integral components of lake ecosystems. Many studies have shown that macrophytes not only play an important role in improving sediment and water quality but also play a wide range of ecological functions in aquatic ecosystems [1–5]. Macrophytes can directly absorb nutrients such as nitrogen and phosphorus from water and sediment and can also inhibit the growth of algae through allelopathy and nutrient competition, thereby reducing phenomena such as algal blooms [6–9]. At the same time, they are also the main provider of organic matter in lake ecosystems, providing abundant food sources and habitats for fish and birds [10–13]. Over the past century, lake ecosystems worldwide have undergone severe degradation owing to climate change and human activities. In 65.2% of lakes globally, macrophytes significantly decreased, with the reduced coverage area of submerged macrophytes accounting for 65.3% of all macrophytes [14]. The decline of macrophytes can lead to the transformation of lakes from clear-water stable lakes to turbid-water stable lakes [15,16].

Lake Erhai, as a representative of lakes with good water quality in China, is one of the critically protected lakes among the "three new lakes". In the 1980s, the water quality of Lake Erhai was classified as Class II according to the Chinese Surface Water Environment Quality Standard. Since then, the water quality of Lake Erhai has shown a general downward trend, and in recent years, the water quality of Lake Erhai has fluctuated between Class II and Class III [17,18]. The Chinese government has continuously strengthened efforts to prevent and control water pollution in Lake Erhai [19]. Degradation of the macrophyte community in Lake Erhai has serious negative effects on the provision of ecosystem services. Lake Erhai faces the threat of cyanobacterial blooms during macrophyte decline. Since the first report of a lake's widespread algal bloom in 1996 [20], Lake Erhai has experienced frequent occurrences of large-scale blooms in 1998, 2003, 2006, 2009, 2013, 2016, and 2021 [21–25]. In recent years, local governments have taken several measures to reduce external and internal pollution loads and achieve certain results. However, indicators such as total nitrogen (TN), total phosphorus (TP), chemical oxygen demand ($COD_{Cr}$), the permanganate index ($COD_{Mn}$), and comprehensive trophic level index (*TLI*) [26] still showed a general upward trend [27]. The TN concentration increased rapidly at a rate of 0.01 mg/L per year. The permanganate index increases by 0.02 mg/L per year [28]. In 2023, the water quality of Lake Erhai will average that recommended for Class III. The chemical oxygen demand was 15.6 mg/L, which was 1.3 mg/L higher than that in 2022.

Combined with the targeted restoration of macrophytes in critical areas along the entire coastline of Lake Erhai, the area covered by macrophytes reached 33.14 $km^2$ in June 2020, accounting for 13.2% of the lake area, which was the largest area in nearly 15 years [29]. The densities of macrophyte communities such as *Vallisneria natans* and *Hydrilla verticillata* have increased and the distribution area of the endemic species *Ottelia acuminata* has significantly expanded, thereby gradually optimizing the structure of the macrophyte community. However, the current coverage of macrophytes in Lake Erhai only recovered to 34.5% of the 96.03 $km^2$ in the late 1980s and the early 1990s. Dominant species such as *Ceratophyllum demersum*, *Potamogeton maackianus*, and *Hydrilla verticillata* have not yet gained a competitive advantage over algae. Exotic macrophytes, such as *Myriophyllum aquaticum* and *Eichhornia crassipes*, are widely distributed along the coast of the northern bay of Lake Erhai. Lake Erhai is currently in the early stages of eutrophication and its aquatic ecosystem is sensitive and fragile. The aquatic ecosystem of Lake Erhai is reversible, thereby making this a critical period for protection, management, and habitat improvement.

The academic community has conducted considerable research on macrophytes in Lake Erhai and gained profound insights into macrophyte diversity, distribution characteristics, and driving mechanisms [30–32]. However, most field surveys and monitoring data began after the degradation of the lake environment, without systematically tracing the historical succession of macrophytes in Lake Erhai or analyzing the causes of macrophyte degradation. This limits the systematic understanding of the long-term evolution of macrophytes in eutrophic lakes. This study elucidates the current distribution of macrophytes in Lake Erhai based on comprehensive surveys of macrophytes in Lake Erhai. By combining literature data and retracing the historical succession of macrophytes in Lake Erhai, we further identified the driving factors of macrophyte degradation while aiming to propose countermeasures for the natural restoration of macrophytes in Lake Erhai and the sustainable improvement of water quality. This study aimed to provide a reference for the ecological restoration of aquatic ecosystems in the early stages of eutrophication and sustainable improvement of water quality.

## 2. Materials and Methods

### 2.1. Study Area

Lake Erhai (25°36′–25°58′ N, 100°06′–100°18′ E) is a typical plateau lake in the Yunnan-Guizhou Plateau of China (Figure 1). It is located in the Dali Bai Autonomous Prefecture of Yunnan Province and belongs to the Lancang-Mekong River system, which originates from Lake Cibi in Eryuan County. The lake ecosystem is relatively closed, with a north-south ear-shaped planform, and serves as a major source of agricultural, industrial, and domestic water supply for Dali Prefecture. Lake Erhai has a maximum water level of 1966.00 m, which corresponds to a storage capacity of $2.96 \times 10^9$ $m^3$. The statutory minimum operating water level is 1964.30 m, with a corresponding storage capacity of $2.53 \times 10^9$ $m^3$. The average annual inflow into the lake is $8.78 \times 10^8$ $m^3$, while the average annual evaporation from the lake surface reaches $3.16 \times 10^8$ $m^3$. The lake covers an area of 252 $km^2$, with a maximum depth of 21.3 m. Its average depth is 10.8 m, with a basin morphology factor of 0.10, a lake shoreline development coefficient of 2.295, a shoreline length of 129.14 km, and a lake replenishment coefficient of 10.14 [33]. The elevation in the Lake Erhai Basin ranges from 1964.3 m to 4113.7 m, thereby experiencing a typical low-latitude subtropical southwestern monsoon climate with an average temperature of 15.1 °C. This climatic pattern features distinct dry and wet seasons, with mild temperatures and abundant sunshine. The average annual rainfall in the lake area is 1048 mm, and the rainy season accounts for over 85% of the total precipitation. The warm climate and ample sunlight promote the growth and reproduction of macrophytes in Lake Erhai, thus extending their growth period. However, these conditions also favor the rapid reproduction of phytoplankton, which leads to the formation of cyanobacterial blooms that negatively impact the lake's aquatic environment and ecology [34].

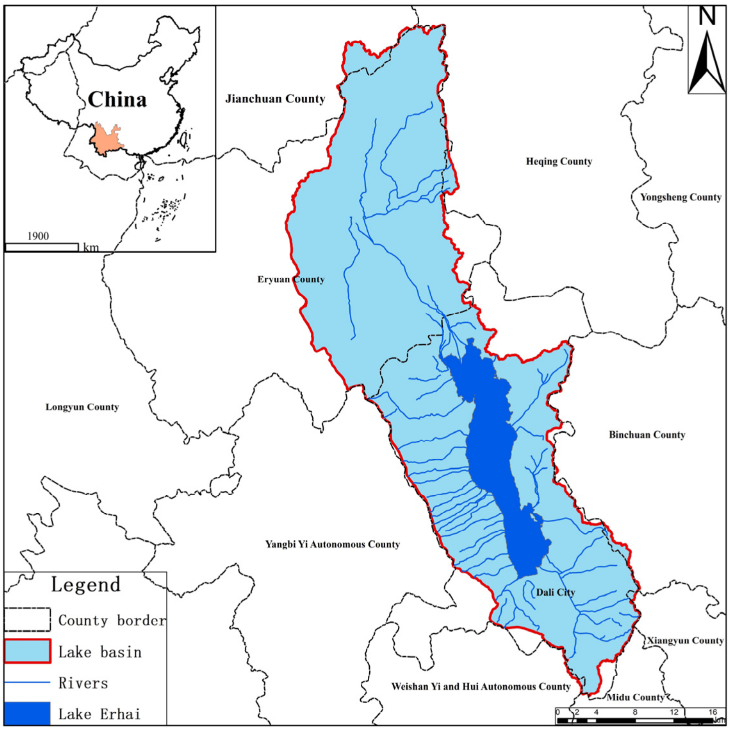


**Figure 1.** Location of the study area.

### *2.2. Data Collection*

From June to August 2022, 100 transect lines perpendicular to the shoreline were randomly laid across Lake Erhai (Figure 2) for macrophyte surveys. Each transect line was spaced at random intervals of 30–50 m and extended from the shoreline to the macrophyte distribution boundary. A quadrat sampler with a rotating sickle (sampling area of 0.196 $m^2$) was used to collect three plant samples randomly from each sampling point along the transect line. The macrophyte within the quadrats were washed, dried, sorted by species, and weighed on site after species identification, while referring to "Flora of China" And "Aquatic Plant" [35,36]. Additionally, 22 transect lines perpendicular to the shoreline were established along the coastal zone of Lake Erhai. At each transect line, sampling points were randomly set at intervals of 1–2 m from the shoreline to the boundary of the macrophyte distribution. Plant samples were collected from 1 m × 1 m quadrats at each sampling point. All macrophytes within the quadrats were quantitatively collected, including wetland and macrophyte parts above the ground surface, using sickles, and whole floating-leaved and submerged macrophytes using quadrat samplers. The collected macrophytes were identified on site, weighed to determine the fresh weight, and recorded. The boundary points of macrophyte distribution were determined using a handheld GPS (Garmin GPS map 60csx, Garmin, Olathe, KS, USA). Subsequently, the distribution areas of macrophytes in the entire lake and central bays were calculated using ArcMap 10.6 software based on boundary point information.

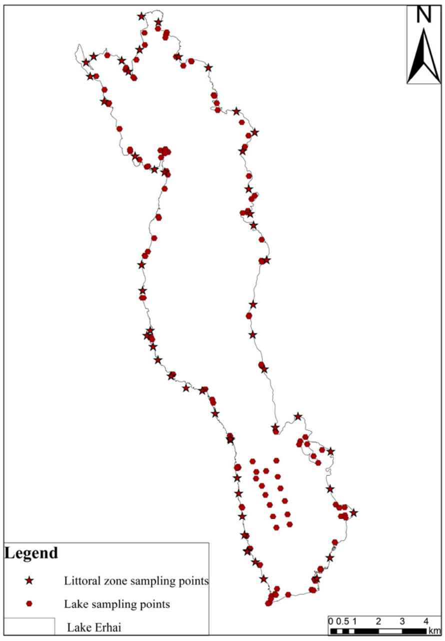


**Figure 2.** Sampling points.

Plant density has often been used to calculate species diversity indices. However, owing to their special biological characteristics, most macrophytes reproduce by branching or tillering rather than simply increasing the population biomass by increasing the number of individuals. Therefore, this study refers to the method of Chen Hong Da [37] and uses biomass to calculate the dominance and diversity indices of submerged macrophytes; that is, the dominance value (DV) of a species is calculated using relative biomass (RB) and relative frequency (RF). Data on macrophyte area, species, distribution depth, dominant species, etc., mainly came from historical literature and Yunnan Provincial Institute of Ecological Environment research results. The biased data in numerous historical datasets were averaged, and the data of 12 months were averaged and converted into annual average data. Past data for macrophyte areas were reasonably estimated.

## 3. Results

### 3.1. Macrophyte Species Composition

According to a survey conducted in 2022, there will be 72 species of macrophytes in Lake Erhai (Table 1). According to the growth form, there were 19 species of submerged macrophytes, which accounted for 26.39%; 4 species of floating macrophytes, which accounted for 5.56%; 5 species of floating-leaved macrophytes, which accounted for 6.94%; 4 species of emergent macrophytes, which accounted for 5.56%; and 40 species of hygrophytes, which accounted for 55.56%. Macrophytes in Lake Erhai were classified by family and species. The family Cyperaceae consists of four genera and six species, all of which are small herbaceous plants with strong adaptability and wide distribution. The Poaceae family has the most species, with 10 genera and 11 species, all of which are herbaceous plants, including *Zizania*, *Phragmites*, *Echinochloa*, *Paspalum*, *Leersia*, and *Arundo*. The family Nymphaeaceae comprises two genera and two species, all of which are floating macrophytes, including *Nelumbo* and *Nymphaea*. The family Hydrocharitaceae comprises five genera and seven species: *Hydrilla*, *Ottelia*, *Elodea*, *Najas*, and *Vallisneria*.

**Table 1.** Results of the 2022's survey on macrophytes in Lake Erhai.

| Life Form | Species | Family | Genus |
|---|---|---|---|
| submerged macrophytes | *Myriophyllum verticillatum* | *Haloragaceae* | *Myriophyllum* |
| | *Potamogeton crispus* | *Potamogetonaceae* | *Potamogeton* |
| | *Hydrilla verticillata* | *Hydrocharitaceae* | *Hydrilla* |
| | *Potamogeton wrightii* | *Potamogetonaceae* | *Potamogeton* |
| | *Ceratophyllum demersum* | *Ceratophyllaceae* | *Ceratophyllum* |
| | *Ottelia acuminata* | *Hydrocharitaceae* | *Ottelia* |
| | *Stuckenia pectinata* | *Potamogetonaceae* | *Stuckenia* |
| | *Elodea canadensis* | *Hydrocharitaceae* | *Elodea* |
| | *Najas marina* | *Hydrocharitaceae* | *Najas* |
| | *Potamogeton lucens* | *Potamogetonaceae* | *Potamogeton* |
| | *Vallisneria natans* | *Hydrocharitaceae* | *Vallisneria* |
| | *Potamogeton perfoliatus* | *Potamogetonaceae* | *Potamogeton* |
| | *Potamogeton maackianus* | *Potamogetonaceae* | *Potamogeton* |
| | *Stuckenia filiformis* | *Potamogetonaceae* | *Potamogeton* |
| | *Potamogeton pusillus* | *Potamogetonaceae* | *Potamogeton* |
| | *Chara corallina* | *Characeae* | *Chara* |
| | *Potamogeton intortifloius* | *Potamogetonaceae* | *Potamogeton* |
| | *Potamogeton oxyphyllus* | *Potamogetonaceae* | *Potamogeton* |
| | *Najas minor* | *Hydrocharitaceae* | *Najas* |
| floating macrophytes | *Azolla pinnata* | *Salviniaceae* | *Azolla* |
| | *Lemna minor* | *Araceae* | *Lemna* |
| | *Spirodela polyrhiza* | *Araceae* | *Spirodela* |
| | *Nymphaea tetragona* | *Nymphaeaceae* | *Nymphaea* |
| floating-leaved macrophytes | *Trapa incisa* | *Lythraceae* | *Trapa* |
| | *Nymphoides peltata* | *Menyanthaceae* | *Nymphoides* |
| | *Potamogeton natans* | *Potamogetonaceae* | *Potamogeton* |
| | *Eichhornia crassipes* | *Pontederiaceae* | *Eichhornia* |
| | *Persicaria amphibia* | *Polygonaceae* | *Persicaria* |
| emergent macrophyte | *Zizania latifolia* | *Poaceae* | *Zizania* |
| | *Typha orientalis* | *Typhaceae* | *Typha* |
| | *Phragmites australis* | *Poaceae* | *Phragmites* |
| | *Nymphaea tetragona* | *Nelumbonaceae* | *Nelumbo* |
| Hygrophyte | *Salix matsudana* | *Salicaceae* | *Salix* |
| | *Salix babylonica* | *Salicaceae* | *Salix* |
| | *Populus przewalskii* | *Salicaceae* | *Salix* |
| | *Metasequoia glyptostroboides* | *Cupressaceae* | *Metasequoia* |
| | *Taxodium distichum var. imbricatum* | *Cupressaceae* | *Taxodium* |
| | *Persicaria hydropiper* | *Polygonaceae* | *Persicaria* |
| | *Persicaria lapathifolia* | *Polygonaceae* | *Persicaria* |
| | *Eclipta prostrata* | *Asteraceae* | *Eclipta* |
| | *Paspalum distichum* | *Poaceae* | *Paspalum* |
| | *Pontederia cordata* | *Pontederiaceae* | *Pontederia* |
| | *Cyperus involucratus* | *Cyperaceae* | *Cyperus* |
| | *Canna indica* | *Cannaceae* | *Canna* |
| | *Schoenoplectus tabernaemontani* | *Cyperaceae* | *Schoenoplectus* |
| | *Leersia hexandra* | *Poaceae* | *Leersia* |
| | *Alternanthera philoxeroides* | *Amaranthaceae* | *Alternanthera* |
| | *Thalia dealbata* | *Marantaceae* | *Thalia* |
| | *Equisetum hyemale* | *Equisetaceae* | *Equisetum* |
| | *Echinochloa crus-galli* | *Poaceae* | *Echinochloa* |
| | *Acorus calamus* | *Acoraceae* | *Acorus* |
| | *Impatiens uliginosa* | *Balsaminaceae* | *Impatiens* |
| | *Juncus effusus* | *Juncaceae* | *Juncus* |
| | *Cyperus serotinus* | *Cyperaceae* | *Cyperus* |
| | *Cortaderia selloana* | *Poaceae* | *Cortaderia* |
| | *Arundo donax 'Versicolor'* | *Poaceae* | *Arundo* |

Table 1. *Cont.*

| Life Form | Species | Family | Genus |
|---|---|---|---|
| Hygrophyte | *Dysphania ambrosioides* | *Amaranthaceae* | *Dysphania* |
| | *Iris tectorum* | *Iridaceae* | *Iris* |
| | *Pycreus sanguinolentus* | *Cyperaceae* | *Pycreus* |
| | *Symphyotrichum subulatum* | *Asteraceae* | *Symphyotrichum* |
| | *Coix lacryma-jobi* | *Poaceae* | *Coix* |
| | *Cyperus difformis* | *Cyperaceae* | *Cyperus* |
| | *Lythrum salicaria* | *Lythraceae* | *Lythrum* |
| | *Bidens pilosa* | *Asteraceae* | *Bidens* |
| | *Echinochloa caudata* | *Poaceae* | *Echinochloa* |
| | *Polypogon fugax* | *Poaceae* | *Polypogon* |
| | *Bolboschoenus planiculmis* | *Cyperaceae* | *Bolboschoenus* |
| | *Colocasia esculenta* | *Araceae* | *Colocasia* |
| | *Oenanthe javanica* | *Apiaceae* | *Oenanthe* |
| | *Cynodon dactylon* | *Poaceae* | *Cynodon* |
| | *Ageratina adenophora* | *Asteraceae* | *Ageratina* |
| | *Commelina communis* | *Commelinaceae* | *Commelina* |

The size of families and genera is an essential quantitative characteristic in the study of macrophyte flora and can reflect the ancient characteristics of the macrophyte flora in a region. In terms of the differences in the number of genera in macrophyte families in Lake Erhai (Table 2), families with three or more genera included *Poaceae*, *Hydrocharitaceae*, *Cyperaceae*, and *Asteraceae*, which accounted for 13.33% of the total number of macrophyte families, with the total proportion of genera reaching 42.59%. Families with two genera included *Cupressaceae*, *Nymphaeaceae*, *Araceae*, *Amaranthaceae*, and *Acanthaceae*, which accounted for 16.67% of the total number of families, with the full proportion of genera reaching 18.52%. There were 21 families with only one genus, which accounted for 70.00% of the total number of families, dominating the number of genera, with a full proportion reaching 38.89%. In terms of differences in the number of species in macrophyte families, families with six or more species included *Lemnaceae*, *Poaceae*, *Cyperaceae*, and *Hydrocharitaceae*, which accounted for 13.33% of the total number of families, with the full proportion of species reaching 47.22%, thereby indicating that dominant families were more evident in Lake Erhai. Species within these families are essential components of the macrophyte resources in this region. There were eight families with 2–4 species, which accounted for 26.67% of the total number of families, with the full proportion reaching 27.78%. Eighteen families had only one species, which accounted for 6.00% of the total number of families, with the total proportion of species reaching 25.00%. Regarding the differences in the number of species in macrophyte genera, there were 18 genera with only one species, which accounted for 34.62% of the total genera and 25.00% of all species and showed an absolute advantage.

**Table 2.** Composition of genera and species within the families of the 2022's survey on macrophytes in Lake Erhai.

| Species | Number of Genera | Genus Proportion (%) | Species Number | Species Proportion (%) |
|---|---|---|---|---|
| *Cupressaceae* | 2 | 3.70 | 2 | 2.78 |
| *Acoraceae* | 1 | 1.85 | 1 | 1.39 |
| *Juncaceae* | 1 | 1.85 | 1 | 1.39 |
| *Balsaminaceae* | 1 | 1.85 | 1 | 1.39 |
| *Lemnaceae* | 1 | 1.85 | 1 | 1.39 |
| *Poaceae* | 10 | 18.52 | 11 | 15.28 |
| *Ceratophyllaceae* | 1 | 1.85 | 1 | 1.39 |

**Table 2.** *Cont.*

| Species | Number of Genera | Genus Proportion (%) | Species Number | Species Proportion (%) |
|---|---|---|---|---|
| *Asteraceae* | 4 | 7.41 | 4 | 5.56 |
| *Polygonaceae* | 1 | 1.85 | 3 | 4.17 |
| *Trapaceae* | 1 | 1.85 | 1 | 1.39 |
| *Characeae* | 1 | 1.85 | 1 | 1.39 |
| *Azollaceae* | 1 | 1.85 | 1 | 1.39 |
| *Cannaceae* | 1 | 1.85 | 1 | 1.39 |
| *Equisetaceae* | 1 | 1.85 | 1 | 1.39 |
| *Lythraceae* | 1 | 1.85 | 1 | 1.39 |
| *Apiaceae* | 1 | 1.85 | 1 | 1.39 |
| *Cyperaceae* | 4 | 7.41 | 6 | 8.33 |
| *Hydrocharitaceae* | 5 | 9.26 | 6 | 8.33 |
| *Menyanthaceae* | 1 | 1.85 | 1 | 1.39 |
| *Nymphaeaceae* | 2 | 3.70 | 2 | 2.78 |
| *Araceae* | 2 | 3.70 | 2 | 2.78 |
| *Amaranthaceae* | 2 | 3.70 | 2 | 2.78 |
| *Typhaceae* | 1 | 1.85 | 1 | 1.39 |
| *Haloragaceae* | 1 | 1.85 | 1 | 1.39 |
| *Commelinaceae* | 1 | 1.85 | 1 | 1.39 |
| *Potamogetonaceae* | 1 | 1.85 | 11 | 15.28 |
| *Salicaceae* | 1 | 1.85 | 3 | 4.17 |
| *Pontederiaceae* | 2 | 3.70 | 2 | 2.78 |
| *Iridaceae* | 1 | 1.85 | 1 | 1.39 |
| *Marantaceae* | 1 | 1.85 | 1 | 1.39 |
|  | 54 | 100.00 | 72 | 100.00 |

### *3.2. Macrophyte Community Composition*

#### 3.2.1. Submerged Macrophyte Community

The submerged macrophyte community in Lake Erhai comprised seven species. The *Vallisneria natans* community is distributed in nearshore areas, excluding the outlet area of the West Erhai River, and often forms patches of varying sizes. The community coverage is generally low, with biomass typically ranging from 400–6500 $g/m^2 \cdot FW$. Common accompanying species included *Ceratophyllum demersum*, *Stuckenia pectinata*, *Myriophyllum spicatum*, *Potamogeton maackianus*, and *Hydrilla verticillata*. The distribution depth ranges from 1.0–5.5 m, with the optimal distribution depth typically between 3.5 and 4.5 m. The *Ceratophyllum demersum* community usually constitutes a single dominant or the main dominant species, distributed around the entire lake, with biomass typically ranging from 200–5000 $g/m^2 \cdot FW$. It often dominates, with proportions exceeding 80% in the dominant communities. In the northern bays and some areas of the eastern shore, *Ceratophyllum demersum* biomass is relatively high and is often associated with species such as *Vallisneria natans*, *Potamogeton wrightii*, *Potamogeton maackianus*, *Myriophyllum spicatum*, and *Potamogeton lucens*. The *Ottelia acuminata* community primarily occurs along the southwestern coast of Lake Erhai and appears patchy and scattered in areas approximately 20–100 m from the shoreline. In areas where it is distributed in patches, the water quality near the shore appears clear and *Ottelia acuminata* grows well. The *Potamogeton maackianus* community is distributed around the entire lake, mainly in the northern and western parts of Lake Erhai and some bays in the eastern part. They were relatively less distributed in the southern region. The distribution depth ranges from 0.5–5.0 m, with an optimal distribution depth between 3 and 3.5 m. As a dominant species, *Potamogeton maackianus* typically occupies large areas of medium-depth water, with higher species diversity in adjacent shallow-water areas, accompanied by species such as *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Vallisneria natans*, *Hydrilla verticillata*, and *Potamogeton lucens*. Community coverage generally exceeds 75%. The *Potamogeton wrightii* community was mainly distributed along the west coast, with some presence in the eastern bays. The biomass usually ranges from 100–4200 $g/m^2 \cdot FW$, commonly accompanied by species such as *Potamogeton maackianus*, *Stuckenia pectinata*, *Vallisneria natans*, and *Myriophyllum spicatum*. *Vallisneria natans* and *Hydrilla verticillata* are primarily distributed along the coast of Lake Erhai, with some distribution in the southeastern bays. The biomass typically ranges from 100–3000 g/m$^2$·FW, commonly accompanied by species such as *Myriophyllum spicatum*, *Ceratophyllum demersum*, and *Potamogeton maackianus*. The *Elodea canadensis* community was mainly distributed near the West Erhai River, with the macrophyte community proportion reaching 100%, and the community biomass was relatively high.

### 3.2.2. Floating-Leaved Macrophyte Community

The *Nymphoides peltata* community was distributed along the west coast of Lake Erhai, with a relatively small distribution area. The biomass ranged from 100–2000 g/m$^2$·FW. It often constitutes a dominant species in communities formed on the water surface, accounting for proportions ranging from 70–90%. Companion species included *Ottelia acuminata*, *Hydrilla verticillata*, *Vallisneria natans*, and *Potamogeton wrightii*.

### 3.2.3. Emerged Macrophyte Community

The emerging macrophyte communities mainly consisted of *Zizania latifolia*, *Phragmites australis*, and *Persicaria amphibia*. The *Zizania latifolia* community was the dominant community along the shores of Lake Erhai and was distributed throughout the circumference of the lake. It is the dominant species within the community and grows predominantly at the land-water interface. Though it occurs in patches in shallow areas, it rarely extends into the lake itself. Biomass typically ranges from 300–8000 g/m$^2$ FW, thereby constituting 80–90% of the dominant community. Common accompanying species included *Phragmites australis*, *Cynodon dactylon*, *Persicaria hydropiper*, and *Paspalum distichum*. The *Phragmites australis* community primarily inhabits the western and northern shores of Lake Erhai and surrounding wetland parks. *Phragmites australis* is a widely distributed macrophyte that grows at the land-water interface along the shores of Lake Erhai. Its biomass is relatively high, ranging from 800 to 13,800 g/m$^2$·FW, constituting 65–80% of the dominant community. Common accompanying species included *Zizania latifolia*, *Cynodon dactylon*, *Alternanthera philoxeroides*, and *Paspalum distichum*. The *Persicaria amphibia* community in Lake Erhai, especially near the Haise Peninsula, is distributed approximately 50 m from the shoreline. The biomass ranges from 100–620 g/m$^2$·FW, with accompanying species such as *Potamogeton wrightii* and *Ceratophyllum demersum*.

### 3.2.4. Hygrophyte Community

The hygrophyte communities in the littoral zone of Lake Erhai mainly comprised *Cynodon dactylon*, *Alternanthera philoxeroides*, *Eclipta prostrata*, and *Paspalum distichum* communities. Among these, the *Cynodon dactylon* community is the dominant community along the shores of Lake Erhai, with a biomass ranging from 100–1000 g/m$^2$·FW, which constitutes approximately 50% of the dominant community. Common accompanying species included *Ageratina adenophora* and *Alternanthera philoxeroides*. The *Alternanthera philoxeroides* community primarily inhabits the western and northern shores of Lake Erhai, with biomass typically ranging from 50–2500 g/m$^2$·FW. It constitutes approximately 80% of the dominant community and is often accompanied by *Cynodon dactylon*, *Paspalum distichum*, and *Bidens pilosa*. The *Eclipta prostrata* community is mainly distributed along the western shore of Lake Erhai, with a biomass ranging from 200–3560 g/m$^2$·FW. It constituted approximately 90% of the dominant community and was commonly accompanied by *Ageratina adenophora*, *Persicaria hydropiper*, and *Alternanthera philoxeroides*. The *Paspalum distichum* community also primarily occurs along the western shore of Lake Erhai, with biomass typically ranging from 60–1450 g/m$^2$·FW. It constituted approximately 70% of the dominant community and was commonly accompanied by *Alternanthera philoxeroides*, *Persicaria hydropiper*, and *Echinochloa caudata*.

### 3.3. Spatial Distribution of Macrophytes

Macrophytes in Lake Erhai are distributed throughout the lake, primarily concentrated within 100–200 m of the shore, appearing in bands or patches. The submerged macrophytes included *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Hydrilla verticillata*, *Potamogeton wrightii*, *Nymphoides peltata*, and *Ottelia acuminata*. The floating-leaved macrophytes mainly consist of *Azolla pinnata* and *Trapa incisa*. The emerging macrophytes include *Phragmites australis* and *Zizania latifolia*. The community structure was comprised of *Ceratophyllum demersum* communities, *Trapa incisa*, *Zizania latifolia*, *Myriophyllum spicatum*, and *Ottelia acuminata*. The total distribution area of macrophytes in the lake was 27.04 km$^2$, with a coverage of 10.71%.

In quantitative sampling across Lake Erhai, the maximum biomass of macrophytes reached 4695 g/m$^2$·FW, with an average biomass of 2035.61 g/m$^2$·FW. The species with the highest average biomass is *Vallisneria natans*, with an average biomass of 557.98 g/m$^2$·FW, thereby accounting for 27.41% of the total macrophyte biomass. Following *Vallisneria natans* is *Ceratophyllum demersum*, with an average biomass of 505.37 g/m$^2$·FW, comprising 24.83% of the total macrophyte biomass. The species with the smallest average biomass are *Potamogeton lucens*, *Potamogeton maackianus*, and *Nymphoides peltata*, with average biomasses of 9.26 g/m$^2$·FW, 5.99 g/m$^2$·FW, and 0.95 g/m$^2$·FW, respectively, which constituted only 0.45%, 0.29%, and 0.05% of the total macrophyte biomass. The total fresh weight of macrophyte biomass in Lake Erhai was estimated to be approximately 55,000 tons (Figure 3).

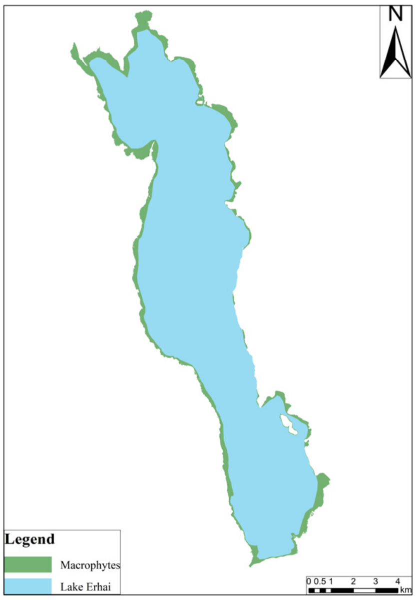


**Figure 3.** Distribution map of the 2022's survey on macrophytes in Lake Erhai.

### 3.4. Species Dominance

In August 2020, during a survey in Lake Erhai, significant differences were observed in the frequencies of various submerged macrophytes, as shown in Table 3. In terms of distribution frequency, the most frequently occurring macrophyte in Lake Erhai is *Vallisneria natans*, followed by *Ceratophyllum demersum*, *Hydrilla verticillata*, and *Potamogeton wrightii*, with distribution frequencies of 21.25%, 18.75%, 13.13%, and 12.50%, respectively. In terms of average biomass, the most frequently occurring macrophyte in Lake Erhai is *Vallisneria natans*, followed by *Ceratophyllum demersum*, *Ottelia acuminata*, *Potamogeton wrightii*, and *Hydrilla verticillata*, with distribution frequencies of 27.41%, 24.83%, 11.61%, 11.21%, and 10.98%, respectively.

**Table 3.** Calculation of the 2022 survey on macrophytes species dominance in Lake Erhai.

| Species | Frequency | Relative Frequency | Biomass (Wet Weight) (g) | Relative Biomass | Dominance Value |
|---|---|---|---|---|---|
| *Stuckenia pectinata* | 9 | 0.63% | 50.98 | 2.50% | 4.06% |
| *Najas marina* | 6 | 3.75% | 19.11 | 0.94% | 2.34% |
| *Potamogeton lucens* | 1 | 0.63% | 9.26 | 0.45% | 0.54% |
| *Ottelia acuminata* | 10 | 6.25% | 236.33 | 11.61% | 8.93% |
| *Hydrilla verticillata* | 21 | 13.13% | 223.45 | 10.98% | 12.05% |
| *Myriophyllum spicatum* | 8 | 5.00% | 49.52 | 2.43% | 3.72% |
| *Nymphoides peltata* | 3 | 1.88% | 11.13 | 0.55% | 1.21% |
| *Ceratophyllum demersum* | 30 | 18.75% | 505.37 | 24.83% | 21.79% |
| *Vallisneria natans* | 34 | 21.25% | 557.98 | 27.41% | 24.33% |
| *Potamogeton lucens* | 2 | 1.25% | 14.90 | 0.73% | 0.99% |
| *Trapa incisa* | 6 | 3.75% | 56.47 | 2.77% | 3.26% |
| *Chara corallina* | 2 | 1.25% | 8.29 | 0.41% | 0.83% |
| *Potamogeton maackianus* | 1 | 0.63% | 5.99 | 0.29% | 0.46% |
| *Potamogeton pusillus* | 1 | 0.63% | 0.95 | 0.05% | 0.34% |
| *Elodea canadensis* | 3 | 1.88% | 20.87 | 1.03% | 1.45% |
| *Potamogeton wrightii* | 20 | 12.50% | 228.27 | 11.21% | 11.86% |
| *Potamogeton crispus* | 3 | 1.88% | 36.74 | 1.81% | 1.84% |

After calculating species dominance, the dominant species of macrophytes in Lake Erhai are *Vallisneria natans*, *Ceratophyllum demersum*, *Hydrilla verticillata*, and *Potamogeton wrightii*, with dominance percentages of 24.33%, 21.79%, 12.05%, and 11.86%, respectively, accounting for 70.03% of the total dominance of the community, as shown in Figure 4. Among them, *Vallisneria natans* and *Ceratophyllum demersum* were the dominant species, with extensive distribution areas and high biomass per sample plot, resulting in a significantly higher average biomass and dominance than the other submerged macrophyte species. However, the average biomass and dominance of *Hydrilla verticillata* varied only slightly. *Hydrilla verticillata* has strong adaptability and can appear in various environments; however, it often lacks a competitive advantage and tends to exist as a companion species in sample plots. Therefore, although its distribution frequency was relatively high, its RB compared to *Potamogeton wrightii* was still relatively low.

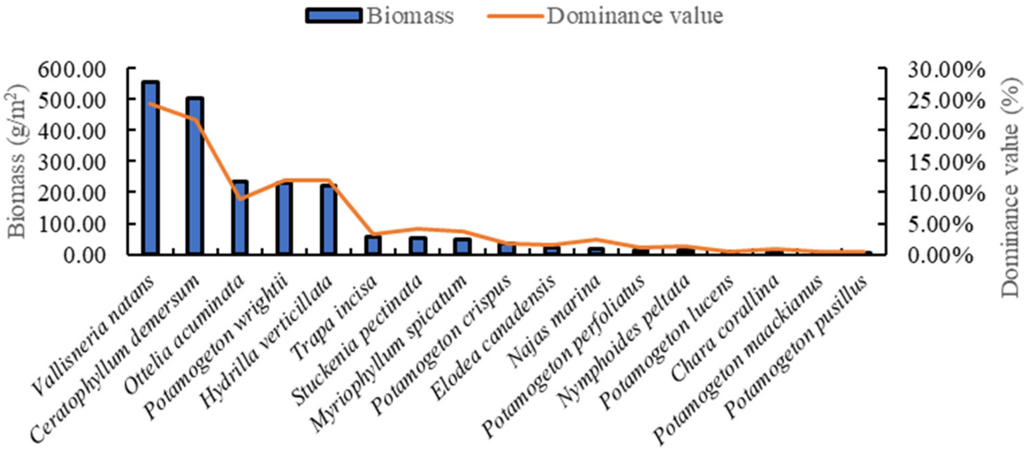


**Figure 4.** Comparison of frequency and biomass of macrophytes in Lake Erhai (2022).

### *3.5. Succession of Macrophyte Species Composition in Lake Erhai*

Compared with historical records, from 1944–2022, the macrophyte species in Lake Erhai underwent a process of transition from a few to many, then from prosperity to decline, and finally gradually stabilized and slowly recovered. Before the 1950s, sporadic collections of macrophytes in Lake Erhai were conducted by individual botanists; however, owing to the dispersion of specimens, no systematic identification or analysis was performed.

The only scholars with records were Hsiao et al., who collected 21 species (Figure 5) that were mainly dominated by submerged macrophytes (48.24%) [38]. In 1957, according to reports by Li Shanghao and others, apart from the 14 common macrophytes that Yunnan the coastal zone of Lake Erhai is relatively rich in, there were no macrophytes deeper than 3 m [39]. From the 1950s to the 1960s (Tables 4 and 5), except for the *Trapa incisa* and *Ottelia acuminata* communities, most submerged macrophyte communities had a coverage of approximately 50% [40], which was dominated by species such as *Najas marina*, *Stuckenia pectinata*, and *Ottelia acuminata* [41]. From the 1950s to the 1970s, with the development of watershed agriculture, the use of pesticides and fertilizers increased, leading to a continuous increase in nutrient concentrations in lake water, which greatly promoted the growth of macrophytes along the lake. The macrophyte coverage area continued to expand into deeper waters, and the water depth suitable for submerged macrophytes increased. The dominant macrophyte species shifted from clear water to *Hydrilla verticillata*, *Ceratophyllum demersum*, and *Potamogeton maackianus*. In the 1980s, the coverage area of macrophytes in the entire lake decreased and the biomass plummeted. The macrophyte area decreased from 7727.00 $hm^2$ in the early 1980s to 6254.00 $hm^2$ in the mid-1980s, and biomass decreased from $79.9 \times 10^4$ t to $47.9 \times 10^4$ t. During this period, the coverage of communities, such as *Hydrilla verticillata* and *Potamogeton maackianus*, increased by 100% [42]. *Vallisneria natans* began to appear at a depth of 8.6 m, and at a depth of 10 m, *Hydrilla verticillata* communities were found on the lakebed with a coverage of 80% [43]. At this time, there were significant changes in the composition of the macrophyte communities, with a decrease in the diversity of submerged macrophytes (accounting for only 30%), simplified community structures, and fewer occurrences of communities such as *Stuckenia pectinata*, which prefers shallow sandy lake beds. Interspecific competition among *Ottelia acuminata* species in the lake, slight water pollution, and excessive harvesting of leaves began to decline, whereas *Hydrilla verticillata*, *Vallisneria natans*, *Potamogeton maackianus*, and *Ceratophyllum demersum*, which prefer nutrient-rich environments, reproduced abundantly in the lake, becoming the three largest and most widely distributed populations in Lake Erhai [42]. In the 1990s, with the gradual deterioration of water quality and the continuous decline in water transparency in Lake Erhai, macrophytes in the deep-water areas continued to decline. The depth range suitable for macrophytes gradually decreased to approximately 8–9 m. The diversity of species, community types, coverage area, and biomass decreased, leading to a simplification of species and a change in the dominant species groups. Compared to the early 1980s, by 1994, the coverage area of macrophytes decreased by 3235.00 $hm^2$, and the biomass decreased by $51.5 \times 10^4$ t. Compared to the mid-1980s, the number of species decreased by 15, and the number of community types decreased by 6 (communities such as *Ottelia acuminata*, *Stuckenia pectinata*, *Phragmites australis*, *Leersia hexandra*, and *Persicaria lapathifolia*). Communities such as *Potamogeton perfoliatus*, reported in the 1970s, are sparsely distributed. *Eichhornia crassipes* became a single-species community, with an area of approximately 2.5 $hm^2$. The range of *Vallisneria natans* communities expanded, whereas *Ottelia acuminata* communities were sparsely distributed only in Xiaohewan and Manjiangwan, owing to excessive human harvesting. The first dominant species, *Hydrilla verticillata*, was replaced by *Vallisneria natans* as the third most dominant species, and the third most dominant species, *Potamogeton maackianus*, became the second most dominant species [43]. In the 2000s, local governments implemented timely governance measures, and the macrophytes in Lake Erhai began to recover slowly. In a 2009 lakeshore survey, 145 species were found (including 15 species of trees and shrubs, with submerged macrophytes accounting for only 20.00%). Compared to the early 1990s, the introduction of lake shore restoration work led to an increase of 100 species, with pollution-tolerant species such as *Zizania latifolia*, *Ceratophyllum demersum*, *Vallisneria natans*, *Potamogeton wrightii*, and *Myriophyllum spicatum* being the main dominant communities. However, the depth range of their distribution gradually decreases to approximately 6–7 m. Macrophyte coverage area decreased by 2492.00 $hm^2$, and biomass decreased by $3.41 \times 10^4$ t. macrophytes on the southern lake platform have disappeared [44]. Since 2010, the distribution depth of submerged macrophytes has decreased to 4–5 m. The lake platform, previously extensively covered by submerged macrophytes, now has a non-macrophyte distribution. During this period, the macrophyte distribution area remained at approximately 10% [45]. Since 2016, the degradation of submerged macrophytes in Lake Erhai has been severe, with the number of species is significantly lower than that in 2008, and the distribution area decreased by over 70% compared to that in the 1980s. The dominant species changed from *Ottelia acuminata*, *Stuckenia pectinata*, and *Najas marina* in the 1960s to *Potamogeton maackianus*, *Ceratophyllum demersum*, and *Vallisneria natans*. Moreover, deep-water areas (>4 m) face the risk of shrinking distribution. By 2022, the proportion of macrophyte area in Lake Erhai remained small, accounting for only 10.71%, with a total distribution area of 2704.00 hm$^2$ and a biomass of $5.50 \times 10^4$ t. The dominant species include pollution-tolerant species, such as *Vallisneria natans*, *Potamogeton maackianus*, and *Ceratophyllum demersum*. Although there has been a slow recovery of macrophytes in Lake Erhai compared to 2009, there is still the possibility of a continued decline in the macrophyte area in the short term under the current trend of eutrophication.

**Table 4.** Macrophyte community succession of Lake Erhai in 1944–2022.

| **Years** | **Number of Species** | **Macrophyte Area (hm$^2$)** | **Coverage Rate (%)** | **Biomass (Wet Weight) ($\times 10^4$ t)** | **Distribution Depth** | **References** |
|---|---|---|---|---|---|---|
| 1944 | 11 family, 19 genus, 21 species | - | - | - | - | [38] |
| 1957 | - | - | - | - | >3 m no macrophytes | [39] |
| 1977 | 20 family, 31 genus, 51 species | - | - | - | >7 m no macrophytes | [46] |
| 1975–1983 | 18 family, 30 genus, 40 species | - | - | - | >10 m no macrophytes | [46] |
| 1981–1983 | 17 family, 24 genus, 32 species | 7727.00 | 30.90 | 79.96 | >8.6 m no macrophytes | [47] |
| 1985–1986 | 21 family, 37 genus, 50 species | 6254.00 | 25.10 | 47.90 | >10.5 m no macrophytes | [42] |
| 1994 | 19 family, 26 genus, 35 species | 4492.00 | 17.69 | 28.40 | >10.5 m no macrophytes | [43] |
| 1997 | 45 species | 6533.00 | 26.58 | 76.50 | >10 m no macrophytes | [48] |
| 1998 | 6 family, 6 genus, 13 species | 9602.50 | 40.39 | 39.57 | >9 m no macrophytes | [49] |
| 2008 | 20 family, 26 genus, 25 species | - | - | - | >7 m no macrophytes | [50] |
| 2009 | 47 family, 108 genus, 145 species | 2000.00 | 8.00 | 24.99 | >6 m no macrophytes | [44] |
| 2016 | 3 family, 7 genus, 13 species | 2636.00 | 10.50 | - | >4 m no macrophytes | [30] |
| 2017–2018 | 9 family, 11 genus, 18 species | - | - | - | - | [51] |
| 2020–2021 | 56 family, 156 genus, 206 species | | | | >5.5 m no macrophytes | [52] |
| 2022 | 30 family, 54 genus, 72 species | 2704.00 | 10.71 | 5.50 | >5 m no macrophytes | - |

**Table 5.** Macrophyte coenotype succession of Lake Erhai in 1944–2022.

| **Coenotype** | **1977** | **1975–1983** | **1981–1983** | **1985–1986** | **1994** | **1997** | **1998** | **2008** | **2009** | **2016** | **2017–2018** | **2020–2021** | **2022** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Zizania latifolia* | + | + | + | + | | | + | | + | | | | + |
| *Trapa incisa + Myriophyllum spicatum* | + | + | | | | | | | | | | | |
| *Potamogeton crispus* | + | + | | + | | | + | | | | | | |
| *Potamogeton wrightii* | + | + | + | + | + | | + | | + | + | | + | + |
| *Potamogeton lucens* | + | + | | | + | | + | | | + | | | + |
| *Potamogeton perfoliatus* | + | + | | | | | + | | | | | | |
| *Ottelia acuminata* | + | + | | + | | | + | | | | | | + |
| *Myriophyllum spicatum* | + | + | + | + | + | | + | + | | + | | | |
| *Hydrilla verticillata* | + | + | + | + | + | + | + | | | + | | + | |
| *Ceratophyllum demersum* | + | + | + | + | + | + | + | + | + | + | + | + | + |
| *Potamogeton maackianus* | + | + | + | + | + | + | + | | + | + | + | + | + |
| *Vallisneria natans* | + | + | + | + | + | + | + | + | + | + | + | + | + |
| *Stuckenia pectinata* | | | + | + | | | + | | | | | | + |
| *Azolla pinnata* | | | + | | + | | + | | | | | | + |
| *Phragmites australis* | | | + | + | | | | | + | | | | + |
| *Leersia hexandra* | | | | + | | | | | | | | | |
| *Persicaria lapathifolia* | | | | + | | | + | | | | | | |
| *Nymphoides peltata* | | | | + | + | | + | | + | | | + | + |
| *Elsholtzia bodinieri Vaniot* | | | | + | | | | | | | | | |
| *Alternanthera philoxeroides* | | | | + | | | + | | | | | + | |
| *Trapa incisa* | | | | + | | | + | | + | | | + | |
| *Eichhornia crassipes* | | | | + | | | + | | | | | | |
| *Zannichellia palustris* | | | | | | | + | | | | | | |
| *Vallisneria natans + Potamogeton wrightii* | | | | | | | | + | | | | | |
| *Vallisneria natans + Myriophyllum spicatum* | | | | | | | | + | | | | | |
| *Vallisneria natans + Ceratophyllum demersum* | | | | | | | | + | | | | | |
| *Myriophyllum spicatum +Potamogeton maackianus* | | | | | | | | + | + | | | | |
| *Tamarix ramosissima Ledeb* | | | | | | | | | + | | | | |
| *Persicaria amphibia* | | | | | | | | | + | | | | + |
| *Najas marina +Myriophyllum spicatum + Vallisneria natans* | | | | | | | | | + | | | | |
| *Najas marina +Myriophyllum spicatum + Potamogeton maackianus* | | | | | | | | | + | | | | |
| *Hydrilla verticillata + Vallisneria natans* | | | | | | | | | + | | | | |
| *Trapa incisa + Utricularia Vulgaris + Hydrilla verticillata* | | | | | | | | | + | | | | |
| *Potamogeton maackianus + Ceratophyllum demersum + Vallisneria natans* | | | | | | | | | + | | | | |
| *Ceratophyllum demersum + Vallisneria natans + Potamogeton wrightii* | | | | | | | | | | | | | |
| *Cynodon dactylon* | | | | | | | | | | | | + | |
| *Ageratina adenophora* | | | | | | | | | | | | + | |
| *Echinochloa caudata* | | | | | | | | | | | | + | |
| *Elodea canadensis* | | | | | | | | | | | | | + |
| *Eclipta prostrata* | | | | | | | | | | | | | + |
| References | [46] | [46] | [47] | [42] | [43] | [48] | [49] | [50] | [44] | [30] | [51] | [52] | - |

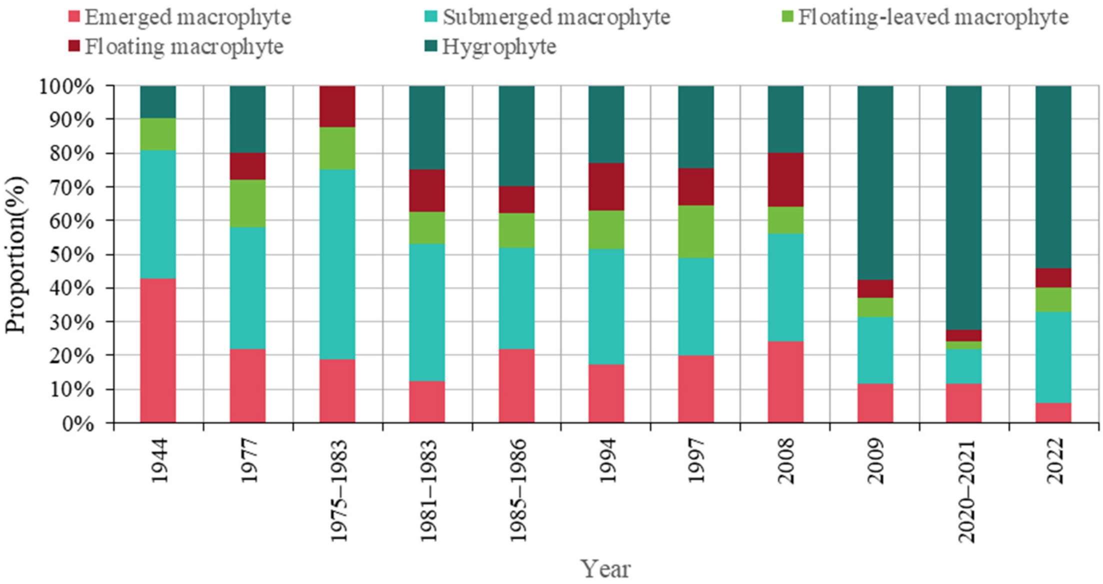


**Figure 5.** Change of macrophytes community structure composition of Lake Erhai in 1944–2022.

## 4. Discussion

### 4.1. Water-Level Fluctuation

Since 1952, the average water-level changes in Lake Erhai have been divided into four stages. In the first stage (1952–1969), Lake Erhai had an intermediate water level of 1974.0 m, the highest historical flood level recorded at 1975.67 m (September 1966), and the lowest water level in 1973.28 m. Although there was dam control at the mouth of the Xi'er River at a bottom elevation of 1972.5 m, Lake Erhai was essentially a natural lake during this period. Despite the overall decline in water levels, the volume of water remained sufficient to maintain a dynamic balance. During the rainy season (May–October), water-level fluctuations are closely related to changes in precipitation following natural processes. Villages, urban areas, and farmlands along the lake's edge were often flooded between elevations of 1974 and 1975.5 m during this period [53]. Approximately 25.35 km$^2$ of cropland along the lakeshore is submerged during floods. Additionally, large areas of farmland to the north and south of the lake are inundated annually during the rainy season. Many studies have reported a close relationship between sunlight and water levels [54–56]. Typically, an increase in the water level reduces the availability of light, especially at the bottom. If the underwater light intensity falls below the light compensation point for macrophytes, the species disappears from the community. Furthermore, high water levels inhibit the average growth of macrophytes [57]. The high-water level in Lake Erhai results in turbidity in coastal areas, rendering it unsuitable for the average growth of macrophytes in areas deeper than 3 m [39].

The second stage (1970–2003) saw a rapid decline in the water level of Lake Erhai following the successive operation of the Xi'er River cascade power stations and increased the outflow capacity of Lake Erhai [58,59]. From 1971 to 1982, the average water level of Lake Erhai was 1973.1 m, which was 0.9 m lower than the natural intermediate water level and 0.18 m lower than the lowest water level. Particularly in 1982, during an extremely dry year, the water level dropped to 1970.66 m, which was 3.34 m lower than the natural average water level and 2.62 m lower than the natural lowest water level. There are periodic fluctuations of 2–3 m in the water level each year, resulting in increased water level fluctuations and reduced water exchange retention time. The decrease in water level led to an increase in suitable areas for the distribution of submerged macrophytes [60,61]. The community of macrophytes *Vallisneria natans* transitioned into a community of beach hygrophytes, increasing macrophyte density. The numbers of *Stuckenia pectinata* and *Najas marina*, which were initially distributed in shallow-water areas, decreased. In contrast, *Stuckenia pectinata*, *Hydrilla verticillata*, and *Ceratophyllum demersum* increased, thereby resulting in a trend toward swampification in some shallow bays. Macrophytes continued to expand toward the western lake heart area, and submerged macrophytes covered the entire western lake heart platform area. From 1983 to 1992, Lake Erhai had low average water levels and drastic interannual variations, providing the hydraulic conditions for maintaining the peak stage of the macrophyte area. From 1993 to 2003, Lake Erhai remained at a low water level (approximately 1964.20 m), but the magnitude of the interannual variation significantly decreased. However, during this period, the water quality of Lake Erhai gradually deteriorated, water transparency decreased, and the distribution range and area of macrophytes decreased rapidly. Large-scale blue-green algae blooms occurred in 1996, 1998, and 2003. The southern lake heart platform area, the main distribution area of submerged macrophytes, also lost submerged macrophytes in 2003, which resulted in the proportion of the macrophyte distribution area in Lake Erhai falling below 10% for the first time in 2003.

The third stage (2004–2016) saw revisions in 2004 to the "Lake Erhai Management Regulations of Dali Bai Autonomous Prefecture", which adjusted the maximum operating water level of Lake Erhai from the original 1965.69 m to 1966.00 m and the minimum operational water level from the original 1962.69 m to 1964.30 m. The water level regulations of Lake Erhai have focused more on ecological restoration, leading to most of the lake shore being submerged again, thereby partially restoring the environmental functions of the lake shore, such as the expansion of wetland areas. During this period, the function of the Xi'er River cascade hydroelectric power station shifted from power generation to water level regulation [62]. Subsequently, from 2003 to 2008, the water level of Lake Erhai continued to increase, with macrophytes covering approximately 8% of the area in 2006. From 2009 to 2016, Lake Erhai operated at a relatively high water level owing to artificial regulations. During this period, the recovery of macrophytes was prolonged and the proportion of macrophyte area remained at approximately 10% for an extended period.

The fourth stage (2017–present) began in 2017 when the local government launched the "Save Lake Erhai" initiative and implemented low-water-level scheduling for the lake. By combining the conditions of the water resources in the basin, conscious efforts were made to implement low-water-level scheduling, reducing the average water level from April to July to 1964.30 m. Macrophyte recovery remained significant, with the average area increasing from 26.8 km$^2$ in 2014–2016 to 32.3 km$^2$ in 2017–2019. Seasonal fluctuations in water levels throughout the year are conducive to the germination, growth, and development of macrophytes [63]. The proportion of the macrophyte distribution area also increased to over 13%, especially with the reappearance of some emblematic macrophytes, such as *Ottelia acuminata* in Lake Erhai.

### *4.2. Lake Eutrophication*

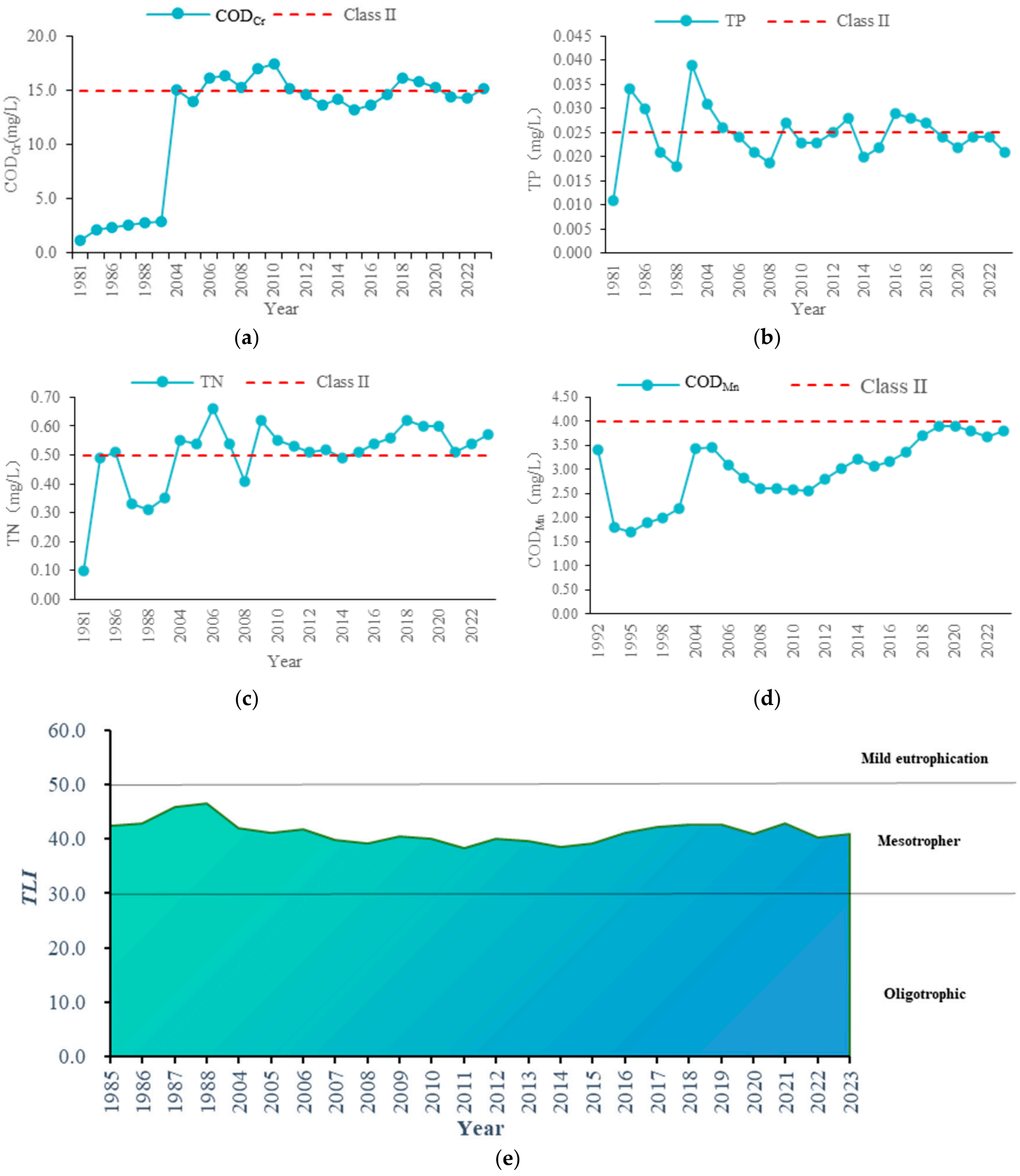
Lakes within the Yunnan-Guizhou Plateau region of China typically have higher elevations and deeper basins than the shallow-water lakes in the eastern plains [64–66]. Consequently, they exhibit characteristics distinct from those found in the eastern plain lake regions. The data from the Seventh National Population Census in 2020 show that the permanent population in the Lake Erhai Basin is 1.02 million, with a population density of 397 people per square kilometer. The basin area's gross domestic product (GDP) was CNY 55.09 billion [67]. Although the Lake Erhai Basin accounts for only 8.71% of the province's total land area, it supports 30.48% of the total population and 37.12% of the regional GDP of the Dali Prefecture. This is the most economically developed region in the Dali Prefecture and one of the fastest-growing economic regions in the Yunnan Province. Compared with lakes in the eastern plains of China, Lake Erhai has a relatively smaller catchment area, and its sources are close to lakes with short inflow channels. Lake Erhai is prone to rapid changes from drought to flooding and frequent localized heavy rain during the flood season. This leads to a concentrated input of pollution loads into the lake during the flood season, especially in the north and west, which has a certain impact on water quality. The semi-closed nature of the lake, its high population density, and high nutrient input make it extremely prone to eutrophication.

Before the 1970s, the water environment of Lake Erhai was stable with a low nutrient salt content. There was no macrophyte growth beyond a depth of 3 m, and macrophyte biomass and coverage were low. The dominant species were *Najas marina* and *Ottelia acuminata*, which preferred clean water. Water quality was categorized as Class I, and nutrient status was low [39]. In the 1970s, owing to the construction of the Xi'er River hydropower station and changes in traditional agricultural practices with the use of chemical fertilizers and pesticides, large amounts of nutrients, such as nitrogen and phosphorus, flowed into the lake through surface runoff from farmland. This has led to changes in water levels, increased nutrient salt content, expansion of macrophyte coverage, and continuous encroachment into deeper waters. The macrophyte community was dominated by pollution-tolerant and nutrient-loving species, such as *Potamogeton maackianus*, *Hydrilla verticillata*, *Ceratophyllum demersum*, and *Vallisneria natans*. Consequently, the water quality declined, and the nutrient status shifted to mid-nutrient level [68]. In the 1980s, the water level of Lake Erhai decreased further, leading to further differentiation in macrophyte distribution. The number of floating and emergent macrophytes declined rapidly. At this time, the water quality deteriorated to Class II and the nutrient status gradually shifted from low to mid-nutrient levels [49]. Total phosphorus (TP) was the main pollutant exceeding the standard, with an average concentration of 0.023 mg/L from 1981 to 1988. In the 1990s, with the booming tourism industry around Lake Erhai and the rapid increase in industrial wastewater due to industrial development, there was excessive feeding in cage aquaculture, which accelerated the input of nutrients into the water. Additionally, excessive harvesting of macrophytes to feed grass carp in cages leads to extensive destruction of macrophytes. This causes severe damage to macrophytes, resulting in catastrophic degradation of the lakeshore zone. In 1996, the average TP concentration in Lake Erhai reached its historical peak (0.039 mg/L), which triggered a cyanobacterial bloom. At this point, the water quality of Lake Erhai had deteriorated further to Class III, with a significant decline in macrophyte populations, and the submerged macrophytes receded to a depth of 6 m. Subsequently, the local government implemented policies such as returning farmland to forests, ponds to lakes, houses to wetlands, and canceling all motorized fishing boats and cage aquaculture policies in the Lake Erhai area. They also prohibited arbitrary harvesting of macrophytes and implemented a "phosphorus ban" policy. Consequently, there was a significant improvement in water quality. In addition to agricultural nonpoint source pollution, there are no reports of industrial or other types of pollution [69]. In the 2000s, agricultural nonpoint source pollution was the main contributor to the cyanobacterial blooms in Lake Erhai. Local government departments have begun to focus on agricultural nonpoint source pollution. They implemented various projects such as the Ecological Engineering Project around Lake Erhai, sewage treatment and interception projects, nonpoint source pollution control projects, garbage collection and disposal projects in villages and along inflowing rivers, greening projects on the hillsides around Lake Erhai, soil erosion control projects, and Lake Erhai water environmental management projects [70]. They also established projects for constructing pollution interception systems around lakes, building sewage collection and treatment systems in towns and villages, collecting and disposing garbage in the basin, and ecological restoration [71]. At this time, the submerged macrophytes in Lake Erhai had retreated to a depth of 4 m, and pollution-tolerant species, such as *Ceratophyllum demersum*, *Vallisneria natans*, and *Myriophyllum spicatum*, still existed. Although the eutrophication process in Lake Erhai slowed, there was a significant upward trend in the $COD_{Cr}$ and TN water quality indicators (with $COD_{Cr}$ concentration at 15.1 mg/L and TN concentration of 0.55 mg/L in 2004) (Figure 6), and they had consistently remained high. TP showed a significant downward trend (decreasing to 0.019 mg/L in 2008). Overall, the water quality ranged between Class II and Class III, with the area of Class III continuously expanding. The lake has fully developed into a moderately eutrophic state, with certain lake bays facing the risk of eutrophication. It is worth noting that the water quality changes experienced by Lake Erhai are not isolated cases. Across the globe, numerous lakes are facing similar challenges. Taking Lake PaiJane in Finland as an example, it has also undergone a similar eutrophication process as Lake Erhai. Despite implementing multiple governance measures, certain water quality indicators of Lake PaiJane, especially those related to nutrients, still show an upward trend [72]. This trend is not limited to Lake Erhai and Lake PaiJane, but exists in multiple lakes worldwide, highlighting the universality and severity of eutrophication in lakes.

Since the 2010s, there has been a significant strategic transformation in the governance of the Lake Erhai Basin, shifting from a predominant focus on “engineering pollution control” to a balanced approach of “structural emission reduction and engineering pollution control”. By the end of 2015, the Lake Erhai Basin had reduced $COD_{Cr}$ by 4144.6 t/a, TN by 654.3 t/a, TP by 67.9 t/a, and $NH_3$-N by 73.6 t/a. The water quality of Lake Erhai remained at the Class III level, with a slight increase in the distribution area of macrophytes. The biodiversity index reached a moderate level, indicating that the health of the aquatic ecosystem is in a “good” state and has improved [71]. This suggests that the conservation model initiated in 2016 was effective in slowing the eutrophication of Lake Erhai and protecting its water quality [45]. Since 2020, with the implementation of the “14th Five-Year Plan” for the protection and governance of Lake Erhai, Yunnan Province’s Lake Erhai “One Lake One Policy” Protection and Governance Action Plan (2021–2025), and other initiatives, the nutrient status index of Lake Erhai has decreased to 40, thereby showing a stable and slowing trend. The eutrophication trend in Lake Erhai slowed, and the water quality fluctuated between Class II and Class III. Although there have been some recent improvements in TP, overall indicators such as TN, $COD_{Cr,}$ and $COD_{Mn}$ continue to show an upward trend annually. However, the aquatic ecosystems of Lake Erhai have not yet recovered effectively. The distribution depth of submerged macrophytes is approximately 5 m, and pollution-tolerant species such as *Ceratophyllum demersum* and *Stuckenia pectinata* are still dominant in Lake Erhai. Water purification and ecological functions remained poor, and the water quality of Lake Erhai continued to fluctuate for a certain period.

### *4.3. Discharge of Pollutants from the Watershed Exceeds the Environmental Capacity of the Lake*

Agriculture is the foundational industry in the Lake Erhai Basin, with farmland primarily located in flat areas close to the lake and often distributed along rivers. Agricultural fertilizers and pollutants easily enter the lake, exerting adverse effects on its water quality [73]. Agricultural pollution accounted for 52.74% of the total pollution load in the water environment of Lake Erhai Basin, whereas livestock pollution accounted for 47.26% [74]. Moreover, nonpoint source pollution caused by excessive and improper fertilizer application contributed as much as 42.58% and 38.83% of the basin’s TN and TP pollution loads, respectively [75]. In particular, since the 1990s, with the rapid development of tourism around Lake Erhai and the gradual acceleration of urbanization, human activities have increasingly contributed to the pollution load (Table 6). In 2001, the total amounts of N and P input into Lake Erhai from agricultural runoff and soil erosion reached 6.315 million tons and 0.85 million tons, respectively, accounting for 54.8% and 70.4% of the total annual input of N and P into the lake [76]. During the Eleventh and Twelfth Five-Year Plans, the input of pollutants, such as TP, TN, and $COD_{Cr}$, into the lake significantly increased. Since 2011, local government departments have attached great importance to nonpoint source pollution control and enhancing control over pollution sources in the basin. The number of sewage treatment macrophytes increased from three in the late Twelfth Five-Year Plan to ten in 2018, and the treatment capacity increased from $13.9 \times 10^4$ $m^3$/day to $20.3 \times 10^4$ $m^3$/day, with a growth rate of 46%. During this period, as the scale of urban sewage treatment continued to increase, the emissions of TN, TP, and other standard pollutants in the Lake Erhai Basin decreased year-on-year from 2016 to 2018, which indicates significant achievements in fertilizer nonpoint source pollution control. These achievements are closely related to measures, such as banning high-fertilizer crops, particularly garlic, promoting green ecological planting, and actively implementing land transfer [73]. The capacity to reduce the pollution load was significantly enhanced, and the degree of water quality deterioration was partly controlled. However, as of 2020, the total input of significant pollutants in the Lake Erhai Basin still exceeds the requirements of the water environment capacity (the $COD_{Cr}$, TN, and TP water environment capacities for the "Fourteenth Five-Year Plan" are 7106 t/a, 1100 t/a, and 95 t/a, respectively). These excess pollutants continue to enter Lake Erhai, causing water quality degradation and eutrophication in highland lakes with a limited storage capacity, small runoff volume, and poor self-purification ability. This drives the degradation of aquatic ecosystem functions and succession of macrophyte communities. Currently, agricultural nonpoint source pollution remains one of the main sources of nitrogen and phosphorus pollution loads in Lake Erhai [75,77], posing severe challenges to protecting the lake's ecological environment.



(**a**) (**b**)

(**c**) (**d**)

(**e**)

**Figure 6.** Trend of the nutrient concentrations of Lake Erhai in the past 40 years. (**a**) chemical oxygen demand ($COD_{Cr}$), (**b**) total phosphorus (TP), (**c**) total nitrogen (TN), (**d**) permanganate index ($COD_{Mn}$), and (**e**) comprehensive trophic level index (*TLI*).

**Table 6.** Pollution load generation and discharge from Lake Erhai watershed.

| **Year** | **Pollutant Type** | **Pollution Discharge Quality** | | | | **Pollutant Load into Lakes** | | | | **References** |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **$COD_{Cr}$ (t/a)** | **TN (t/a)** | **TP (t/a)** | **$NH_3$-N (t/a)** | **$COD_{Cr}$ (t/a)** | **TN (t/a)** | **TP (t/a)** | **$NH_3$-N (t/a)** | |
| 2004 | Point pollution | - | - | - | - | 7410 | 1185.6 | 140.8 | - | [78] |
| | Nonpoint pollution | - | - | - | - | 7132 | 647 | 95.1 | - | |
| | Soil erosion | - | - | - | - | - | 592.2 | 60.1 | - | |
| | Summation | - | - | - | - | 14,542 | 2424.8 | 296 | - | |
| 2010 | Point pollution | 5132.2 | 694.8 | 57.9 | 480.5 | 722.1 | 82.1 | 6.9 | 56.8 | [79] |
| | Nonpoint pollution | 40,782.3 | 7748.9 | 989.5 | 3489.8 | 9327.5 | 1954.7 | 123.8 | 620.2 | |
| | Soil erosion + dry and wet deposition | - | 403.7 | 42.3 | - | - | 591.4 | 45.4 | - | |
| | Summation | 45,914.5 | 8847.4 | 1089.7 | 3970.3 | 10,049.6 | 2628.2 | 176.1 | 677 | |
| 2015 | - | 30,748 | 4978 | 513 | 2153 | 10,654 | 1873 | 142 | 419 | [80] |
| 2018 | Point pollution | 3685.63 | 638.92 | 51.83 | 452.43 | 1288.22 | 175.1 | 16.3 | 74.07 | [81] |
| | Nonpoint pollution | 18,011.3 | 2968.71 | 270.07 | 1193.03 | 5390.38 | 872.47 | 68.46 | 204.66 | |
| | Soil erosion | 1138.57 | 544.14 | 56.77 | 54.41 | 398.5 | 359.86 | 25 | 15.04 | |
| | Summation | 22,835.5 | 4151.77 | 378.67 | 1699.87 | 7077.1 | 1407.43 | 109.76 | 293.77 | |
| 2020 | Point pollution | 3487.28 | 594.57 | 52.6 | 482.73 | 1214 | 142.16 | 11.68 | 61.69 | [82] |
| | Nonpoint pollution | 15,327.43 | 2458.08 | 224.84 | 996.01 | 5751.81 | 840.49 | 62.65 | 124.98 | |
| | Soil erosion + dry and wet deposition | 1036.28 | 559.33 | 55.85 | 23.91 | 310.78 | 399.15 | 30.93 | 3.29 | |
| | Summation | 19,850.99 | 3611.98 | 333.29 | 1502.65 | 7276.59 | 1381.8 | 105.26 | 189.96 | |

### *4.4. Climate Change Has a Significant Impact on Aquatic Ecosystems*

In recent years, significant climate change has occurred in the Dali region, with the annual average temperature showing both a fluctuating upward trend and a clear warming trend. Overall, there was a fluctuating downward trend in the annual precipitation, thereby leading to a decrease in the basin water resources (Table 7). From 1989 to 2019, the growth rates of the annual average temperature, the lowest temperature, and the highest temperature were 0.0394 °C/year, 0.0500 °C/year, and 0.0189 °C/year [83], respectively. These rates of change are much higher than the national average increase of 0.026 °C/year from 1951 to 2020 [84] and also higher than the growth rate of 0.024 °C/year in Yunnan Province from 1971 to 2004 [85], with the warming amplitude of the annual average minimum temperature higher than that of the maximum temperature. From 2006 to 2023, there was a warming trend in the water temperature of Lake Erhai (Figure 7), which is significantly higher than the warming trend in the Dali region.

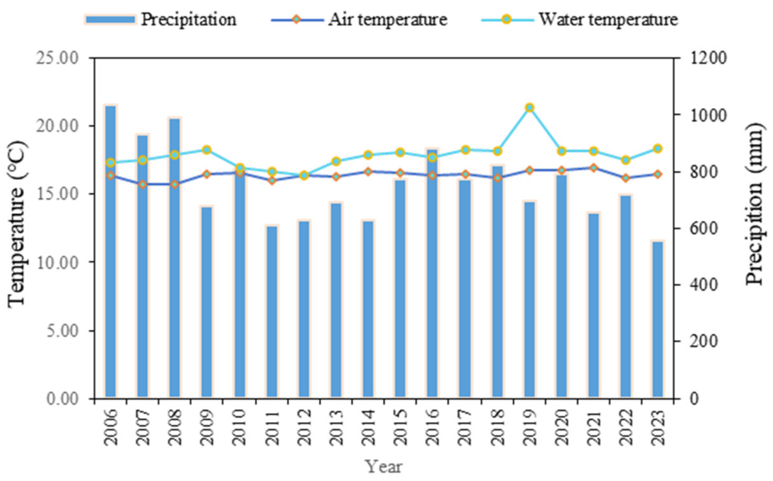


**Figure 7.** Water temperature in Lake Erhai, temperature in Dali Prefecture, and precipitation in Dali Prefecture from 2006 to 2023.

**Table 7.** Changes of annual mean temperature, annual average precipitation and water resource amount over Lake Erhai Basin in the past 60 years.

| | 1960s | 1970s | 1980s | 1990s | 2000s | 2010s | Multi-Year Average |
|---|---|---|---|---|---|---|---|
| Annual average temperature/°C | 14.3 | 14.4 | 14.5 | 14.6 | 15.1 | 16.4 | 14.8 |
| Annual mean precipitation/mm | 997.3 | 892.1 | 826.3 | 937.2 | 890.6 | 725.4 | 878.2 |
| Water resources quantity/billion $m^3$ | 1.021 | 0.783 | 0.659 | 0.790 | 0.683 | - | 0.787 |

Numerous studies have shown that lake water temperatures undergo significant changes with climate change [86–89]. The water temperature of most lakes worldwide shows a rapid upward trend at a rate of 0.34 °C/10a, which is twice the average warming rate on land and has a wide range of changes [90]. This trend may have profound impacts on the ecological environment of lakes. In China, the lake changes in the Yunnan-Guizhou Plateau lake area and the Qinghai Tibet Plateau lake area coincide with the global trend, further confirming that climate change is the most important driving factor for lake changes [91]. Specifically, among the 52 lakes in the Qinghai Tibet Plateau lake area, 31 lakes have shown an upward trend in water temperature, with an average warming rate of $0.055 \pm 0.033$ °C/year [92]. Due to its unique geographical conditions of low latitude and high altitude, Lake Erhai has experienced a climate change pattern of continuous temperature rise, a gradual decrease in relative humidity, and the significant increase in solar radiation over the past 40 years. Lake water temperature is an essential environmental condition for the survival of aquatic organisms and a key determinant of primary productivity in lake ecosystems. It not only affects the metabolism and growth of aquatic organisms, but also determines the composition, structure, and spatial distribution patterns of biological populations. Previous studies have shown that rising water temperatures not only affect the germination and growth of macrophyte reproductive bodies, but also cause some macrophytes to germinate and grow prematurely, thereby becoming the dominant species in the water body, such as *Elodea canadensis*, *Stuckenia pectinata*, and *Ceratophyllum demersum* [93]. Moreover, as the water temperature increases, the distribution depth of submerged macrophytes increases, leading to changes in community distribution, structure, and function. Climate change also affects precipitation. In the Dali region, from 1989 to 2019, there was an overall fluctuating downward trend in precipitation, with growth rates of $-5.7486$ mm/year for annual precipitation and $-4.149$ mm/year and $-3.500$ mm/year for the minimum and maximum annual precipitation, respectively [69]. A continuous decrease in precipitation directly leads to an increase in the number of streams flowing into the lake and drying, which results in a reduction in the inflow of water into the lake. According to statistics on the highest and lowest water levels in Lake Erhai from 2011 to 2019, the annual water level fluctuation ranged from 1.55 to 0.90 m, with the maximum fluctuation occurring in 2011 at 1.55 m and the minimum in 2016 at only 0.90 m, which is far below the prescribed 1.70 m water level fluctuation. The continuous decrease in inflow reduces the water flow velocity and turnover frequency, thereby reducing the dilution effect of nutrients in the water and diminishing the self-purification capacity of the lake. This ultimately led to significant changes in the growth conditions, biomass, and distribution of macrophytes in Lake Erhai [94], as manifested by a decrease in species diversity, simplification of species, changes in dominant species populations, and the transition of macrophyte distribution depth from 3 m gradually downward to 10 m.

## 5. Conclusions

Upon reviewing numerous research results in Lake Erhai Basin, it can be observed that there has been a significant succession of macrophytes. Since the 1980s, the diversity of macrophyte species in Lake Erhai has fluctuated from a few to many, and then from abundance to decline, and finally stabilized gradually with slow recovery. The distribution area of macrophytes has shrunk from over 30% during its peak in the 1980s to approximately 10% by 2020s. The lower limit of the water depth distribution decreased from to 9–10 m to within 5 m, and compared with 2009, the number of submerged macrophyte species decreased by 26.92%. Pollution-tolerant species have developed rapidly, and the dominant species have transitioned from clean-water types, such as *Najas marina*, *Stuckenia pectinata*, and *Ottelia acuminata* in the 1960s, to pollution-tolerant species, such as *Vallisneria natans*, *Hydrilla verticillata*, *Ceratophyllum demersum*, *Potamogeton maackianus*, and *Potamogeton wrightii*.

The successive operation of cascade hydropower stations on the Xi'er River and the increase in the outflow capacity of Lake Erhai led to a rapid decrease in its water level of Lake Erhai. The significant fluctuations in water level within the year have accelerated the transformation of the Lake Erhai ecosystem from a "clear-water state" to a "turbid-water state", thereby resulting in the decline of macrophytes and the disappearance of endemic species. The reduced diversity of macrophytes weakens the resilience of macrophyte communities to disturbance. Eutrophication occurs when the amount of pollutants discharged into the basin exceeds the environmental capacity of the lake. Excessive nutrient concentrations stimulate phytoplankton proliferation, leading to an increase in algal abundance and a decrease in water transparency. In addition, significant climate change has been observed in the Dali region in recent years, with an increasing trend in the annual average temperature and a clear warming trend. The increase in lake water temperature caused some macrophytes to germinate and grow earlier, becoming the dominant species in the water, and increasing the depth of distribution of the submerged macrophytes. With a decrease in rainfall, the inflow into the lake continued to decline, resulting in slower water flow and longer replacement cycles. This reduced the dilution effect of nutrients in the water and lowered the self-purification capacity of the lake. Ultimately, these factors significantly alter the growth conditions, biomass, and distribution of macrophytes in Lake Erhai consequently making them more prone to decline.

In the context of climate change, controlling the total emissions of pollutants at the source and managing inflow pollution loads are crucial. Scientifically devising and implementing reasonable water-level operation schemes are essential for creating favorable habitat conditions for macrophyte restoration. These are necessary measures to maintain the "clear-water stable state" in the early stages of eutrophication in lakes and prevent them from entering the "turbid-water stable state".

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

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