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Article *in* Earth's Future · March 2022

DOI: 10.1029/2021EF002419

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Earth's Future

RESEARCH ARTICLE
10.1029/2021EF002419

Considering the Adaptive Cycle and Resilience of the Ecosystem to Define Reference Conditions for Wetland Restoration

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Key Points:

- Recent anthropogenic pressures triggered a strikingly different community succession with sharp drought compared to natural pressures
- Evaluate ecosystem resilience to anthropogenic pressures based on paleo-biological communities such as plants and diatoms
- We use the characteristics of the early conservation phase which had high resilience and a stable state as the reference conditions

Supporting Information:

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

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Citation:

Liu, H., Gao, C., & Wang, G. (2022). Considering the adaptive cycle and resilience of the ecosystem to define reference conditions for wetland restoration. *Earth's Future*, *10*, e2021EF002419. https://doi.org/10.1029/2021EF002419

Received 7 SEP 2021
Accepted 15 MAR 2022

Abstract

Ecosystem resilience to pressures expanding and contracting within the adaptive cycle as slow variables change. However, little is known about their role in defining reference conditions for wetland restoration. Here, we applied paleoecological data of two wetlands that have been degraded (Honghe, riparian peatland) and disappeared (Shenjiadian, valley peatland) to evaluate ecosystem resilience to anthropogenic pressures as the phases of the adaptive cycle progress. The slow variables of plants and diatoms gradually began to change from moisture to dry loving species under severe disturbances in the late 1970s. Then regime shift took place around 1990 CE (Current Era) based on a sequential T-test analysis and F statistics on the slow variables. A drop in water level caused by human activities rather than climate moisture led to regime shifts in Honghe and Shenjiadian wetlands. Therefore, the ecosystem were in the conservation phase before the late 1970s, and were in the reorganization phase after 1990 CE. The ecosystems had high resilience and a stable state at the early conservation phase, and its characteristics can be used as reference conditions for wetland restoration. The reference water level was 11–13 cm and the NH_4-N ranged from 0.8 to 1.2 mg/L. The dominant vegetation was *Drepanocladus aduncus* and the dominant diatom was *Pinnularia brevicostata*. The referred enrich factors of nitrogen, phosphorus, and heavy metals were under 4.45, 2.12, and 1.11, respectively. Considering both adaptive cycle and resilience to define reference conditions can provide insight into the future restoration and management of wetland ecosystems worldwide.

Plain Language Summary

The restoration and conservation of wetlands has great significance in improving future sustainability of the global ecological environment in the future; defining reference conditions for wetland ecological restoration is key to achieving this goal. In this paper, we propose a method to define reference conditions for wetland restoration by considering the ecosystem's resilience and adaptive cycle using paleoecological data from two wetlands in the Sanjiang Plain, Northeast China. Intense drought associated with recent anthropogenic pressures rather than natural pressures changed the community succession in these wetlands. The state of the ecosystems has become unstable under severe human disturbances since the late 1970s; and based on statistical analysis of biological variables, regime shift took place around 1990 CE. From the late 1970s to 1990 CE was the release phase in the ecosystems' adaptive cycle, before the late 1970s was the conservation phase, and after 1990 CE was the reorganization phase. The ecosystems had strong resilience and a stable state at the early conservation phase, however there was likely slight disturbances at this phase. Setting the characteristics at the early conservation phase as reference conditions for wetland restoration is more reasonable, economical, and sustainable than using the pre-disturbed natural ecological characteristics.

1. Introduction

The wetland ecosystem is an essential and complex aquatic-terrestrial ecosystem with many beneficial functions and services (e.g., maintaining biodiversity, purifying water, controlling runoff, and regulating climate) (Niering, 1978; Woodward & Wui, 2001). Human activities have gradually become the major factor affecting most wetland ecosystem functions and services, with substantial disturbances on the ecosystem being caused by population growth and economic development in the last century (Matthews, 1993). If wetlands are not protected or restored in time, ecosystems may rapidly degrade further under intensive human activities. For example, the rapid shrinking of the Aral Sea (which contains many lakeside wetlands) from the 1960s is overwhelmingly owed to the expansion of irrigation, which is a colossal disaster caused by human beings (Micklin, 2007). Thus, wetland protection and restoration are of great significance to the future sustainability of ecosystems around the world. Reference conditions represent a group of minimally disturbed conditions organized by selected physical, chemical, and biological characteristics, such as water level, nutrition, and biotic communities, and are a point of reference against which to evaluate changes in ecosystems (Moore et al., 1999; Reynoldson et al., 1997). Reference conditions can provide direction for constructing restoration goals and evaluating restoration efforts' consequences (Barnosky et al., 2017; White & Walker, 1997).

The Ramsar Convention has provided general principles and guidelines for wetland restoration based on many different projects worldwide (Ramsar Convention, 2002). “Historical documents” (Hughes et al., 1998; Kress et al., 2019), “reference sites” (Cui et al., 2009; Herlihy et al., 2019), and “paleoecology” (Finlayson et al., 2016; Muxika et al., 2007) are standard methods for establishing reference conditions for wetland ecological restoration. These methods usually set the pre-disturbed natural dynamic ecosystem states and interactive factors as reference conditions for ecosystem restoration. Written and oral history, historical photos, land survey records, fire records, hydrologic records, weather records, etc. can reflect the ecosystem state before human disturbances (Interagency Workgroup on Wetland Restoration, 2003). If there was a lack of historical information, previous research used a more natural local ecosystem as a reference site (Comín et al., 2014; Mahan et al., 2014). Paleoecology, widely used to set up reference conditions for ecosystem restoration, can provide a long-term ecological background of an ecosystem's evolution process. The European Union provided a strategy for the protection and restoration of aquatic ecosystems; the goal was to find a point that did not exhibit impact of human activities based on paleoecology and then use it as a marker for lake restoration efforts (European Union, 2000). There are many examples worldwide defining reference conditions for wetland restoration based on these methods (Clarkson et al., 2017; Dearing et al., 2012; Kress et al., 2019; Proulx et al., 2018; E. Seddon et al., 2019), which contributes greatly to wetland management. Nevertheless, most cases failed to consider the ecosystem's adaptive cycle and resilience to human pressures.

Resilience determines the persistence of relationships within a system and measures the ability of these systems to absorb the impacts of disturbances and retain their basic function and structure (Holling, 1973; Walker & Salt, 2006). Disturbances are trigger that cause an ecosystem to change from one stable state to another in the adaptive cycle, which is a model to describe the dynamics of ecosystems. The adaptive cycle (Figure 5a) has four phases: Exploitation, conservation, release, and reorganization (Gunderson & Holling, 2002), and it is proposed as a fundamental unit for understanding complex systems from cells to ecosystems to societies. As the cycle progresses for an ecosystem, key points in the ecosystem's history can be identified; the resulting factors that may have played a potential role in each ecosystem's future can be assessed. Therefore, it is necessary to consider the adaptive cycle when defining reference conditions for wetland restoration. As the phases of the adaptive cycle progress, a system's ecological resilience expands and contracts. Ecological resilience decreases as stability domains contract in the progression to the conservation phase. Disturbances will provoke crisises and transformation because ecological resilience is low in the shift from conservation to release phase. Tightly bound resources are now released as connections break and regulatory controls weaken. The loss of structure continues as linkages are broken and natural, social, and economic capital leaks out of the system (Walker & Salt, 2006). Therefore, a regime shift occurs when progressing from release to reorganization (Randle et al., 2015; Scheffer et al., 2001). A regime shift is an abrupt shift from one regime to another, representing the shift from the release to reorganization phase of the ecosystem's adaptive cycle (Beaugrand, 2004; Gunderson & Holling, 2002; Scheffer et al., 2001). However, Capon et al. (2015) reviewed studies on regime shifts and found that most studies lack evidence on whether the system can recover after the stress is removed. Even though the system changes are consistent with regime shift models, it is possible that the assemblage shifts here are responding to ongoing regional scale pressures (Kattel et al., 2017).

Wetland restoration usually sets the ecosystem conditions before interference as a reference. However, the ecosystem cannot be restored its original state after the regime shift occurs; it will move further away instead of returning (May, 1977; Scheffer et al., 2009). Restoring lakes to a valuable state requires interventions that greatly strengthen the ecosystem's resilience (Carpenter & Cottingham, 1997; Timpane-Padgham et al., 2017). Endter-Wada et al. (2020) proposed that strategically linking wetland protection to other societal objectives can help wetlands mitigate risks and enhance resilience. This policy can foster collaboration across agencies, facilitate stakeholder engagement, and bring technical and financial resources to improve wetland management at the landscape scale. However, little is known about how the ecosystem's adaptive cycle and resilience can guide the definition of reference conditions for wetland restoration. The role of species diversity (typical slow variables) in ecosystem resilience to human pressures was illustrated by experiments in which ecosystem's toxic chemical stress levels, nutrient input, or climate were manipulated (Dakos et al., 2008; R. Wang et al., 2012; K. Zhang et al., 2018). These experiments aid in understanding the resilience dynamics in the ecosystem's adaptive cycle under human disturbances based on statistical analysis (including autocorrelation coefficients, variance, skewness, *t*-test, and F-test analysis) of ecological community (diatoms) time series.

To better understand recent changes of wetland ecosystems and their driving factors (anthropogenic or natural), it is necessary to comprehensively reconstruct the wetland ecosystem's formation and development history under natural pressures (climate change, volcanic activity, etc.). We can determine the wetland ecosystem's succession stage and identify the autogenic succession based on vegetation variations. Wetland plants are an essential component of all wetland ecosystems, there is a strong ecological basis for using vegetation to identify and characterize wetland ecosystems (Cronk & Fennessy, 2009). Anthropogenic activities can produce chemicals or constituents which transfer to the wetland via atmosphere deposition and surface runoff. For instance, the grain size of sediment and sediment rate (SR) can be used as indicators of soil erosion intensity. Coarser grains and faster sediment rates are typically interpreted as representing higher soil erosion intensity (McManus & Duck, 1993). Black carbon (BC), polycyclic aromatic hydrocarbons (PAHs), and other chemical combustion products in wetland sediments mainly come from the burning and use of fossil fuels. Agricultural activities can be reflected by chemical fertilizers (total nitrogen [TN], total phosphorus [TP]), and pesticides (heavy metals) which can accumulate in wetlands through surface runoff. The accumulated amount of heavy metals in wetland sediments are not only influenced by pesticide application, but also by mine exploration (Olid et al., 2010). Human activity intensity can be reflected by heavy metal enrichment factors. In addition, some major human activities events were recorded in local historical documents. Therefore, anthropogenic pressures on wetland ecosystems can be reflected by geochemical indicators (sedimentary facies, composition products, nutrient elements, heavy metals) and historical records.

Here we present high-resolution palaeoecological records (plant macrofossils and diatoms) from a degraded Ramsar wetland (Honghe) and a disappearing wetland (Shenjiadian) in the Sanjiang Plain, Northeast China. We aim to answer the question of how to define reference conditions for wetland restoration by considering the ecosystem's adaptive cycle and resilience. We hypothesized that the ecological states at the beginning of the ecosystem's conservation phase could be used as reference conditions for wetland restoration. To test this hypothesis, we discuss the formation and development of wetland ecosystems under natural pressures (especially climate change), which is essential to understand wetland changes under human disturbances. In this way, we can compare the changes of the wetland ecosystem under natural pressure and human disturbance, distinguishing whether the change of the ecosystem is caused by human influence or natural succession. Human pressures in wetland ecosystems on the Sanjiang Plain were revealed by geochemical indicators and historical records. Sequential T-test Analysis of Regime-shifts algorithm (STARS) and F statistics of plant and diatom palaeoecological communities time series (slow variables) were used to understand the ecosystem resilience dynamics to pressures in the adaptive cycle. The ecosystem characteristics, including vegetation composition (slow variables), nutrients, and heavy metals, are the specific composition of the reference conditions. Our study provides a framework to define reference conditions for future wetland restoration by considering the ecosystem's adaptive cycle and resilience.

2. Materials and Methods

2.1. Site and Sampling Description

The Sanjiang Plain is a low (average elevation is 50–60 m above sea level) and flat alluvial plain. Many wetlands developed in this area due to low topography, abundant water flow, and suitable climate conditions, precipitation is concentrated in the summer and autumn. Sanjiang Plain has a temperate humid and semi-humid monsoon climate, with an average annual temperature of 1.6–3.9°C and an average annual precipitation of 500–700 mm. When the temperature drops, a large amount of water freezes in the soil before being drained. More than 70% of wetlands have disappeared with the increase of population and land reclamation since the founding of the People's Republic of China in 1949 CE (Current Era) when the wetland area was 360×10^4 hm^2; almost all existing

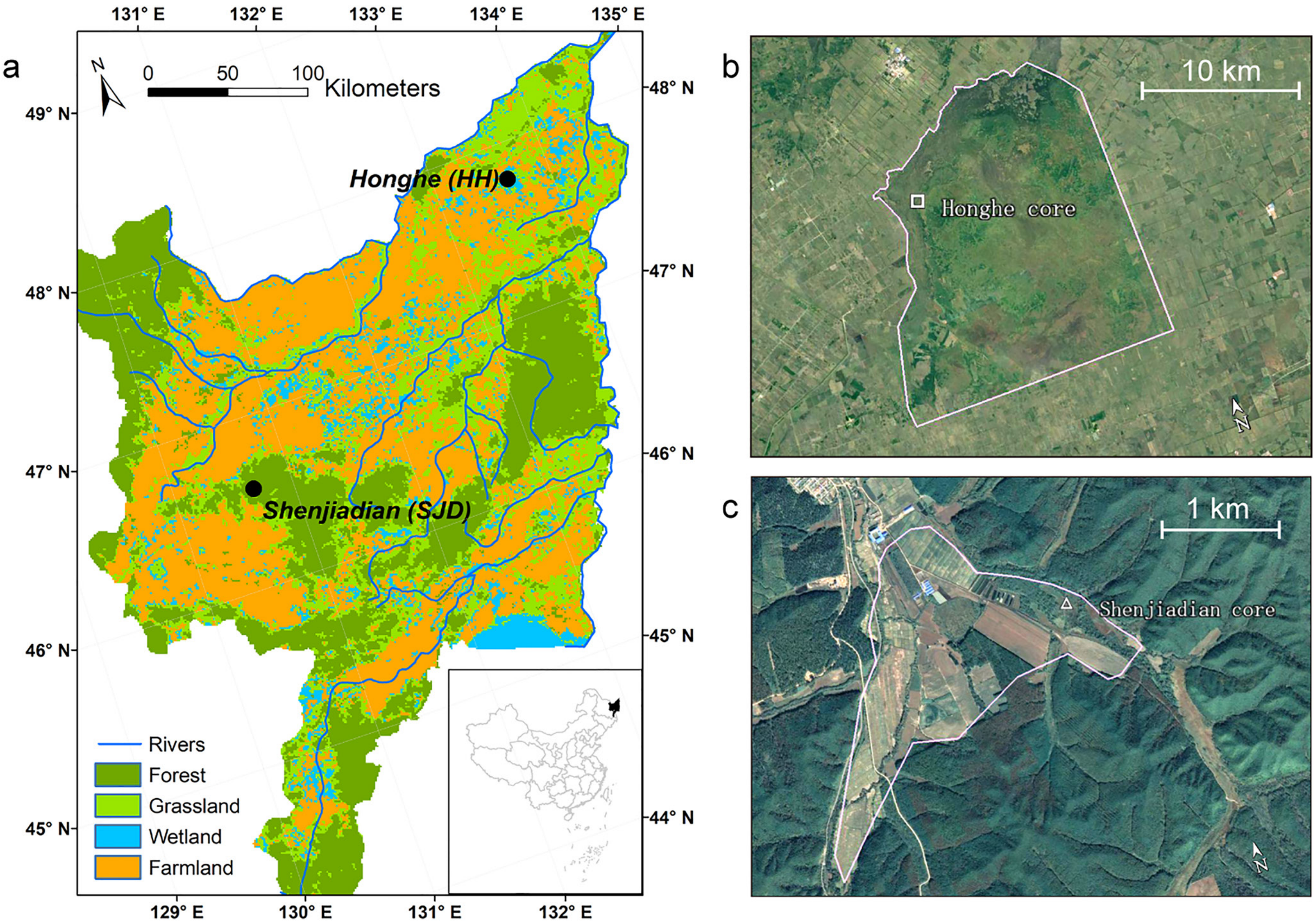

Figure 1. Study area and sampling sites. (a), land type map of the Sanjiang Plain, Northeast China showing our sampling sites' locations, and the inset shows the Sanjiang Plain location in China. (b and c), Remote sensing images of the Honghe and Shenjiadian peatland selected for paleoecological analyses. The white lines are the Honghe National Nature Reserve boundary and the former border of Shenjiadian peatland. The white square and triangle represent the position of peat cores.

wetlands have degraded (Mao et al., 2018; Z. Wang et al., 2009). Cultivated land is the primary land-use type, accompanied by other land-use types such as forest land, grassland, and wetland (Figure 1a).

The Honghe (47.7886°N, 133.6275°E) and Shenjiadian (46.5796°N, 130.6706°E) peatlands were selected as examples to define reference conditions based on their long records of peat deposit as well as having more paleoecological information compared to other sites on the Sanjiang Plain. Honghe peatland is located in the Honghe National Nature Reserve (Figure 1b), a Ramsar wetland Reserve. The geologic substrate of Honghe peatland is a typical dish-shaped depression; the Honghe river flows through this area, which makes the area rich in water and leads to the formation of peatland. It is roughly circular with a diameter of 2,000 m and an average water depth of 5 cm. The average peat accumulation depth is 150 cm and the grass-root layer is about 20 cm. The peatland surface's main area is dominated by *Carex lasiocarpa* and *Calamagrostis angustifolia* and surrounded by deciduous broadleaved forests. One peat core was collected in the central region of Honghe peatland in July 2011 using a Russian peat corer, the length of the Honghe peat core was 148 cm. Shenjiadian peatland developed in the valley near Shenjiadian village. The bottom of the valley is flat, and its vertical and horizontal slopes are small. As a result, this area became a gathering area for surface runoff, leading to peat development. The white line in Figure 1c indicates the approximate range of peat deposits. The average peat accumulation depth is 200 cm, and the grass-root layer is about 10 cm. The vegetation assemblages in Shenjiadian peatland were dominated by *Carex lasiocarpa*, accompanied by *Menyanthes trifoliata*. We collected a peat core from the northeast of Shenjiandian peatland in July 2010, the length of the Shenjiadian peat core was 193 cm. Regretfully, the landscape of the Shenjiadian peatland is mostly farmland now. The two peat cores (Honghe and Shenjiadian) were sectioned at 1-cm intervals with a stainless-steel hand saw and transported to the laboratory for further analysis.

2.2. ^{14}C and ^{210}Pb Dating

We used both ^{14}C and ^{210}Pb dating methods to ensure the chronology accuracy based on the two dating methods' distinct characteristics on the time scale. The age frame of 1–42 cm peat sediments was constructed using the ^{210}Pb dating method (Appleby & Oldfield, 1978) because the ^{210}Pb reaches radioactive equilibrium at 42 cm in the Honghe peat core. The ages of the deeper peat sediments (60–148 cm) were determined using the ^{14}C dating method (Ramsey, 2008). We established the ages of 43–59 cm peat sediments using linear interpolation of the two dating methods' results of the Honghe peat core (Figure S1a in the Supporting Information S1). In the Shenjiadian peat core, the ages of 1–26 cm peat sediments were determined using the ^{210}Pb dating method due to the ^{210}Pb reaching radioactive equilibrium at 26 cm. The ages of the deeper peat sediments (58–193 cm) were determined using the ^{14}C dating method. The ages of 27–57 cm peat sediments were established by linear interpolation of the two dating methods' results in the Shenjiadian peat core (Figure S1b in the Supporting Information S1).

2.3. Sedimentary and Statistical Analyses

2.3.1. Identify Historical Human Disturbances

The analyses of TN, TP, heavy metals, and PAHs in the sediments of eight wetlands (including Honghe and Shenjiadian peatlands) were performed by Liu et al. (2018). We also measured the SR, grain size, and BC analysis of these eight wetland cores in this study. The SR was calculated based on the sediment thickness over a unit of time (^{14}C and ^{210}Pb dating results). The calculation equation is:

$$\mathrm{SR} = h/t \tag{1}$$

where h is the sediment thickness (cm); t is the accumulated time (yr), which is determined by ^{14}C and ^{210}Pb dating. The grain size was measured using a Mastersizer 2,000 laser grain-size analyzer according to the method described by Lu and An (1998). BC in the wetland sediments was measured using the dichromate oxidation method developed by Lim and Cachier (1996). We used Min-Max normalization to normalize the data of SR anomaly, mean grain size, BC, TN, TP, heavy metals, and PAHs. Then, we calculated the average value of normalized TN and TP to represent the nutrient variations (nutrient index) in wetland cores. The average value of normalized SR anomaly and mean grain size represent the sedimentary facies variations (sedimentary index), the average value of normalized BC and PAHs represent the combustion products variations (combustion products index). We also calculated the average value of heavy metals enrichment factors to represent the heavy metals variations (heavy metals index).

2.3.2. Quantitative Analyses of the Ecosystem Resilience and Adaptive Cycle

The STARS (A. W. Seddon et al., 2014) and F statistics (Zeileis et al., 2002) analyses of the slow variables (plant and diatom communities) in Honghe peatland are shown in Liu et al. (2018). We also carried out the STARS and F statistics analyses of the plant communities in Shenjiadian peatland. We extracted out about 1 cm^3 sub-samples from the peat samples and washed them with a strong water jet over a 125 μm sieve after estimating the abundance of unidentifiable organic matter (UOM). The variations of UOM can reflect the decomposition of peat. Then the residues were inspected under a stereomicroscope at 7.3–120 × magnification and 400 × magnification where necessary. The relative abundance of plant species at each depth interval was estimated semi-quantitatively for each macrofossil type using a 10 × 10 square grid salver (Barber et al., 1994). The plant data of Shenjiadian peatland had been Hellinger transformed to reduce the influence of abundant species, the temporal series of the plant were sorted into 5-year bins and can be formed by combining with the age frame established by ^{14}C and ^{210}Pb dating. We extracted the principal component factor 1 (PC1) scores from plant communities based on principal component analysis to represent the most critical communities' information among all the main components extracted. The statistically significant shift in PC1 was detected by the STARS and F statistics of the temporal series of PC1.

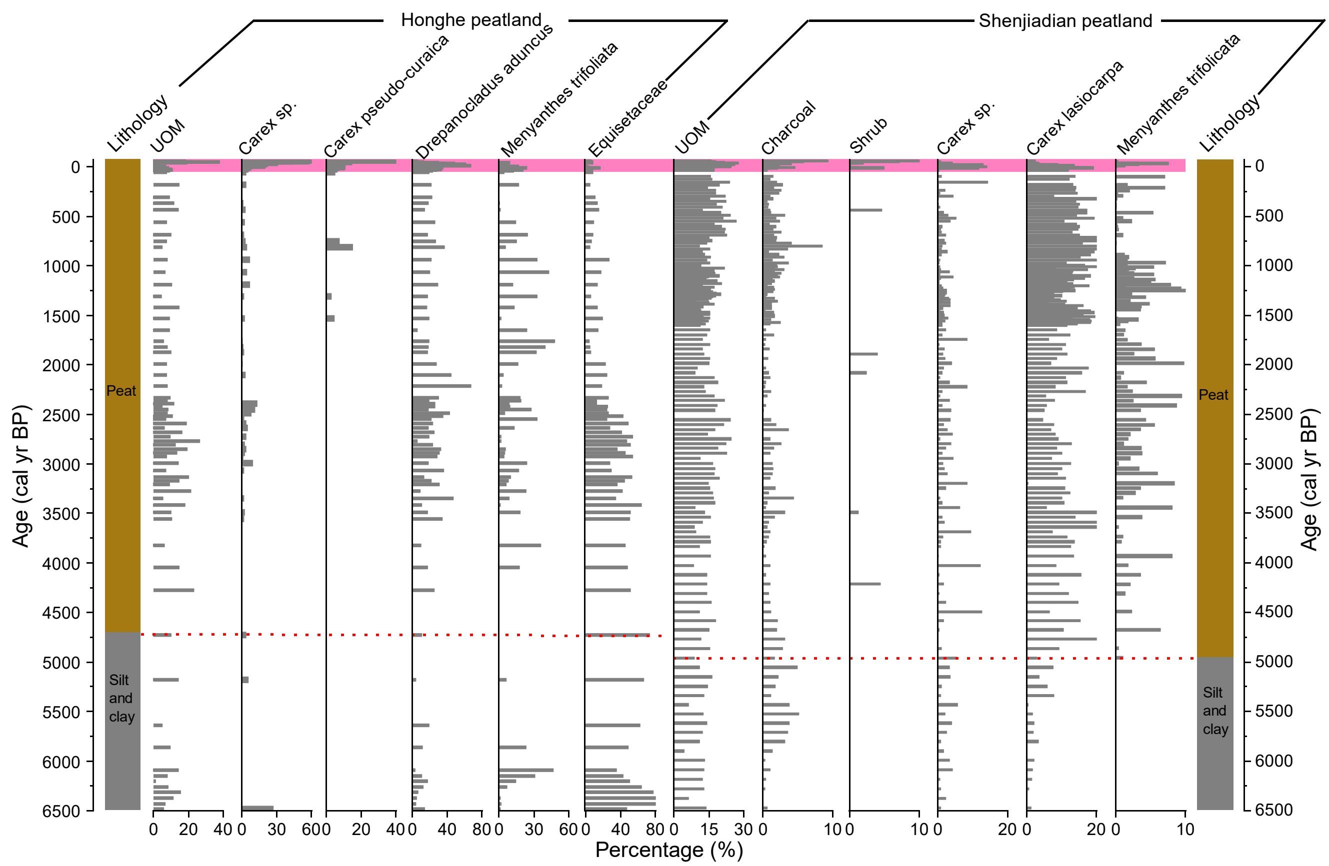

Figure 2. The plant species of Honghe and Shenjiadian peatlands with their lithology. Different colors of the rectangular column represent the changes in lithology. The red dot lines represent the dominant species' shifts, and the pink shadow represents the sharp species changes.

3. Results and Discussions

3.1. Natural Evolution After the Formation of the Wetland Ecosystem

The plant species of Honghe and Shenjiadian peatlands over the past 6,500 years are presented in Figure 2. From 6,500 to 4,700 cal yr BP, the plant community of Honghe peatland was dominated by *Equisetaceae*, a typical moisture-loving vegetation which often grows in humid places (Simpson, 2010). *Equisetaceae* firstly decreased and then increased, reaching the highest value at 4,700 cal yr BP. The depth of 133–134 cm (~4,700 years cal BP) is the boundary between peat and silt according to Honghe peatland sediments' stratigraphy (Figure 2). Honghe peatland ecosystem began to form and develop since 4,700 cal yr BP. Peatland formation and development are the natural development processes of lake paludification in which plant remains gradually fill up the lake (Partanen & Luoto, 2006). A sudden drought caused by the weakening of the East Asian Summer Monsoon around 4,700 cal yr BP was a main reason for lake paludification and peat expansion in the Sanjiang Plain (Z. Zhang et al., 2015). From 4,700 to 2,400 cal yr BP, there was a decrease in *Equisetaceae* (from 70% to 30%) and increase in *Menyanthes trifoliata* and *Drepanocladus aduncus*, which are typical wetland vegetations with the ability to grow in low oxygen conditions. Marsh vegetation began to develop, and plant communities have changed with the lacustrine-marsh facies shift. From 2,400 to 50 years BP, the abundance of *Equisetaceae* was the lowest according to historical standards, with higher *Drepanocladus aduncus* and *Menyanthes trifoliata*. Marsh vegetation succeeded in Honghe peatland since 2,400 cal yr BP, indicating the wetland ecosystem had reached a mature stage. The dominant plants, *Drepanocladus aduncus* and *Menyanthes trifoliata*, maintained dynamic stability, changing little from 2,400 to 50 cal yr BP. However, the plant communities underwent dramatic changes during the last hundred years. The relative abundance of UOM, *Carex sp.*, and *Carex pseudo-curaica* in the past 100 years is abnormally high compared to the changes driven by natural forcing in the past 6,000 years.

There are also striking differences in the succession of plant communities in Shenjiadian peatland. The amount of *Carex lasiocarpa* was low, and no *Menyanthes trifolicata* appeared in Shenjiadian peatland from 6,500 to 4,900 cal yr BP. The depth of 162–163 cm (~4,900 years cal BP) is the boundary between peat and silt according to the stratigraphy of Shenjiadian peatland sediments (Figure 2). Shenjiadian peatland ecosystem began to form and develop since 4,900 cal yr BP from lake paludification, with the *Carex lasiocarpa* and *Menyanthes trifoliata* prevailing. There was a decrease in *Carex lasiocarpa* from 4,900 to 2,600 cal yr BP, then the *Carex lasiocarpa* started to increase from 2,600 to 700 cal yr BP. From 700 to 50 cal yr BP, *Carex lasiocarpa* and *Menyanthes trifoliata* had no apparent increasing or decreasing trends, indicating that the evolution of the wetland ecosystem was relatively stable during this period. The relative abundance of UOM, Shrub, charcoal, and *Carex sp.* in the past 100 years is abnormally high compared to the changes driven by natural pressures in the past 6,000 years in the Shenjiadian peatland. Shrubs are highly tolerant to hydrological conditions and more adaptable to drought than *Carex sp.*. The presence of charcoal also indicated a drier environment. The drought that impacted plant communities in the last 100 years is the most severe drought since the formation of the peatlands. If the reason was only natural succession, there would not be such a large-scale xerophyte vegetation succession.

The basic succession of vegetation in the last 100 years shows a drastic difference from the past 6,000 years in Honghe and Shenjiadian peatlands. For thousands of years, dominant vegetation species succeeded from pond to marsh species. Certainly, the accretion of nearly 2 m of peat in the two peatlands occurred over multiple adaptive cycles over a 6,000-year period under natural pressures (climate change). However, we only focus on the dramatic cycle during the last 100 years in this study, because during this time there was unprecedented pressure from human activities.

3.2. Changes of Wetland Ecosystem and Its Adaptive Cycle Under Anthropogenic Pressures

With the development of industry and agriculture and the dramatic increase in population, human disruptions have substantially impacted the environment during the last hundred years in the Sanjiang Plain, Northeast China (Research group on Chinese wetland development and protection, 1998). We performed geochemical analyses (grain size, SR, TN, TP, BC, PAHs, heavy metals) of wetland sediments to reflect changes in the intensity of human disturbances on the wetland ecosystem. The wetland cores' SR anomalies were almost all positive in 1950–2010 CE (Common Era), the mean grain sizes also showed increasing trends during this stage (Figure S2 in the Supporting Information S1). There was no pronounced increase in rainfall from 1950 to 2010 CE (Figure S3 in the Supporting Information S1) in Sanjiang Plain, so soil erosion was mainly caused by human activities. The BC concentrations showed almost the same increasing trend as PAHs concentrations (Figure S4 in the Supporting Information S1). Futhermore, the sedimentary and combustion product indexes showed similar change patterns with the nutrient and heavy metal indices during the last 100 years (Figure 3e). There was a slight increase in the sedimentary index from the 1920s. All geochemical indictors recorded an increasing trend from the 1950s, a dramatic increase occurred since the late 1970s (Figure 3e). The variations of human activity indexes (sedimentary index, nutrient index, combustion products index, heavy metals index) in wetland sediments were in line with the history of the Sanjiang Plain, Northeast China. Because the Qing dynasty protected and barred Northeast China, the indexes of sediment, combustion products, nutrients, and heavy metals were low and stable before the 1920s. According to historical documents, some cities and mining activities were developed after the completion of the Chinese East Railway in the 1920s (Fang et al., 2005). Thus, some wetlands began to be disturbed in the 1920s. Almost all wetlands were influenced by the sharp increase in population and land reclamation since the founding of the People's Republic of China in 1949 CE (Research group on Chinese wetland development and protection, 1998). The sedimentary index, the combustion products index, the nutrient index, and the heavy metals index of the wetlands all showed dramatic increases after China's reform and opening up since the late 1970s (Figure 3). For this reason, the drop in the water level of the existing wetlands started to accelerate in the face of increasing reclamation and subsoil water use since the late 1970s (Figure S3 in the Supporting Information S1).

Honghe and Shenjiadian peatlands' plant communities underwent dramatic changes in the last hundred years (Figure 4). Dramatic changes in plant communities are not the result of the wetland ecosystem's natural succession. Based on plant macrofossils paleo-records, the dominant plant species did not change much under natural forcing from 700 to 50 cal yr BP. Recent human activities triggered a strikingly different community succession with more extreme drought than natural pressures (Figure 2). Compared with *Menyanthes trifoliata* and *Drepanocladus aduncus*, *Carex sp.* is more adaptable to dry environments (Lou et al., 2013). The relatively

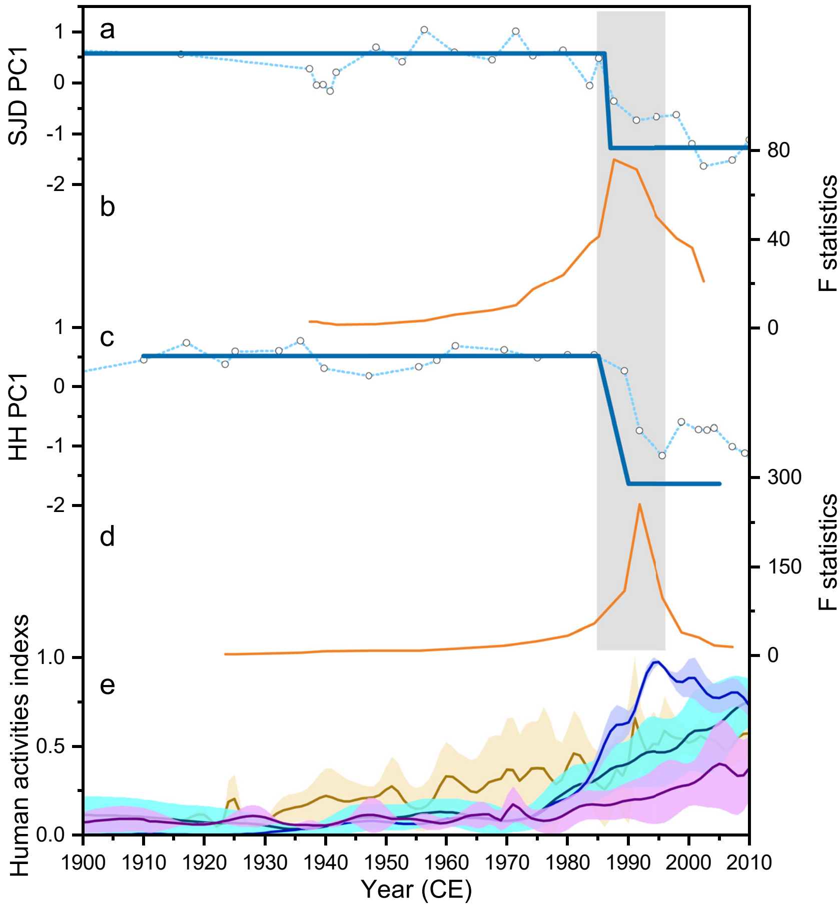

Figure 3. The regime shift of Honghe and Shenjiadian peatland ecosystems responded to the severe human disturbances. (a and c), Sequential T-test Analysis of Regime-shifts algorithm analysis (light blue dot lines) with mean values (blue horizontal lines) of principal component factor 1 scores for 1900–2010 CE, using Student's *t*-test in the Honghe and Shenjiadian peatlands, respectively. (b and d), F statistics (orange lines) of the Honghe and Shenjiadian peatlands, respectively, showed significant ($p < 0.01$) breakpoints in about 1990 CE. (e), The human activity indexes in the wetlands of Sanjiang Plain. The sedimentary index (brown line), nutrient index (blue line), heavy metal index (cyan line), and combustion products index (purple line) revealed the degree of human disturbance in the Sanjiang Plain's wetland ecosystems. The color shadows show their standard errors, respectively.

drought-tolerant *Carex sp.* has slowly replaced the indicator species for wet conditions, *Menyanthes trifoliata* and *Drepanocladus aduncus*, in the Honghe peatland since the late 1970s (Figure 4), which is the beginning of dramatic human activities. Simultaneously, the diatom community gradually changed from wet to dry species in the Honghe peatland (Liu et al., 2018). Relatively more drought-adapted vegetation increased from the 1980s, and the relatively wet species *Carex lasiocarpa* almost disappeared in the Shenjiadian peatland. The other typical wetland vegetation *Carex sp.* also decreased. The charcoal amount increased significantly, which further shows that the drought in Shenjiadian peatland was irefutable. Compared with Honghe peatland, the degree of drought in Shenjiadian peatland was more substantial. In the Honghe peatland, carex is more drought-tolerant compared to *Menyanthes trifoliata* and *Drepanocladus aduncus*, but carex in the Shenjiadian peatland is more moisture-tolerant compared to shrubs.

STARS algorithm and F statistics on the PC1 scores of the plant community showed that the Shenjiadian peatland ecosystem's regime shift occurred in approximately 1990 CE (Figures 3a and 3b). The time of the regime shift in the Shenjiadian peatland is the same as that of the Honghe peatland (Figures 3c and 3d). In summation, although the wetlands suffered slight human disturbances since the 1920s, the Honghe and Shenjiadian wetland ecosystems' states did not change much before the late 1970s in the past hundred years. The dominant plants were typical marsh vegetation, with mature and stable ecosystems. The future was more predictable and less driven by

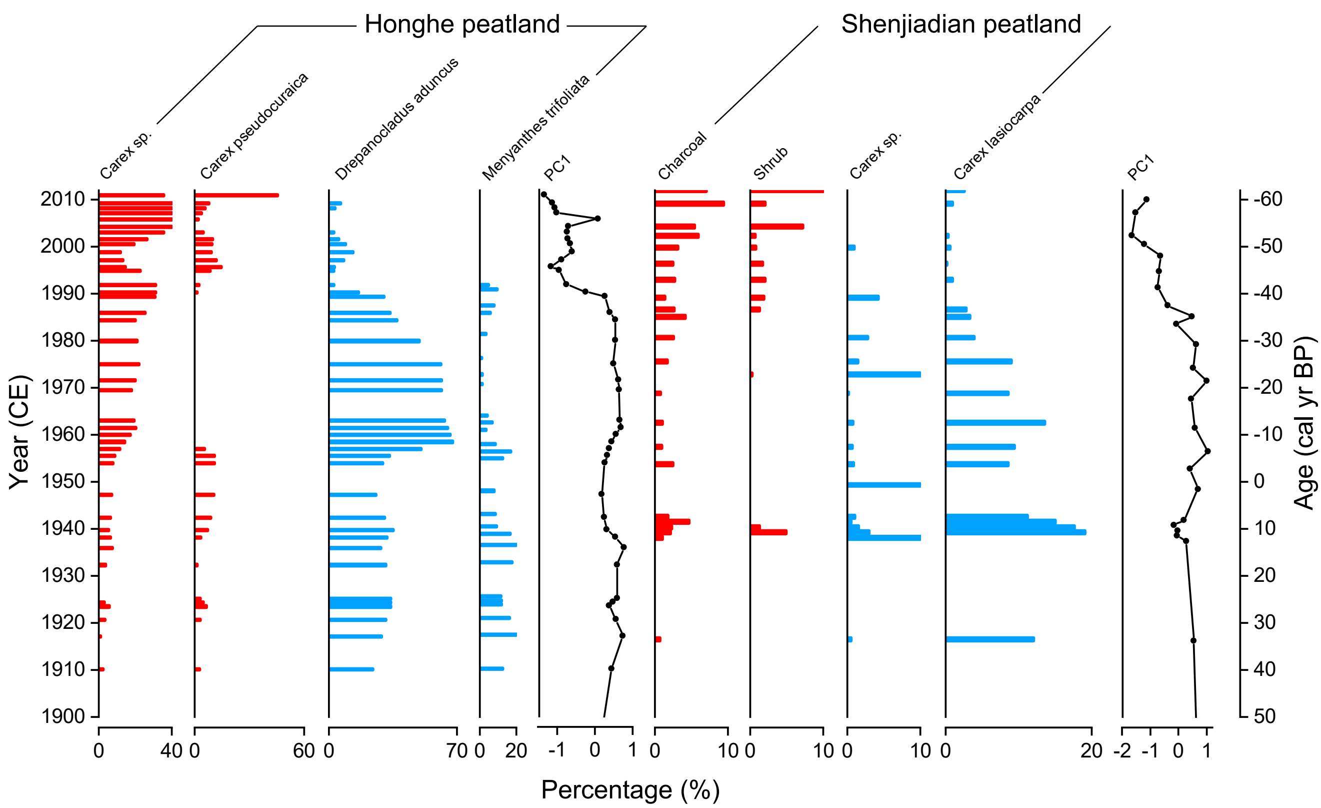

Figure 4. The significant shifts of plant communities in Honghe and Shenjiadian peatlands during the recent hundred years. The plant communities were arranged according to the relative degree of adaptation to the water level. Red bars represent the relatively dry-loving biological community's changes, and blue bars represent the relatively moisture-loving biological community's changes.

uncertain forces outside the system's control. The ecosystems have undergone dramatic changes when the systems have been severely disturbed since the 1970s. Therefore, the period before the late 1970s in the past 100 years was the conservation phase of the ecosystems' adaptive cycle (Figure 5a). The disturbances during the late 1970s provoked crisis and transformation of the Honghe and Shenjiadian peatlands. They were the trigger that caused the ecosystems to change from oligotrophic, nontoxic, and moisture-loving species, and so on, equilibrium to eutrophic, toxic, and dry-loving species, and so on, equilibrium in the adaptive cycle. The average TN enrichment factors increased from 5 during 1900–1990 CE to 19 during 1990–2018 CE, the average TP enrichment factors rose from 2 to 9, and the heavy metals enrichment factors increased from 1 to 2 (Table S1 in the Supporting Information S1). After that, the regime shifts of the wetland ecosystems occurred in 1990 CE. More than 70% of wetlands in the Sanjiang Plain disappeared due to an increase of population and land reclamation since the founding of the People's Republic of China in 1949 CE, with almost all existing wetlands have now degraded. The scale of the changes within the Sanjiang Plain makes it unlikely that the pressures which brought about such widespread changes will be removed. We are unable to get direct evidence of whether the grassland will return to sedgeland if the drivers of land use are removed. However, we believe that it is difficult for the wetland ecosystem in this area to return to its original state after undergoing such major changes, even if the pressures are removed. There is a time gap between the regime shift (~1990 CE) and severe disturbances (the late 1970s), which is the wetland ecosystem adaptive cycle's release phase. During the release phase, the slow variable of vegetation changed rapidly, the ecosystem states was unstable, and resilience reduced dramatically. After 1990 CE, the carex in Honghe peatland and shrub in Shenjiadian peatland began to capture opportunity to appear or expand—the pioneer vegetations. The peatland ecosystems entered the reorganization phase, in which soil processes minimize nutrient loss and reorganize nutrients so they become available for the next phase of exploitation. However, as the ecosystems shift from reorganization to exploitation (Figure 5a), some of the accumulated resources leave the system because of the organization's collapse (Holling & Gunderson, 2002). The critical functionalities of the wetland ecosystem were worse or even damaged. The water conservation function of Honghe peatland has been

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injured since 1990 CE, similarly to Shenjiadian peatland. The damage to the water conservation function of the wetland ecosystems were caused by a falling water level driven by anthropogenic activities, such as the excessive use of groundwater for irrigation purposes and wetland drainage for reclamation. There was no pronounced increase in rainfall from 1950 to 2010 CE, and the amount of artificial groundwater exploitation increased from 8×10^8 in 1986 to 110×10^8 m^3/yr in 2013 CE (G. Zhang et al., 2018; Figure S3 in the Supporting Information S1). Furthermore, most of the Shenjiadian peatland disappeared after 2010 CE, with the rest was arid and turning into grassland.

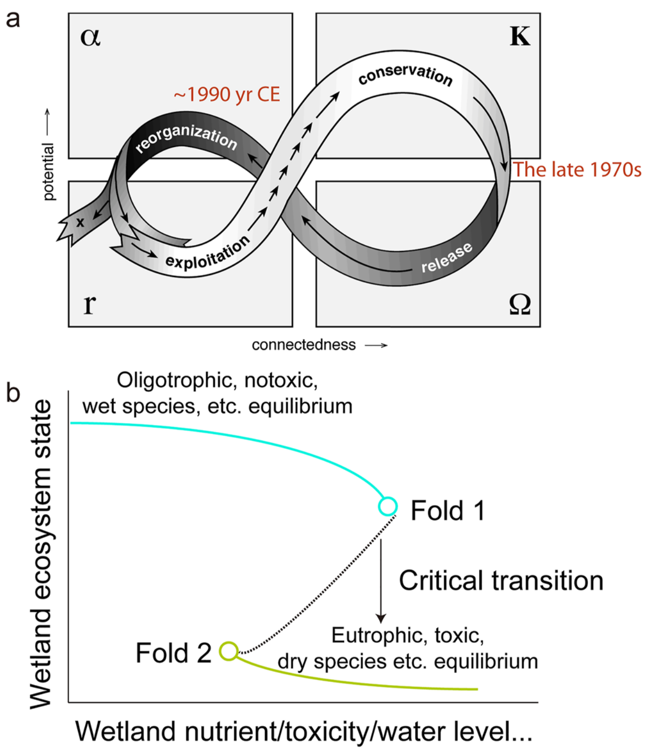

Figure 5. The adaptive cycle and the state changes of the wetland ecosystems responded to the decreasing ecological conditions. (a), A stylized representation of the four phases (r, K, Ω, α) and the flow of events among them in the adaptive cycle of the wetland ecosystems. The fore loop includes two phases of exploitation and conservation, and the back loop comprises two phases of release and reorganization. The arrows show the speed of that flow in the cycle, where short arrows indicate a slowly changing situation and long arrows indicate a rapidly changing situation. *Y*-axis–the potential that is inherent in the accumulated resources of biomass and nutrients; *X*-axis–the degree of connectedness among controlling variables (Holling & Gunderson, 2002). (b), Bifurcation diagram of an ecological model of wetland ecosystem state under decreasing ecological conditions. Solid lines represent equilibria; the dashed line marks the boundary between the Oligotrophic, nontoxic, wet species, and so on, equilibrium (cyan) and eutrophic, toxic, dry species, and so on, equilibrium (yellow).

3.3. Reference Conditions for Wetland Ecological Restoration

The state of wetland ecosystems began to worsen, and the water level declined after severe human disturbances based on the variations of geochemical indicators and ecological communities (Figures 3e and 4, Table S1 in the Supporting Information S1). Ecological communities (slow variables), hydrological conditions, nutrient status, and so on, are critical variables indicating the wetland ecosystem's development. Not only have the water levels changed, but the nutrition and heavy metal contents of the ecosystems have also changed (Figure 3e). The state of wetland ecosystems changed from oligotrophic, nontoxic, moisture-loving species, equilibrium to eutrophic, toxic, dry-loving species, and so on, equilibrium (Figure 5b). As nutrients and poisonous substances increase, water level decreases (*x*-axis), wetland ecosystem state gradually declines up to a critical threshold that function undergoes a critical transition through a fold bifurcation (Fold 1). The wetland ecosystem state collapses at this bifurcation to the alternative eutrophic, toxic and dry species state. The wetland ecosystem cannot recover to its original status after the regime shift occurs. If the wetland nutrient, toxicity, and the water level are restored, the water ecosystem state returns to the previous oligotrophic, nontoxic, and moisture-loving species state at another threshold (Fold 2).

Considering the ecosystem's resilience and adaptive cycle, we do not need to restore the wetland ecosystem's ecological conditions to its pre-disturbed state. Furthermore, we are unable to repair the ecosystem to its exact initial state after a regime shift occurs. We propose that the reference conditions are the characteristics at the beginning of the ecosystem's conservation phase, with strong resilience and a stable state. The environmental attributes at the beginning of the conservation phase, such as vegetation composition, nutrients, and heavy metals, can be clearly reflected by the paleo-biological and geochemical data. Further, some paleo data, such as pollen, plant macrofossil, and diatoms, can reconstruct the water level. For example, the water level changes in the Honghe peatland during the Holocene were reconstructed by paleo-diatom data based on the inferred diatom-water level regression model (Ma et al., 2018). The water level at the beginning of the conservation phase was 11–13 cm which is higher than now (Ma et al., 2018), and the NH_4-N reconstructed by diatoms in the Honghe peatland was 0.8–1.2 mg/L (Liu, 2019). The dominant vegetation composition was *Drepanocladus aduncus-Carex* community (Figure 4), and the dominant diatom was *Pinnularia brevicostata* (Liu et al., 2018). To reconstruct the moisture-loving ecological communities, the drainage ditches should be filled and provide a more suitable environment for aquatic species. The referred enrich factors of TN, TP, and heavy metals should be under 4.45, 2.12, and 1.11, respectively (Table S1 in the Supporting Information S1). To reach that goal, there is a need to consider changes in management in relation to farming, such as fertilization patterns. The pesticide management should be strict to reduce heavy metal use. In the conservation phase, the Honghe and Shenjiadian peatland ecosystems were slightly disturbed by human activities (Figures 3e and 5a). Compared with the pre-disturbed natural state as the reference conditions, this approach has a lower restoration effort. It can save the cost of artificial restoration (water system remediation and connectivity engineering, pollution control, treatment engineering, etc.). The wetland will recover to the previous oligotrophic, nontoxic, and moisture-loving species state at another threshold (Figure 5b). This approach can be used in both Honghe and Shenjiadian peatlands, showing this method's reliability.

4. Conclusions

We used paleoecological records to reconstruct the natural variabilities of Honghe and Shenjiadian wetland ecosystems. The dominant plant species did not change much under natural forcing from 700 to 50 cal yr BP and have undergo dramatic changes in the last 100 years. Wetlands in the Sanjiang Plain have been slightly disturbed since the 1920s and were severely disturbed due to the mechanization and modernization of agriculture after China's reform and opening up from the late 1970s. The sedimentary index, nutrient index, heavy metal index, and combustion products index reveal the degree of human disturbance in the Sanjiang Plain's wetland ecosystems. Recent anthropogenic pressures triggered a strikingly different community succession with sharp drought compared to natural pressures. The ecosystem state was not stable, resilience decreased during the late 1970s–1990 CE in Honghe and Shenjiadian peatlands under anthropogenic disturbances based on the STARS algorithm and F statistics of the typical slow variables (ecological communities). According to the characteristics of high resilience and a stable ecosystem state at the beginning of the conservation phase (before the late 1970s) of the ecosystem's adaptive cycle, its ecological state can be used as reference conditions for Honghe and Shenjiadian peatlands' restoration. The reference water level was 11–13 cm, and the reference NH_4-N concentration ranged from 0.8 to 1.2 mg/L. The dominant vegetation composition was *Drepanocladus aduncus-Carex* community, and the dominant diatom was *Pinnularia brevicostata* at the beginning of the conservation phase. The referred enrich factors of TN, TP, and heavy metals should be under 4.45, 2.12, and 1.11, respectively in the Sanjiang Plain. According to the reference conditions we set, the wetland ecosystem will be restored to a fair and stable state at another threshold. Compared with the pre-disturbed natural conditions, this approach considers the ecosystem resilience and the adaptive cycle, which is more in line with ecosystem evolution and can save on artificial restoration. It can provide important lessons for the future management and restoration of this type of wetland worldwide.

Data Availability Statement

The sedimentary, geochemical, and biological species data involved in the article is available at figshare (https://doi.org/10.6084/m9.figshare.13655588).

Acknowledgments

This work was supported by the National Natural Science Foundation of China (No. 42001081, 42171103); and the China Postdoctoral Science Foundation (No. 2020M680694); and the Youth Innovation Promotion Association CAS (No. 2020235); and the Special Research Assistant Project of the Chinese Academy of Sciences.

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