

Research Article

Plasticity and rooting behaviour of *Pontederia crassipes* under vernal water level rise: Implications for biological invasion and management

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Abstract

As global warming continues, increasing minimum winter temperatures may no longer limit the northward expansion of invasive species, particularly those from tropical zones. A mesocosm experiment with a chronosequence approach (space-for-time trade-off) was used to examine the effects of water level variation on the traits of the invasive aquatic plant water hyacinth [*Pontederia crassipes* (formerly *Eichhornia crassipes*)] collected from freezing, chilling and warm overwintering locations in China. We hypothesized that the phenotypic plasticity of the plant, particularly its ability to adjust its root morphology and topology in response to vernal water level rise, enhances its capacity to invade freshwater ecosystems. The results revealed significant plasticity in the response of the plants to water level, with plant traits such as total biomass, diaspore number, leaf area, specific leaf area, root length, and photosynthetic efficiency significantly increasing under a 10-cm water level, which can be regarded as a moderate overwintering water level. However, the plants from the warm location did not perform better than did those from the freezing or chilling locations, possibly because the harsh winter conditions reduced plant biomass but did not negatively affect the plants at the gene level. These findings highlight phenotypic plasticity in rooting behavior, which enables plant survival and growth during overwintering in the littoral zone, allowing *P. crassipes* to withstand low temperatures and to rapidly proliferate during the vernal water rise period. This study highlights the importance of early detection and management strategies to control the spread of *P. crassipes*, particularly given the trends in global climate change, which may facilitate its northward expansion. The use of *P. crassipes* as a model plant is recommended for studying the responses of invasive aquatic plants to global change in freshwater ecosystems.

Key words: Clonal propagation, invasive species management, freshwater ecosystems, global climate change, root Architecture, vernal water rise

Introduction

The spread of invasive species has been regarded as a cosmopolitan phenomenon, which has not yet reached saturation (Seebens et al. 2017). Invasive aquatic plants can negatively affect the water quality and limit aquatic biodiversity in freshwater ecosystems (Fleming and Dibble 2015; Wang et al. 2016; Hussner et al. 2017). Low winter temperatures significantly restrict the growth and limit the distribution ranges of invasive species, as most invasive species originate from tropical zones such as the Amazon drainage basin (Clements and Ditommaso 2011; Liu et al. 2017). There are two effects of low temperatures on plants: when the temperature is below -1°C , plants die quickly. This damage is referred to as freezing injury. The other effect, which is referred to as chilling injury, refers to plant damage or death when the temperature is above 0°C . Chilling injury occurs mainly because of destruction of the cell membrane structure, and such injuries are the main obstacle preventing the spread of plants to high latitudes or northward in the Northern Hemisphere (Schulze et al. 2005; García et al. 2018). Invasive species have spread under global warming (Hellmann et al. 2008; Early et al. 2016; Ren et al. 2021). As global warming continues, we face threats from not only the increase in the average temperature but also the increase in the minimum temperature in winter (IPCC 2018). The low temperature in winter once served as a threshold determining the potential growth and spread of invasive species; however, as global warming continues, it may no longer function as a limiting factor (Kerr and Kharouba 2007). This change facilitates the spread of invasive species, allowing them to invade areas previously unsuitable (Walther et al. 2009; Bellard et al. 2013; Liu et al. 2017). Global trends suggest that for every 1°C increase in the minimum winter temperature, the potential habitable range of tropical invasive species increases by approximately 150–200 km northward (Kerr and Kharouba 2007; IPCC 2018). For example, the geographic range of water hyacinth [*Pontederia crassipes* Mart. (formerly *Eichhornia crassipes* (Mart.) Solms)] has expanded northward in China, with studies indicating successful overwintering in northern provinces during warm winter seasons (You et al. 2014; Wu and Ding 2020).

Originating from the Amazon Plain and Caribbean zones, *P. crassipes* is a noxious weed found all over the globe, and its growth is limited by low winter temperatures (Villamagna and Murphy 2010; Adebayo et al. 2011). The plant has nearly the same negative impact on nature, nature's contributions to people and good quality of life (IPBES 2023). Fortunately, without the introduction of obligate pollinators, this species rarely reproduces sexually in China (Zhang et al. 2010; Liu et al. 2013). Vernal water level rise, refers to the seasonal increase in water levels driven by spring rainfall and upstream hydrological regulation (Bauder 2005; Collinge and Ray 2009). This phenomenon typically occurs from March to May in the Yangtze River Basin and Pearl River Basin of China, coinciding with rising temperatures after winter. *Pontederia crassipes* can only drift with currents and winds from warmer southern regions during the vernal water level rise period (Figure 1). In the Taihu Lake Basin, its leaves and stipes dry and wilt, whereas their roots and stolons survive in mud within the littoral zone during the water drawdown period. In this case, warm mud could protect roots from frost-induced death in winter, and the overwintering vegetative biomass could respond quickly to elevated temperatures (Njambuya and Triest 2010; Yang and Everitt 2010; Liu et al. 2016). Thus, climate change may increase the invasion success of *P. crassipes* by expanding its distribution range and increasing its negative impacts. As a result, *P. crassipes* diaspores may suppress other free-floating species by occupying the empty niches left on the water surface due to freezing-induced mortality in spring. The successful overwintering of *P. crassipes* encompasses two stages: first, the plant can overwinter as mentioned; second, it can successfully

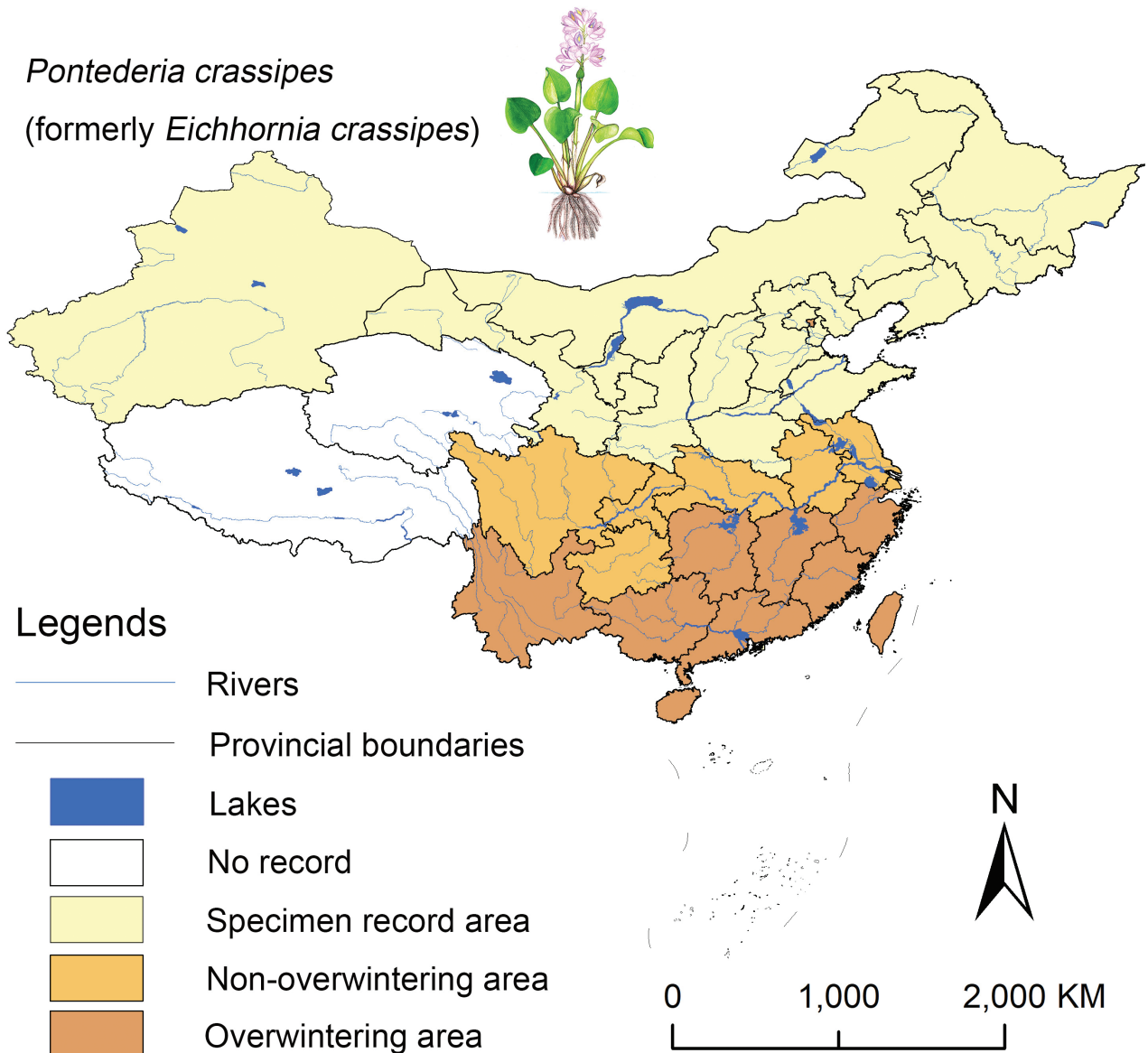


Figure 1. Distribution of *Pontederia crassipes* (formerly *Eichhornia crassipes*) in China. The figure was drawn based on previous field investigations and historical records.

proliferate and produce diaspores in spring. When the increase in the water level is high enough, the connection between mother ramets and daughter diaspores is disrupted, and diaspores can drift away to occupy new habitats, thus expanding the invasion range. Ramets and diaspores fulfill complementary roles in determining the invasion success of *P. crassipes*. Ramets, which are genetically identical clones, remain connected and share resources with the parent plant during growth, although they can survive independently if separated. Diaspores, as dispersal units, detach from the parent plant to colonize new habitats, thus facilitating their geographical expansion. Furthermore, studies indicate that the root systems of *P. crassipes* respond plastically to variations in water depths. For instance, shallow submergence enhances the growth of root systems and biomass allocation (Liu et al. 2016). Under deeper water levels, stem bases (and roots) are protected from environmental stress, allowing the plant to survive harsh winter conditions (You et al. 2013), and a water depth of 10 cm can significantly enhance root elongation and rootlet development, facilitating survival during overwintering and niche expansion. However, root topology remains stable

across treatments, indicating that *P. crassipes* maintains a consistent dichotomous root branching structure (Huang et al. 2022). These studies demonstrate that the roots of *P. crassipes* are critical for their adapting to variations in water levels, influencing root biomass, morphology, and topology under changing environmental conditions. Overall, these strategies enable the widespread distribution and persistence of this species in various environments. When *P. crassipes* produces new diaspores, this proliferation may allow plants to expand into northern waters, as global warming causes water temperature changes. *Pontederia crassipes* can survive (even on a small scale) after harsh winters and may produce a large population. However, whether the plant survives and spreads given vernal water level rise remains unexplored.

Several studies in China, such as those by You et al. (2013), You et al. (2014), Liu et al. (2016), Yu et al. (2019), and Huang et al. (2022), have focused on the impact of increasing temperatures on overwinter growth of *P. crassipes*. However, the following question remains: Will the surviving ramets perform better than non-chilling ramets do? We hypothesize that variations in the overwintering traits of *P. crassipes* across different latitudes are influenced by phenotypic plasticity. The determination of the relative importance of these mechanisms is crucial for predicting the potential range expansion under climate change. Moreover, we hypothesize that chilling conditions may result in ramets with greater survival potential (i.e., survival of the fittest). The results of this study highlight a novel rooting phenomenon, and the potential ecological impacts of this phenomenon were predicted.

Materials and methods

Plant material collection

We employed a chronosequence approach (space-for-time trade-off) in which, more than 200 live overwintered *P. crassipes* ramets were collected from different sampling locations (Table 1) and cultivated under three water levels to explore the effects of water level variation on plant growth in spring. The chronosequence approach, in which spatial differences are replaced by temporal changes, was adopted to study the effect of water level variation on plant growth and to determine the unique survival and phenotypic plasticity strategies of plant roots. Instead of waiting for global warming changes to occur over time, we selected different sampling locations that represent different stages of this process. Notably, January is the coldest month across the three sampling locations.

Table 1. Coordinates of the three ramet sampling locations of *P. crassipes*.

Background	Sampling locations	Coordinates
Freezing	Suzhou	31.0338°N, 120.4228°E
Chilling	Nanping	26.6022°N, 118.1457°E
Warm	Guangzhou	23.3061°N, 113.2773°E

Pontederia crassipes ramets subjected to freezing injury were collected from a bay (31.0338°N, 120.4228°E) outside the Taihu Laboratory for Lake Ecosystem Research (TLLER), Dongshan Branch (DB), in the Yangtze drainage basin on February 22, 2022. The area exhibits a mean January average air temperature of 3.0°C, and the minimum winter temperature (-6°C) occurred on December 26 from 2021–2022 (<https://lishi.tianqi.com/suzhou>). As a region characterized by low winter temperatures, Suzhou contains the northernmost distribution of *P. crassipes*. The littoral zones in this area, such as those around Taihu Lake, offer

nutrient-rich but freezing-prone environments. This setting allows the study of the mechanism through which the plant rooting strategy mitigates freezing damage in mud during winter drawdown periods.

Pontederia crassipes ramets subjected to chilling injury were collected from a riverbank in Nanping city, Fujian Province (26.6022°N, 118.1457°E), in the Minjiang drainage basin on February 25, 2022. The minimum winter temperature (1°C) occurred on February 21, 2022 (<https://lishi.tianqi.com/nanping>). The distance between Nanping and Suzhou is 540 km. Situated in Fujian Province, Nanping exhibits moderate winter temperatures. This area represents regions where chilling injury (not freezing injury) is the dominant limiting factor for invasive aquatic plants. The selection of Nanping enables the evaluation of the adaptability of the plant under intermediate climatic conditions, thus reflecting environments where climate change could shift temperatures toward higher, less restrictive levels.

Pontederia crassipes ramets subjected to a warm location, i.e., neither a freezing nor chilling location, were collected on February 26, 2022, in Guangzhou, Guangdong Province (23.3061°N, 113.2773°E), in the Pearl River drainage basin. The minimum winter temperature (4°C) occurred on February 20, 2022 (<https://lishi.tianqi.com/guangzhou>). The distance between Guangzhou and Nanping is 612 km. Guangzhou represents an environment where *P. crassipes* thrives without temperature-induced stress. The inclusion of this location allows for the comparison of plant traits under optimal growth conditions, thus serving as a baseline for assessing the impact of colder climates.

Study area

The mesocosm experiment was conducted at the TLLER, DB (31.0331°N, 120.4217°E), which is located on the shore of Taihu Lake. This area enjoys a mild subtropical climate.

Experimental setup

Prior to the experiment, young ramets obtained from the three sampling locations were cultivated separately in a greenhouse in the TLLER, DB. The experiment started on March 13, 2022. Sediment was collected from Taihu Lake near the TLLER, DB. A total of 15 cm of sediment was added to each cylinder ($d = 0.30$ m, $h = 1.00$ m). All the cylinders were placed on a platform in a natural setting in the TLLER, DB. No protection measures (for instance, shading and pest control) were implemented. Young ramets of a similar shape and weight were collected, and the biomass was measured. The water level was set to 1, 10 and 20 cm. These water levels were selected on the basis of previous field investigations and experimental evidence (Huang et al. 2022; Wang et al. 2017). The 1-cm depth represents stranded plants in moist littoral zones, highlighting stress conditions during drawdown. The 10-cm depth represents the optimal rooting conditions observed in littoral environments, which enhances nutrient uptake and survival. Finally, the 20-cm depth represents free-floating conditions, which is relevant for understanding the adaptability and dispersion of this plant under water level rise. These levels are consistent with the natural conditions in the Lake Taihu Basin, where seasonal fluctuations significantly influence the growth and spread of *P. crassipes*. Each treatment was replicated six times ($n = 6$). The water level was maintained with a pump after rainfall.

The experiment ended on May 20, 2022, when the weather neared summer conditions. The sediment near the roots was removed along the direction of the roots, and the adhering sediment was gently washed away by a pump during harvesting. The

number of diaspores and the lateral root number c of the ramets in each cylinder were counted. The original root shape was maintained to the greatest extent possible. The root system was cut with tweezers so that the roots were dispersed and did not overlap.

The plant functional traits included the total biomass, shoot/root (S/R) ratio, diaspore number, maximum quantum yield of photosystem II F_v/F_m , leaf area (LA), specific leaf area (SLA), root length (RL), specific root length (SRL), lateral root number c , mean rootlet number a , and topological indices TI, q_a and q_b (Table 2).

Table 2. Descriptions of the measured functional traits.

Abbreviations	Descriptions	Units	Note
Growth traits			
Total biomass	Total plant biomass	g	including diaspores
S/R ratio	Shoot/root ratio		
Diaspore number	Number of daughter plants	ind.	
Photosynthetic trait			
F_v/F_m	Maximum quantum yield of photosystem II		
Morphological traits			
LA	Leaf area	cm ²	excluding diaspores
SLA	Specific leaf area	cm ² g ⁻¹	
RL	Root length	cm	excluding diaspores
SRL	Specific root length	cm g ⁻¹	
Root c	Lateral root number c	ind.	
Mean a	Mean rootlet number a	ind.	
Root topological indices			
TI	Topological index TI		excluding diaspores
q_a	Topological index q_a		excluding diaspores
q_b	Topological index q_b		excluding diaspores

On the harvest day, five randomly chosen leaves were sampled from the plants in each treatment with a 4-mm (0.13-cm²) diameter leaf clip. The leaves were incubated in the dark for 20 minutes before sunrise to ensure that all the reaction centers within the chloroplasts were fully oxidized, which was assessed via a handheld plant efficiency analyzer (PEA) (Hansatech Instruments, Ltd., Norfolk, UK). The initial fluorescence F_0 and maximum fluorescence F_m of the leaves were measured, and the maximum quantum yield or energy trapping efficiency of the photosystem II reaction centers, F_v/F_m , was calculated as follows:

$$F_v/F_m = (F_m - F_0)/F_m.$$

The biomasses of the plant shoots and roots were determined via weighing after drying at 60°C for 48 h in an oven.

Images of the plant leaves and roots were developed by scanning via an Epson 12000XL scanner (Seiko Epson Corp., Suwa, Nagano, Japan). Following the recommendations of Bouma et al. (2000), the image resolution was set to 600 dpi, and the scanned images were saved as 1:1 uncompressed 8-bit high-resolution TIFF files. To increase the contrast between the roots and the background, the nearly transparent roots of *P. crassipes* were stained with a 0.2 mmol/L (0.075 mg/mL) methylene blue solution for 30 s before scanning with a white LED light source. The scanned root images were processed via WinRHIZO root measurement and

analysis software (Regent Instruments Inc., Québec City, Canada). WinRHIZO software was chosen for its ability to provide detailed quantitative data on root morphology and topology, such as the LA, RL, and rootlet number a to better elucidate the adaptive strategies of *P. crassipes*.

The plant SLA was calculated as follows:

$$\text{SLA} = \text{LA}/\text{leaf biomass.}$$

The SRL was calculated as follows:

$$\text{SRL} = \text{RL}/\text{root biomass.}$$

The root system of *P. crassipes* is highly complex and extensively overlapped, making it impossible to obtain a complete image via conventional scanning analysis methods. In this study, we investigated the overall root structure by cutting and individually scanning roots and then combining them with the original root branching.

The root topological indices TI, q_a and q_b were obtained according to our previously published methods (Huang et al. 2019):

$$\text{TI} = \frac{\log a}{\log ca};$$

$$q_a = \frac{a - 1 - \ln ca / \ln 2}{ca - 1 - \ln ca / \ln 2};$$

$$q_b = \frac{(a + 3 - 2/a) / 2 - 1 - \ln ca / \ln 2}{(ca + 1) / 2 - 1/ca - \ln ca / \ln 2}.$$

The topological indices TI, q_a and q_b of *P. crassipes* are indicated by the lateral root number c and the mean rootlet number a .

For herringbone-like branching, the value of the topological index TI is close to 1, with the values of both q_a and q_b approaching 1. In contrast, dichotomous branching yields a TI value close to 0.5, with q_a and q_b values close to 0. According to plant root structure theory, plants with herringbone-like branching are adapted to low-nutrient environments because this branching pattern features more and longer connections and a lower root system hierarchy. However, this branching pattern exhibits a lower transmission efficiency and higher construction cost. Dichotomous branching root systems encompass shorter connections and are easier to construct and maintain than are herringbone-like root systems. This root branching pattern typically occurs in environments in which nutrients and water are more abundant.

Data analysis

Before analysis, all the data were analyzed to ensure that they met the assumption of a normal distribution on the basis of the Shapiro–Wilk test and the assumption of homogeneity of variance on the basis of the Levene test. If the data did not satisfy these assumptions, they were transformed with a $\log(x+1)$ function. An unconstrained unimodal ordination model based on detrended correspondence analysis (DCA) was constructed in Canoco 5.0 (Microcomputer Power, Ithaca, NY, USA). In this study, the results revealed that the lengths of the gradients were shorter than 3, and therefore, the use of linear principal components analysis (PCA) was preferred. A general linear model (GLM) was employed to examine the effects of the

sampling location (SL) and water level (WL) on the plant functional traits. Moreover, the effects of the interaction between SL and WL on plant functional traits were assessed. Post hoc pairwise comparisons of the means were conducted via Duncan's multiple range test at a significance level of $P = 0.05$ to test for differences between treatments. One-way analysis of variance (ANOVA) was employed to test for differences in plant functional traits at a significance level of $P = 0.05$. All statistical analyses were performed via SPSS Statistics 26 (IBM Corp., Armonk, NY, USA).

Results

To determine the influences of sampling location (overwintering location) and water level on the traits of *P. crassipes*, we first employed a PCA to assess the relationships of plant traits with sampling location (SL) and water level (WL). The PCA results showed that the cumulative percentage variance accounted for the relationship among SL and WL with 13 functional traits on the first two canonical axes was 97.29% (57.11% for axis 1 and 40.18% for axis 2) (Figure 2). WL had a closer relationship with these functional traits than SL did (Figure 2).

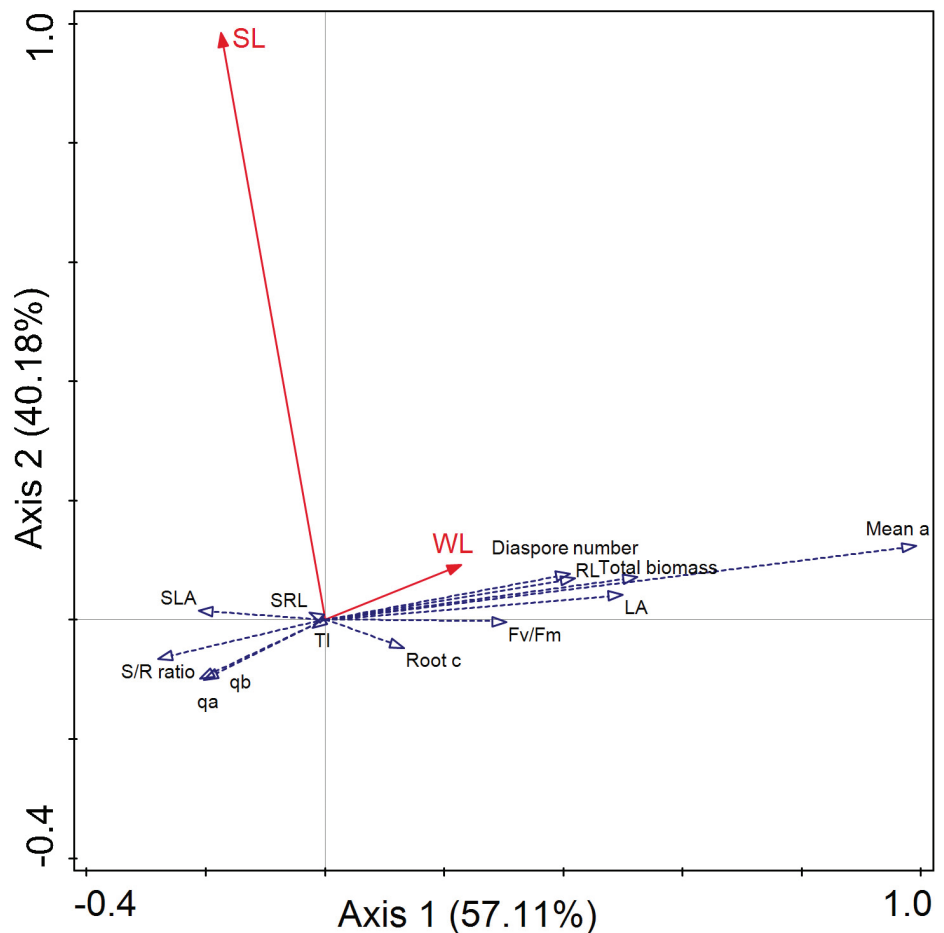


Figure 2. The ordination diagram of the principal component analysis (PCA) of sampling location (SL) and water level (WL) along with the 13 measured functional traits. The definitions of the abbreviations and descriptions are shown in Table 2. Dashed blue vectors with transparent arrows represent the 13 measured functional traits (response variables), and the solid red vectors with filled arrows represent the two explanatory variables, SL and WL. Arrows indicate the increase in values from the ordination center. The angle between the functional traits and factors represents their correlations, and the sharper the angle, the stronger the correlation.

The GLM results revealed that the water level significantly affected several traits, whereas the sampling location and the interaction between the water level and sampling location did not (Table 3). In summary, water level significantly affected the plant traits of *P. crassipes*, including total biomass, diaspore number, F_v/F_m , leaf area, specific leaf area, root length, and mean value. In contrast, only the sampling location and the interaction between the sampling location and water level (SL \times WL) did not significantly affect these traits. These results indicated no significant differences among the sampling locations.

Table 3. General linear model (GLM) results for the effects of sampling location (SL) and water level (WL) on the traits of water hyacinth (*Pontederia crassipes*).

	SL		WL		SL \times WL	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Total biomass	0.116	0.891	118.596	<0.001	0.199	0.937
S/R ratio	0.721	0.492	1.572	0.219	0.443	0.777
Diaspore number	1.119	0.336	64.933	<0.001	0.170	0.952
F_v/F_m	0.047	0.954	12.309	<0.001	0.385	0.818
LA	0.490	0.616	179.972	<0.001	0.671	0.615
SLA	0.562	0.574	14.006	<0.001	0.382	0.820
RL	0.385	0.683	35.247	<0.001	0.127	0.972
SRL	0.601	0.552	0.027	0.974	0.261	0.901
Root <i>c</i>	0.175	0.840	0.660	0.522	0.127	0.972
Mean <i>a</i>	0.907	0.411	18.018	<0.001	1.306	0.282
TI	0.010	0.990	0.256	0.775	0.079	0.988
q_a	0.093	0.911	1.455	0.244	0.201	0.937
q_b	0.102	0.903	1.412	0.254	0.208	0.933

The results that meet the significance level of $P < 0.05$ are highlighted in bold.

Thus, we applied the water depth as the main indicator. The total biomass, diaspore number and F_v/F_m value peaked at a water depth of 10 cm, whereas the variation in the S/R ratio did not differ significantly among the various treatments (Figure 3). The total biomass and diaspore number at water depths of 1 and 20 cm were low and did not significantly differ (Figure 3).

The LA and RL showed similar trends with increasing water depth. Specifically, they peaked at a water depth of 10 cm, and the values at 10 cm were significantly greater than those at the other two water depths (Figure 4). The SLA was greater at a water depth of 1 cm than at the other depths, but there was no significant difference among the three treatments. There was a decreasing trend in the SLA with increasing water depth (Figure 4b). The root *c* did not significantly differ among the three depths (Figure 4e). The mean *a* reached its peak at a water depth of 10 cm and decreased at a water depth of 20 cm, and the lowest value was obtained at a water depth of 1 cm (Figure 4f).

The topological traits TI, q_a and q_b exhibited similar trends across all the treatments (Figure 5), which indicates that the root branching pattern of *P. crassipes* did not differ across the various sampling locations or water levels. The lack of significant differences in plant root topological traits may occur because the plant may form genetic constraints, which may prevent significant structural changes. As a result, the root system may remain consistent across the different experimental treatments.

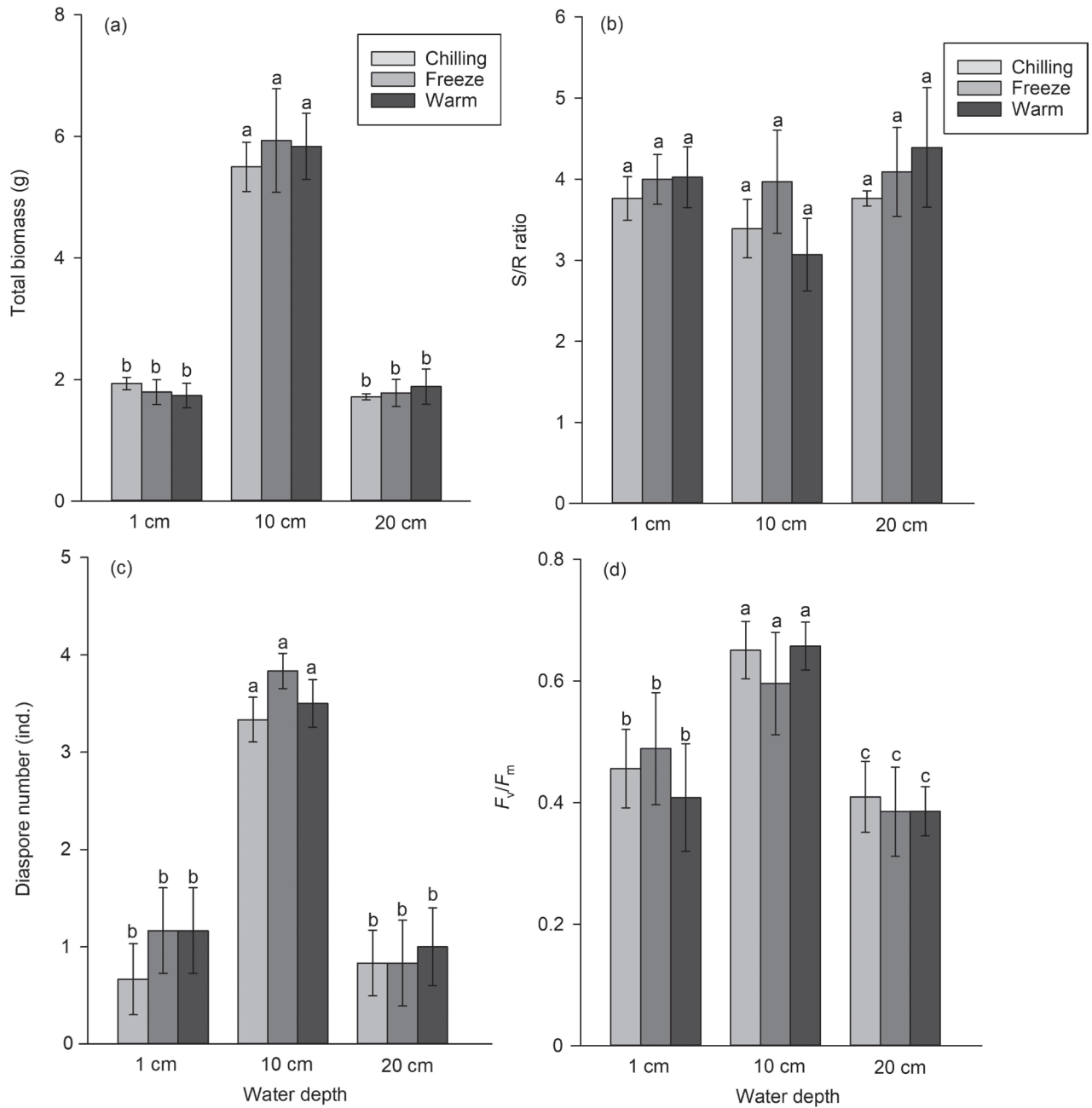


Figure 3. Growth traits, i.e., the total biomass, shoot/root (S/R) ratio, and diaspore number, and photosynthetic traits, i.e., the maximum quantum yield of photosystem II F_v/F_m , observed in the experiment. The values are expressed as the mean \pm standard error (S.E.) ($n = 6$). The different lowercase letters indicate significant differences between treatments ($P = 0.05$).

Discussion

Pontederia crassipes was chosen as a model plant to investigate a new rooting behavior and to elucidate the transformation from being rooted in winter to being free-floating during the vernal flooding period. Our findings demonstrated that the water level significantly affected plant traits, including the total biomass, diaspore number, photosynthetic efficiency (F_v/F_m), LA, RL and mean a . Moreover, the plants from the warm location did not outperform those from the freezing or chilling locations, which could be attributed to biomass damage caused by harsh winter conditions. However, it is also possible that freezing and chilling conditions do not significantly affect the plant at the genetic level, allowing it to

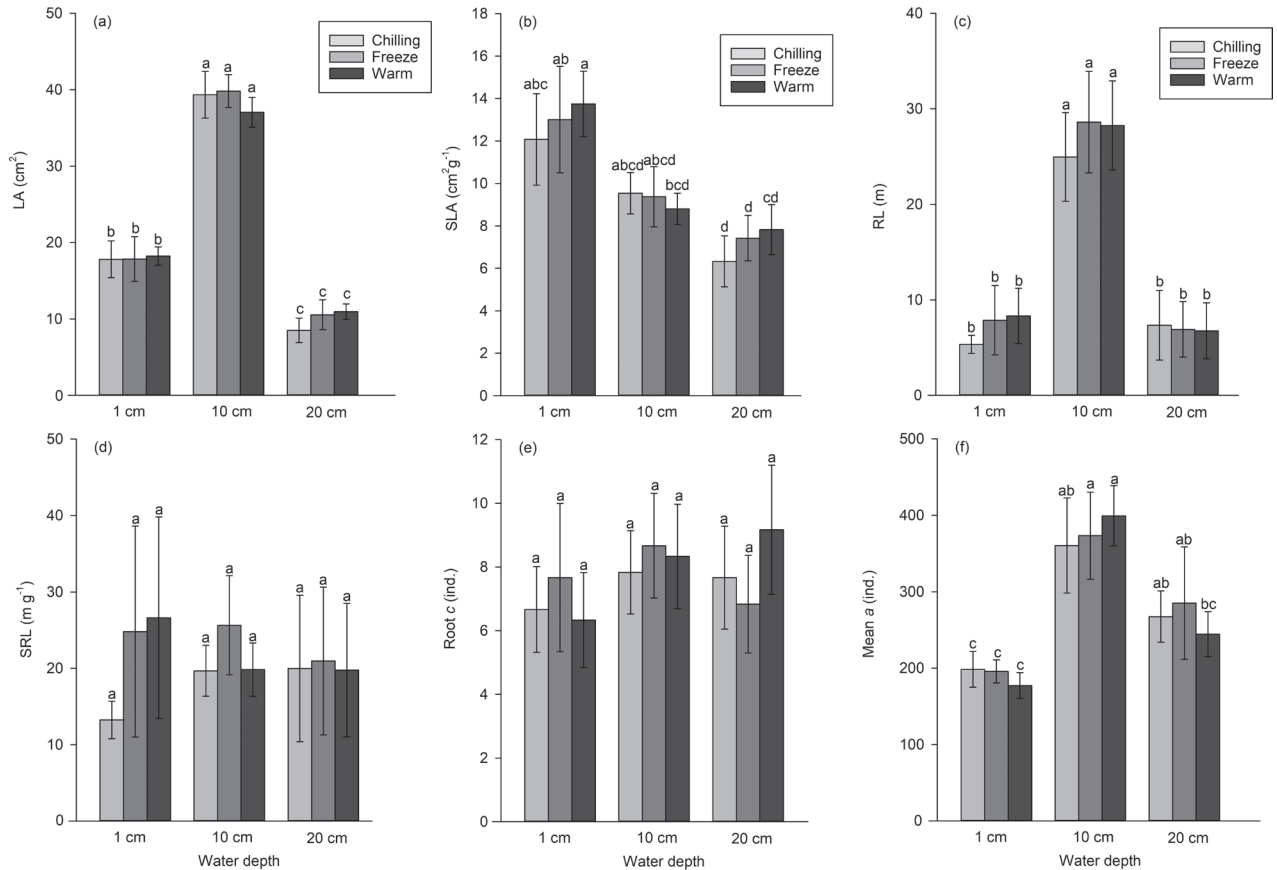


Figure 4. Morphological traits, i.e., the leaf area (LA), specific leaf area (SLA), root length (RL), specific root length (SRL), lateral root number *c* (root *c*) and mean rootlet number *a* (mean *a*), observed in the experiment. The values are expressed as the mean \pm S.E. ($n = 6$). The different lowercase letters indicate significant differences between treatments ($P = 0.05$).

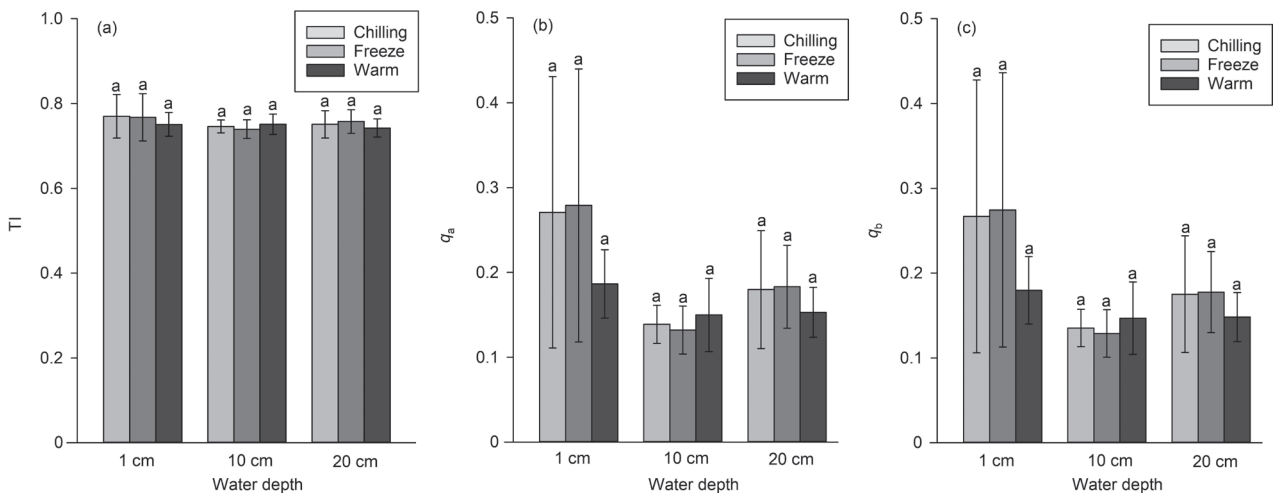


Figure 5. Root topological traits, i.e., topological indices TI, q_a and q_b , observed in the experiment. The values are expressed as the mean \pm S.E. ($n = 6$). The different lowercase letters indicate significant differences between treatments ($P = 0.05$).

maintain certain adaptive traits. These findings conform with a previous study indicating low genetic diversity and differentiation in introduced populations of *P. crassipes* (Zhang et al. 2010), which may contribute to its invasion success. This hypothesis requires further investigation into the genetic basis (for instance, transcriptomic or genomic studies) of resilience in the plant under extreme environmental conditions.

Vernal water levels and rooting behavior: Enhancing the survival and invasion of *P. crassipes* under changing climatic conditions

Unlike Liu et al. (2016), who reported significant impacts of the temperature, our findings highlight the water level as a critical factor influencing plant traits. The littoral zone contains abundant nutrients, and the temperature is higher than the air temperature, which can help plants overwinter, survive and proliferate during the vernal flooding period. The shift in *P. crassipes* from being rooted to free-floating driven by water level may be regarded as a unique survival strategy based on phenotypic plasticity. Other free-floating plants with similar rooting behavior have not been reported to overwinter in China. Thus, the shift in the rooting behavior of *P. crassipes* may indirectly facilitate it to suppress other species in spring. This furthers the plant invade empty niches left on the water surface after freezing-induced mortality of other free-floating plants; this agrees with the empty niche hypothesis, which states that invasive plants exploit new habitats created by fluctuating resources (Hussner et al. 2017; Golivets and Wallin 2018; Mathakutha et al. 2019). These findings suggest that *P. crassipes* exhibits significant plasticity in response to water level changes, which can be considered a crucial survival strategy in dynamic aquatic environments. This plasticity may enable *P. crassipes* to colonize new areas, contributing to invasion success.

The ability of *P. crassipes* to survive at low temperatures by rooting in littoral zones suggests that it can withstand and adapt to colder climates more effectively than previously thought. The 10-cm water depth likely provides optimal conditions for the overwintering of *P. crassipes* by balancing accessibility to water and nutrients while minimizing environmental stress. At this moderate depth, its rooting structures can securely anchor in nutrient-rich littoral sediments, thus supporting growth and biomass accumulation. This depth also protects the roots and stolons against temperature extremes, insulating them within the stable thermal environment of the littoral zone—an advantage during overwintering. Its ability to develop functional traits such as an increased biomass, diaspore number, and root length at this depth highlights its adaptive strategies to survive and proliferate under changing environmental conditions, such as vernal water rise. As global warming continues, the minimum winter temperatures are projected to increase, potentially removing the historical thermal barriers limiting the northward expansion of invasive species. This could lead to expansion of their geographical range, allowing *P. crassipes* to invade new water bodies that were previously unsuitable due to low winter temperatures.

Given the potential for *P. crassipes* to expand its range under climate change, early detection and rapid response strategies are crucial. Monitoring programs should be established in vulnerable areas, such as littoral zones, to detect new invasions early and take prompt action to control their spread before the plant becomes established. By identifying the water level as a critical factor influencing the growth of *P. crassipes*, we provide new insights into the mechanisms that facilitate its invasion and persistence in freshwater ecosystems. This understanding is essential for predicting the spread of *P. crassipes* under future climate scenarios in which hydrological patterns may change. For example, regulating water levels in winter could be a potential method to limit the growth and spread of this invasive species.

Pontederia crassipes can be viewed as a model organism for studying the responses of invasive aquatic plants to global change

The terrestrial plant *Arabidopsis thaliana* has been widely studied as a model plant across almost all plant subdisciplines (Pang and Meyerowitz 1987; Meinke 1998; the Arabidopsis Genome Initiative 2000; Poecke and Dicke 2008).

Among aquatic plants, *Phragmites australis* has been employed as a model organism for environmental changes, highlighting its utility in research on global change (Holdredge et al. 2010; Lambertini et al. 2012; Meyerson et al. 2016; Eller et al. 2017). Most studies on *P. australis* have focused on its ability as a wetland plant to tolerate different water and nutrient conditions but not on specific seasonal rooting behaviors, as observed in *P. crassipes* (Lambertini et al. 2012). The rooting behavior of *P. crassipes* in littoral zones in winter, which allows it to withstand low temperatures and proliferate in spring, is relatively unique. Several models of the growth and yield (Lorber et al. 1984), population dynamics (Gamage and Asaeda 2004), recognition based on airborne hyperspectral imagery (Yang and Everitt 2010), natural resource valuation (Buller et al. 2013), growth and interactions between shoot and root systems (Eid and Shaltout 2017) and root topology (Huang et al. 2019) of *P. crassipes* have been established. Numerous studies on the role of this species in element cycling in freshwater ecosystems (Pinto-Coelho and Barcelos Greco 1999); impact, management and utilization (Malik 2007; Villamagna and Murphy 2010; Coetzee and Hill 2012); relationships with herbivores (Fan et al. 2016); biosorption of chemical pollutants (Mohanty et al. 2006; Alvarado et al. 2008; Malar et al. 2016); response to environmental factors (You et al. 2013; Fan et al. 2015; Wang et al. 2017); and phytoremediation (Feng et al. 2017; Mishra and Maiti 2017) have been published as case studies. The relatively large and abundant leaves of this species make it easier to estimate its foliar traits more precisely, and its root system is relatively easy to quantify. We recommend *P. crassipes* as a model organism for studying the responses of invasive aquatic plants to global changes in freshwater ecosystems because this species is a successful invader. Thus, its use could be beneficial for identifying operative methods to control its spread.

Conclusions

The ability of *P. crassipes* to root in littoral zones to overwinter enables it to withstand low temperatures and to rapidly proliferate in spring, highlighting a unique strategy based on phenotypic plasticity that could facilitate its northward expansion under global climate change. When water levels rise in spring, *P. crassipes* can rapidly regenerate and spread. This adaptability to water level variation, combined with the warming climate, indicates that areas experiencing seasonal floods could exhibit accelerated plant colonization and growth. Control efforts should focus on winter water drawdown periods when the plant is rooted, enabling effective removal of roots and stolons. Moreover, regulating water levels to disrupt ideal growth conditions, such as reducing the water depth to limit root development, is vital. Additionally, manipulating water levels through flooding and draining cycles, particularly under vernal water level rise, can interrupt reproductive cycles. The use of *P. crassipes* as a model organism is also recommended to better understand the responses of invasive aquatic plants to global environmental changes, ultimately contributing to more effective management and control measures.

Authors' contribution

Xiaolong Huang: Data Curation; Writing – Original draft; Writing – Review and Editing; Project administration. Heyun Wang: Conceptualization; Investigation. Songyang Li: Visualization; Investigation. Leyang Xu: Methodology; Investigation. Zhaoshi Wu: Validation; Formal analysis. Hu He: Methodology; Formal analysis. Kuanyi Li: Supervision; Project administration; Funding Acquisition.

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