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Effects of young poplar plantations on understory plant diversity in the Dongting Lake wetlands, China

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This study evaluated the effects of young poplar plantations on understory plant diversity in the Dongting Lake wetlands, China. Poplar plantations resulted in a higher species number and Shannon's diversity. Species compositions were different between areas with poplar and reed populations: a lower ratio of hygrophytes but a higher ratio of mesophytes, and a higher ratio of heliophytes but a lower ratio of neutrophilous or shade plants in poplar areas compared to reed areas. Poplar plantations supported a higher ratio of ligneous plants in the entire Dongting Lake area, but there was no difference in the monitored plots. Unlike reedy areas, poplar plantations had higher light availability but lower soil water content during the growing seasons. These data suggest that young poplar plantations generally increased species richness and plant diversity, but significantly changed species composition due to the reduced soil water and increased light availability.

Large-scale tree plantations have been recognized as one of the greatest threats to biodiversity[1,2]. Generally, exotic tree species such as eucalyptus[3], rubber trees[4], pines[5], and poplars[2] are used for large-scale plantations. Fast-growing trees are generally planted in monocultures and have obvious advantages over native plants in competing for light, nutrient, and water resources. Therefore, large-scale tree plantations have led to increasing concerns regarding their adverse effects on biodiversity[6].

Previous studies have yielded contradictory results concerning the effects of fast-growing tree plantations on understory plant diversity[7]. Poplar plantations usually increased plant diversity compared to that in agricultural areas[8] or in abandoned fields[9] but decreased species richness compared to that in arable fields[2]. Fast-growing tree plantations might have a balanced effect on biodiversity due to habitat heterogeneity and differences in planting pattern or land-use history[10,11]. However, unlike in forest or agricultural ecosystems, flooding has important filter effects in the survival of understory plant species in wetlands, leading to relatively low plant diversity[12]. The effects of large-scale tree plantations on plant diversity might therefore be different in wetlands versus other ecosystems.

Changes in environmental conditions after the establishment of fast-growing tree plantations were generally considered as key factors affecting understory plant diversity[9,13,14]. After tree plantations are established, canopy stratification leads to a light gradient in the habitat, that is, niche separation of different species according to light requirement[15], which might be the main reason for the higher species richness in areas with tree plantations compared to those with herbaceous species[10,16]. Studies have shown that poplar plantations can result in a higher number of shade plants and a lower number of heliophyte species compared to those found in adjacent arable fields[2]. Additionally, fast-growing tree plantations usually have a higher transpiration rate[5,9,17], leading to a lower soil water content[18]. Therefore, changes in the environment play an important screening role in the establishment of understory plant species after tree plantation, due to the considerable differences in life form or ecotype of plant species, for example, heliophytes versus cheliophytes, or hydrophytes versus shade plants[1,19]. Species composition in different ecotypes or life form is more meaningful to reflect the changed environments than species richness expressed by species number. Species richness alone seems to be insufficient to evaluate the effects of fast-growing tree plantations on understory plant diversity; proportional species composition also needs to be considered.

Poplar (*Populus deltoides*), a fast-growing deciduous tree, is the most dominant species in broadleaf forests in China[20]. In 2003, poplar accounted for 13.5% of total forest plantation area in China[21]. In 1970s, *P. deltoides* was introduced into the Dongting Lake area, the second largest freshwater lake in China, for schistosome control, leading to an increase in the forest area from 87 km^2 in 1983 to 640 km^2 (accounting for 26% of the total lake area)

Table 1 | ANOVA (GLM) of plant diversity and species composition (means ± S.E.) in the Dongting Lake wetlands

Plant diversity	East Dongting Lake			South Dongting Lake			West Dongting Lake			Total Dongting Lake		
	Poplars	Reeds	*F*	Poplars	Reeds	*F*	Poplars	Reeds	*F*	Poplars	Reeds	*F*
SN	10.11 ± 1.02	5.33 ± 0.55	16.809***	8.32 ± 0.80	4.57 ± 0.89	9.704**	8.89 ± 0.22	5.57 ± 0.29	46.101***	9.17 ± 0.57	5.17 ± 0.35	36.77***
H	1.43 ± 0.12	0.82 ± 0.13	12.082**	1.30 ± 0.09	0.88 ± 0.16	5.672*	1.22 ± 0.17	0.99 ± 0.04	3.112ns	1.35 ± 0.07	0.89 ± 0.07	21.31***
Water requirement												
RH	48.20 ± 3.07	66.67 ± 3.40	16.234***	45.84 ± 3.49	74.57 ± 7.94	12.843**	74.23 ± 2.75	77.9 ± 6.92	0.092ns	50.83 ± 2.92	72.41 ± 3.45	22.38***
RM	49.33 ± 2.25	33.33 ± 3.40	15.402**	51.44 ± 3.47	25.43 ± 7.94	10.607**	22.76 ± 3.86	22.38 ± 6.92	0.001 ns	46.37 ± 2.78	27.59 ± 3.45	17.53***
RX	2.47 ± 1.39	0.00 ± 0.00	3.134ns	3.09 ± 1.02	0.00 ± 0.00	6.972*	2.96 ± 1.61	0.00 ± 0.00	9.432*	2.81 ± 0.74	0.00 ± 0.00	15.57***
Light requirement												
RHE	58.86 ± 2.86	49.07 ± 3.53	4.643*	59.65 ± 2.05	57.57 ± 8.65	0.070 ns	69.87 ± 3.88	42.14 ± 5.40	9.809*	60.67 ± 1.75	49.50 ± 3.47	7.72**
RN	35.84 ± 2.71	10.65 ± 4.76	21.115***	32.95 ± 4.65	13.01 ± 4.29	7.998*	13.27 ± 3.79	49.52 ± 6.41	12.180**	31.32 ± 2.82	23.20 ± 4.77	4.55ns
RS	5.30 ± 2.09	40.28 ± 6.05	29.793***	7.77 ± 3.88	29.42 ± 7.78	7.107*	16.86 ± 5.06	8.33 ± 4.06	1.440 ns	8.01 ± 1.10	27.25 ± 4.43	10.23**
Life form												
RA	42.95 ± 5.87	45.83 ± 3.40	0.181 ns	31.69 ± 6.29	20.66 ± 8.55	1.131 ns	39.14 ± 5.70	25.95 ± 4.56	2.728 ns	37.56 ± 3.82	32.12 ± 3.89	0.99 ns
RP	57.05 ± 5.87	54.17 ± 3.40	0.181 ns	68.68 ± 6.33	79.34 ± 8.55	1.050 ns	60.86 ± 5.70	74.05 ± 4.56	2.728 ns	62.44 ± 3.82	67.88 ± 3.89	0.99 ns
Growth form												
RV	4.65 ± 1.50	3.70 ± 2.70	0.056 ns	9.40 ± 2.97	10.97 ± 4.64	0.088 ns	0.00 ± 0.00	16.67 ± 8.13	1.680 ns	6.01 ± 1.56	9.86 ± 2.25	1.07 ns
RHP	95.10 ± 1.51	96.30 ± 3.70	0.089 ns	90.63 ± 2.95	89.03 ± 4.64	0.092 ns	97.96 ± 1.03	83.33 ± 8.13	1.291 ns	93.45 ± 1.51	90.14 ± 3.25	0.80 ns
RL	0.24 ± 0.74	0.00 ± 0.00	1.000 ns	0.34 ± 0.33	0.00 ± 0.00	0.766 ns	2.04 ± 1.03	0.00 ± 0.00	10.929 *	0.54 ± 0.25	0.00 ± 0.00	5.04*

SN, species number; H, Shannon's diversity index; RH, ratio of hygrophytes; RM, ratio of mesophytes; RX, ratio of xerophytes; RHE, ratio of heliophytes; RN, ratio of neutrophilous plants; RS, ratio of shade plants; RA, ratio of annual or biennial plants; RP, ratio of perennial plants; RV, ratio of vine; RHP, ratio of herbaceous plants; RL, ratio of ligneous plants.
ns$P > 0.05$;
*$P < 0.05$;
**$P < 0.01$;
***$P < 0.001$.

in 2007[22]. In this study, a large-area field investigation was conducted to compare species richness and composition between areas with 3- to 12-year-old poplar plantations, and areas dominated by native reeds (*Miscanthus sacchariflorus*). Additionally, fixed-plot monitoring of light availability, soil water content, and plant diversity between 6-year-old poplar plantations and reed areas was performed to eliminate the effects of topographical and environmental difference (elevation, disturbance history, and soil physical and chemical characteristics) on plant diversity[23]. This study tested the following hypotheses: 1) That plant diversity (including species number and diversity index) would be higher in poplar plantations compared to that in reed areas, and 2) that the ratio of hygrophyte and heliophyte species would be low in poplar plantations due to lower soil water content and light availability caused by tree transpiration and canopy shading, respectively.

Results

Species diversity and composition in the large-area investigation. Species number was significantly higher in poplar plantations versus reedy areas for the entire Dongting Lake area ($P < 0.01$; Table 1). Shannon's diversity indices were higher in poplar areas than in reedy areas in the East, South, and entire Dongting Lake areas ($P < 0.05$), but not different in the West Dongting Lake area ($P > 0.05$). These results suggested that poplar plantations generally resulted in higher understory plant diversity compared to that in the reed areas.

Hygrophytes were the main ecotype in reed areas in Dongting Lake (66.7–77.9%; Table 1). The ratio of hygrophytes was lower, but that of mesophytes was higher, in poplars versus reeds in the East, South, and entire Dongting Lake areas ($P < 0.01$), but not different in the West Dongting Lake area ($P > 0.05$). The ratio of xerophytes was higher in the South and West Dongting Lake area ($P < 0.05$), but not different in the East Dongting Lake area ($P > 0.05$). Poplar plantations had different effects on species composition of plant communities categorized by light requirements. For example, poplar areas had higher ratios of heliophytes and neutrophilous plants but a lower ratio of shade plants in the East Dongting Lake area, and a higher ratio of neutrophilous plants, lower ratio of shade plants, and the same ratio of heliophytes in the South Dongting Lake area, compared to composition in the reed areas. There was no significant ($P > 0.05$) difference in species composition with regard to life form and growth form, except for a higher ratio of ligneous plants in poplars versus that in reedy areas in the West and entire Dongting Lake areas ($P < 0.05$).

Species diversity and composition in monitored plots. For a given class of vegetation, species number and H were different among the four sampling periods (Fig. 1). For poplars, species number and H were higher in April versus the other three months. For reedy areas, the species number was highest in July, intermediate in October and April, and lowest in January, and H was lower in January than in the other three months. For a given month, species number and H were also different between the two vegetation types. In October, species number was higher in poplar areas (7.9) versus reedy areas (3.5), and H did not differ between the two vegetation types. In January and April, species number and H followed a similar pattern: higher in poplar areas versus reedy areas. However, in July, species number and H did not differ between the two vegetation types. Poplar plantations were therefore generally associated with a higher understory plant diversity, even when seasonal influences were taken into account.

During the monitoring period, the relative ratio of abundance for different species (composition) changed seasonally (Fig. 2). For example, the ratio of hygrophytes was higher in October (86.1%) and January (100%), but lower in April (77.0%) and July (62.4%) in reeds, whereas the ratio of mesophytes was lower in October and January, but higher in April and July in the two vegetation types ($P < 0.05$). Poplar plantations had similar effects on species composition

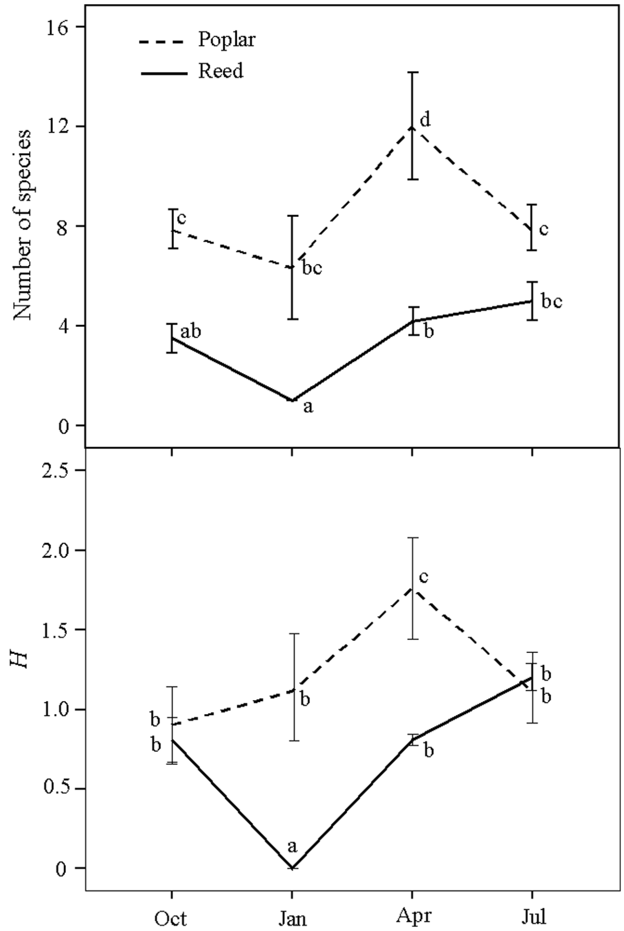

Figure 1 | Number of species and Shannon diversity index (*H*) (means ± S.E.) in poplar plantations and natural reed areas of the Dongting Lake wetlands. Different letters indicate a significant difference ($P < 0.05$).

categorized by water and light requirements as in the entire area; there were higher ratios of mesophytes and heliophytes, but lower ratios of hygrophytes and neutrophilous plants in poplar areas versus reedy areas. However, unlike reedy areas, poplar plantations had no effects on species composition with regard to life form and growth form ($P > 0.05$).

Soil water content and ratio of light availability in the monitored plots. Soil water content in the two vegetated areas showed obvious seasonal dynamics and was relatively higher from March to September, with the exception of July (Fig. 3a). During the investigation period, soil water content was higher in the reed areas versus the poplar plantations ($P < 0.05$).

From December to March, the ratio of light availability was 100% in both vegetation types (Fig. 3b). In the other months, it was higher in poplar areas versus reedy areas ($P < 0.05$). These results suggested that poplar plantations maintained higher light availability during the growing seasons compared to that found in reeds.

Discussion

Young poplar plantations supported higher understory plant diversity compared to that in reed areas, consistent with our first hypothesis. Poplar plantations have been confirmed to increase species richness in other ecosystems, such as farmlands and abandoned lands[8,9]. Establishment of fast-growing tree plantations greatly increase the structural and environmental heterogeneity due to canopy stratification[15]. Increased structural diversity in tree plantations is normally associated with increasing plant diversity[24,25].

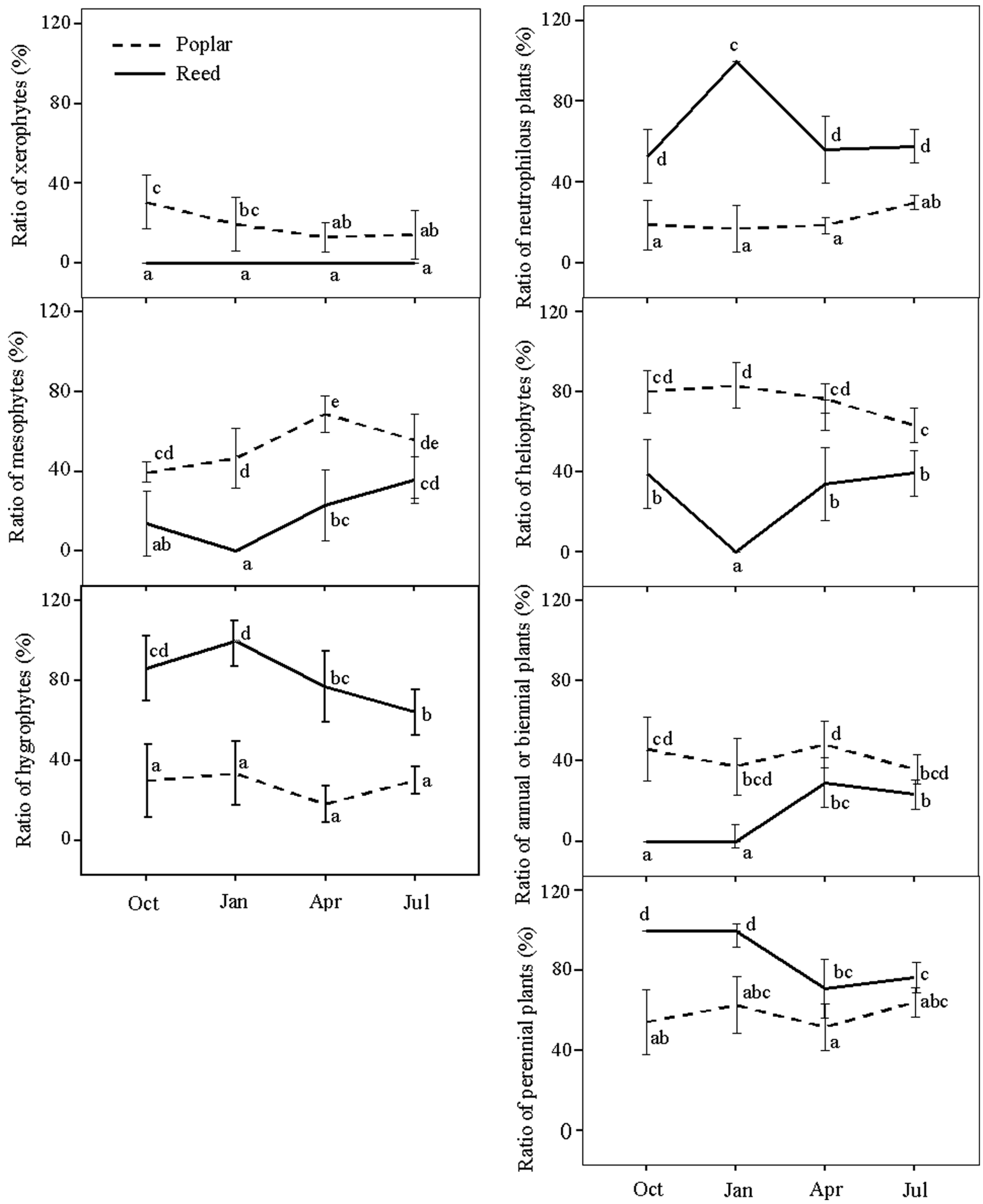

Figure 2 | Species ratios of hygrophytes, mesophytes, heliophytes, neutrophilous plants, annual or biennial plants and perennial plants (means ± S.E.) in poplar plantations and natural reed areas of the Dongting Lake wetlands. Different letters indicate a significant difference ($P < 0.05$).

In this study, the mean ratio of light availability was 1.5 times higher and soil water content was 0.7 times lower in poplar plantations versus reedy areas, indicating that more species can survive in the poplar plantation areas, leading to a higher plant diversity[9,14]. In contrast, the high stand density in reedy areas during the growing seasons not only increased plant competition for light resources but also decreased environmental diversity. In addition to increased competition for light, the relatively stable soil humidity could also promote lower plant diversity in reedy areas[26]. This would be similar to a decrease in understory species richness and plant diversity that would be expected in more mature poplar plantations with increased canopy shading[14].

Poplar plantations had different effects on species composition corresponding to water requirements, in the three parts of the Dongting Lake area: the ratio of hygrophytes was lower, but that of mesophytes was higher, in poplars versus reedy areas in the East, South, and entire Dongting Lake areas, but no different in the West Dongting Lake area. These results are partly consistent with the second hypothesis: the ratio of hygrophyte would be low in poplars versus reedy areas, and the possible reason might be the difference in elevation between the two investigated vegetation types[27,28]. In wetland ecosystems, studies have shown that elevation had a strong influence on understory vegetation due to the hydrological conditions such as soil moisture and water level fluctuations[14]. In monitored plots at the same elevation, the mean soil water content was lower in poplar areas (23.5%) versus in the reedy areas (31.3%), presumably due to higher transpiration capacity in the poplars[17]. Excessive loss of soil water might have changed wetlands to dry lands

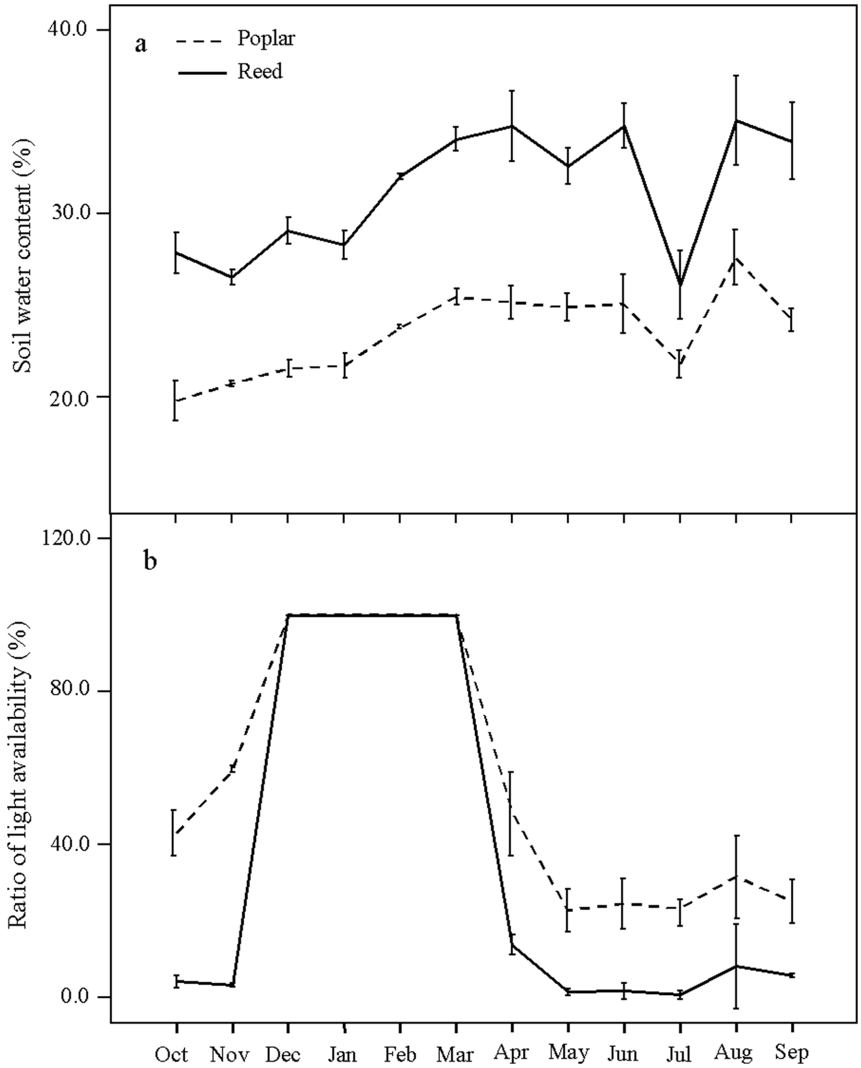

Figure 3 | Soil water content (a) and ratio of light availability (b) in poplar plantations and natural reed areas of the Dongting Lake wetlands (means ± S.E.).

and resulted in a lower ratio of hygrophytes, but a higher ratio of mesophytes or xerophytes, in the poplar areas compared to that in the reed areas.

In the Dongting Lake wetlands, poplar plantations resulted in a higher ratio of heliophytes but a lower ratio of neutrophilous or shade plants compared to those in the reed areas. These results are inconsistent with the second hypothesis, and are also inconsistent with the previously reported results from farmlands[2]. Our study clearly showed that poplar plantations resulted in a higher understory light availability in the growing seasons, which can be explained by two factors. First, a dense reed population (148,000 plants ha^{-1}) leads to a lower light availability at the ground level, which is unfavorable for the growth of heliophytes. Second, poplars in a young-aged stand have an undeveloped canopy. The understory light availability in these areas was therefore still relatively high[9]. Higher light availability in young poplar plantations is favorable for the growth of heliophytes; lower light availability in older plantations is more favorable for neutrophilous or shade plants[14].

Only a few ligneous and vine plants were recorded occasionally in the poplar areas, and the ratios of these species did not differ from those in the reed areas, except for a higher ratio of ligneous plants in the West Dongting Lake area. This result is inconsistent with previous findings in forest ecosystems, where fast-growing tree plantations, including eucalypt species, favored recolonization of ligneous plants by changing the understory microclimate, including light and water availability[29,30]. However, seasonal flooding from July to August usually led to the submergence of the investigated area. Therefore, seedlings of the ligneous plants in poplar and reedy areas might not have survived after the floodwaters receded, which might be the reason for no difference in most areas.

Although species number and Shannon's diversity were higher in young poplar versus reedy areas, poplar plantations had different effects on relative proportions of species composition: a higher ratio of mesophytes but a lower ratio of hygrophytes, and a higher ratio of heliophytes but a lower ratio of neutrophilous or shade plants. Changes in relative proportions of species also reflect the changes in understory environmental conditions. Therefore, species richness alone is incomplete and species composition of different ecotypes or life forms cannot be neglected when evaluating the extent to which understory plant diversity is affected by fast-growing tree plantations. Additionally, poplar plantations might also have far-reaching effects on the diversity of animal species. In the South Dongting Lake wetlands, poplar plantations have led to a significantly lower diversity of migratory birds[31]. Considering that it is a wetland of international importance, the Dongting Lake region should be protected by applying some measures, such as rational planning of poplar planting, wetland restoration, and water level control, to conserve the habitats of important species, and maintaining a certain

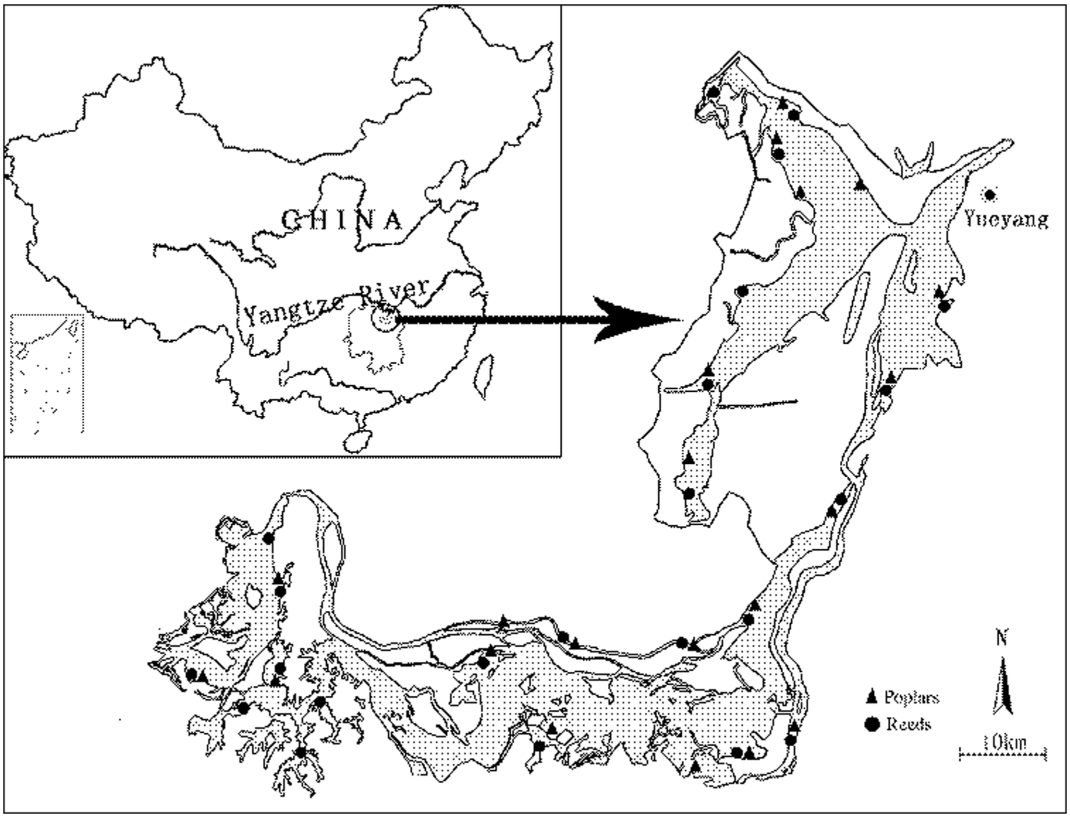

Figure 4 | Investigation plots corresponding to poplar plantations and natural reed areas in the Dongting Lake wetlands. It was generated by the authors of Xu Li and Youzhi Li using the software of Adobe Photoshop CS3.

variety of disturbances over a certain proportion of the landscape, e.g. prescribed burning, cutting, etc., might also maximize diversity.

Methods

Study sites. The Yangtze River is connected to Dongting Lake through three inlets (Songzikou, Taipingkou, Ouchikou) and one outlet (Chenglingji). Dongting Lake covers an area of 2625 km^2 (28°38′–29°45′N, 111°40′–113°10′E) and is divided into East, South, and West Dongting Lake. The lake is characterized by a subtropical monsoon climate, with an average annual temperature of 16.2–17.8°C and 259–277 frost-free days. The mean annual precipitation ranges from 1,200 to 1,415 mm, with the rainy season from April to August; average humidity is 80%, and average evaporation is 1,270 mm[32]. The annual mean wind speed is 2.0–3.0 m s^{-1}, and the elevation 28–35 m above sea level (a.s.l). Since 1970, poplars have been planted extensively in the Dongting Lake area for industrial pulp, and have now become the dominant vegetation type.

The site of the large-area investigation covered East, South, and West Dongting Lake areas. In May 2011, poplar areas were randomly chosen from map coordinates corresponding to poplar plantations with nearby natural reedy areas (controls). The reedy areas were dominated by *M. sacchariflorus*, harvested annually during November–December for making paper and germinated during March–April. A total of 21 poplar and 23 reed areas were chosen for this study. The understory reeds in poplar plantations were not harvested. The were nine poplar and nine reed areas in the East Dongting Lake area, nine poplar areas and seven reed areas in the South Dongting Lake area, and three poplar areas and seven reed areas in the West Dongting Lake area (Fig. 4). In each vegetated area, stand age was determined by questioning local inhabitants, and stand density was measured by counting. The stand age ranged from 3 to 12 years and stand density from 285 to 2,000 trees ha^{-1}.

Considering the effects of the difference in topography and environment between the investigated poplar and reed areas on plant diversity, fixed plots were chosen at the same site to monitor environmental factors (including light availability and soil water content) and plant diversity between the poplar plantations and reeds. The site of the monitored plots located on the beach of the Yangtze River, Guangxingzhou Town (29°32′N, 112°55′E), Yueyang City, Hunan Province, China and the elevation was 30 m a.s.l[17]. The site is approximately 15 km from the Chenglingji outlet and belongs to the East Dongting Lake area. In October, 2011, two vegetated areas were

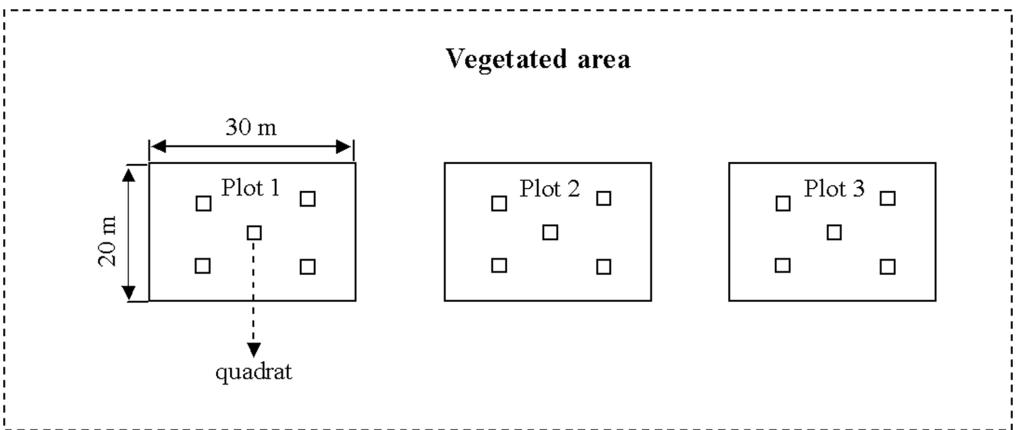

Figure 5 | Experimental design in plant species investigation in the Dongting Lake wetlands.

chosen for this study: poplar plantation (planted in 2005) and reeds. The areas covered by poplar and reeds were approximately 3 and 8 ha, respectively. The density was 148,000 plants ha^{-1} for reed and 1,666 trees ha^{-1} (in rows spaced 2 m × 4 m) for poplar plantations. Average heights were 10.5 m and 3.7 m for poplars and reeds, respectively. The average diameter at breast height (DBH) was 11.1 cm for poplar. The two vegetated areas were separated by a distance of approximately 30–40 m and lacked external disturbance except annual harvest of reeds and initial planting of poplars. Environmental conditions, including hydrological and meteorological factors, were the same in the two study areas. The soils were deposited by flooding and physical and chemical properties are similar between the two vegetated areas ($P >$ 0.05). Mean soil pH at a depth of 0–60 cm was 8.01–8.22. Total carbon, total nitrogen, total phosphorus, and total potassium were 21.59–25.25, 1.43–1.51, 0.70–0.73, and 19.35–22.51 g kg^{-1}, respectively. Before the poplar plantations were established from stem cuttings, the plant community in the study sites was occupied by reeds, including *M. sacchariflorus*, and *Phragmites australis*.

Investigation and classification of species. The nested quadrats sampling design suggested by Avery and Burkhart[33] was used to form sampling units to determine plant diversity. In each vegetated area, three plots (20 m × 30 m) with equal spacing were established as replicates. In each plot, five quadrats (2 m × 2 m) with equal spacing (5–6 m) were chosen for investigation. The total number of sampling quadrats in each vegetated area was 15 (Fig. 5). The name and number of each species at each sampling quadrat were investigated in the whole Dongting Lake wetlands in May, 2011, and were monitored in the fixed plots in October, 2011 and January, April, and July, 2012, respectively. According to habitat requirement and plant biological characteristics[34–37], plant species were classified into two ecotypes (ecotype according to water requirement: hygrophytes, mesophytes, and xerophytes; and ecotype according to light requirement: heliophytes, neutrophilous plants, and shade plants), one life form (annual or biennial plants and perennial plants), and one growth form (ligneous plants, vine, and herbaceous plants).

Measurement of community parameters, soil water content, and ratio of light availability in monitored plots. Stand density, plant height (poplar and reed), and DBH of poplars were measured for monitored plots in October, 2011. Soil samples were collected monthly from October, 2011 to September, 2012. In each plot, soil was sampled from the surface layers (0–40 cm) by using a soil sampler, according to the five-point sampling method[38]. The latitude and longitude of each soil sampling point were recorded using a global positioning system. Soils collected from each plot were mixed and stored in a bag for the measurement of soil water content by using the classical method of drying and weighing[39]. Two illuminometers were used for measuring light availability at a height of 1 m above the land, one inside the plots (L1) and the other in an open field (L2). The ratio of light availability was calculated as the ratio of L1 to L2. At monthly intervals from October, 2011 to September, 2012, 40 paired points were measured in each plot.

Statistical analysis. Plant diversity was evaluated using species richness and Shannon's diversity index (H). Species richness was calculated as species number per sampling quadrat in each vegetated area[2,40]. Shannon's diversity index (H) was calculated using the following equation[40]:

$$H = -\sum_{i=1}^{N} pi \ln pi,$$

where N is species number, *pi* the ratio of species *i* to the total number of species.

Species ratio was calculated as the ratio of the species number of a target ecotype or life form to the total species number in each sampling quadrat.

In the large-area investigation, species number, H index, and ratios of hygrophytes, mesophytes, xerophytes, heliophytes, neutrophilous plants, shade plants, annual or biennial plants, perennial plants, vine, herbaceous plants, and ligneous plants in the East, South, West, and total Dongting Lake were analyzed using analysis of variance (ANOVA) general linear modeling (GLM), due to hydrological differences in the three parts of Dongting Lake.

In the monitored plots, seasonal mean species diversity and composition were compared using Tukey's test at the 0.05 significance level. Homogeneity of variances was tested using Levene's test, and data were $\log_{10}$- or square root-transformed where necessary to reduce any significant heterogeneity of variances. There was back-transformation of data presented in the figures and tables. All statistical analyses were performed using SPSS V17.0 software (SPSS Inc., USA).

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Author contributions

Y.L., X.C. and Y.X. designed the study. Y.L., X.L. and F.L., performed the field large-area investigations, Y.L., X.C. and Z.H. conducted the fixed-plots monitoring. All authors wrote the manuscript.

Additional information

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