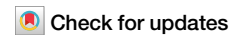


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# Water-surface photovoltaic systems have affected water physical and chemical properties and biodiversity

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The implementation of water-surface photovoltaic systems as a source of renewable power has expanded rapidly worldwide in recent decades. Water-surface photovoltaic avoids negative impacts on terrestrial ecosystems, while the impacts on aquatic physical and chemical properties and biodiversity are unclear. To understand the ecological and environmental impacts of water-surface photovoltaic systems, here we conducted a field survey on water physical and chemical properties, plankton and bird communities of 26 water-surface photovoltaic systems in the Yangtze River basin in China during the winter and summer of 2022. We found that water-surface photovoltaic systems decreased water temperature, dissolved oxygen saturation and uncovered area of the water surface, which caused a reduction in plankton species and individual density, altering the community composition. Water-surface photovoltaic systems also caused an overall decrease in bird diversity and changed bird community compositions. These findings suggested that water-surface photovoltaic systems have impacts on the water environment and ecology. Since water-surface photovoltaic systems will continue to expand in the future, our results emphasize that rational planning is critical for the sustainable development of water-surface photovoltaic systems and the protection of the aquatic environment and biodiversity.

The use of renewable energy sources has gained increasing attention worldwide in recent decades<sup>1</sup>. Especially in recent years, the photovoltaic (PV) industry has been substantially advanced, and the contribution of PV systems to the renewable energy sector is expected to continue to grow rapidly in the future<sup>2,3</sup>. At present, PV systems are typically constructed on land. However, terrestrial PV plants occupy large areas of land and can negatively impact local biodiversity and ecosystem services<sup>4,5</sup>. To avoid negative impacts of PV system on terrestrial ecosystems, water-surface photovoltaic (WSPV) systems, in which PV panels are installed on the water surface, have become the fastest-growing power generation technology in the past decades<sup>6,7</sup>. The global installation capacity of WSPV systems has been expanding rapidly by over 40 times, from 68 MW in 2015 to 3 GW at the end of 2020, and the deployment continues to accelerate as the technologies mature<sup>8</sup>.

Compared with traditional ground-mounted PV systems, WSPV systems have many advantages, including avoiding the need for land acquisition and site preparation<sup>9–11</sup>, reducing water evaporation losses and

thus saving water resources, and improved power efficiency due to the cooling effect by water evaporation<sup>6,12,13</sup>. Consequently, WSPV systems provide enormous opportunities for the global expansion of solar energy capacity<sup>7,13</sup>. As an emerging technology for exploiting solar energy on waterbodies, WSPV systems undoubtedly avoid the impacts of traditional PV arrays on terrestrial ecosystems, yet they may impact the physical and chemical features of water and aquatic organisms, but these impacts are largely unknown<sup>14,15</sup>. Most studies on WSPV systems have focused on engineering feasibility, and few have explored the impacts on the aquatic environment and biodiversity<sup>1,16</sup>.

Large areas of PV panels cast shadows on the water surface and thus can reduce light availability to waterbodies, and floating materials on the water surface reduce contact between the air and waterbody, which may lead to reductions in water temperature and dissolved oxygen<sup>17,18</sup>. These changes might impact aquatic organisms. Many waterbodies are habitats for birds, including some threatened species, such as *Mergus squamatus* and *Aythya baeri*<sup>19</sup>. Large areas of PV panels on water occupy habitats for birds; human

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activities associated with WSPV system maintenance may also disturb birds and their habitats<sup>20</sup>. Clarifying the potential impacts of WSPV systems on the aquatic environment and biodiversity will enable the integration of conservation measures into WSPV system development plans. However, although some studies have investigated the impacts of WSPV systems on aquatic organisms, these have generally focused on the function of PV panel coverage in inhibiting algae growth and thus reducing the risk of bloom outbreaks<sup>21,22</sup>. Some studies have indicated that WSPV systems can impact water quality (e.g. decrease water temperature and dissolved oxygen concentration), but these studies were conducted using model simulations or were based on surveys at a local scale<sup>17,23</sup>. Hence, the impacts of WSPV systems on water environments and biodiversity are still unclear. Due to the lack of a comprehensive understanding of the ecological impacts of WSPV systems, mitigation measures for adverse impacts have been absent from project designs, potentially exacerbating the impacts on ecologically vulnerable waterbodies<sup>24–26</sup>.

China is the country with the largest area of PV installations in the world<sup>1</sup>. Supported by policies and funding from the government, the installation of WSPV systems has expanded rapidly, reaching 960 MW in 2018, which was 73% of the global total capacity<sup>27</sup>. China's large area of waterbodies, including lakes and reservoirs, also gives it a high potential for future WSPV installations<sup>12</sup>. To understand the impacts of WSPV systems on the aquatic environment and biodiversity, we investigated physical and chemical features of the water and community structure and diversity of plankton (including phytoplankton, microzooplankton, and macrozooplankton) and birds in the waterbodies of 26 WSPV plants in the Yangtze River basin, the most concentrated area of WSPV systems in China<sup>28</sup>. The physical and chemical properties of water directly reflect the impacts of WSPV systems on water environmental conditions<sup>29</sup>. Plankton plays a pivotal role in material recycling and energy flow in aquatic ecosystems<sup>30,31</sup>. Moreover, plankton is sensitive to changes in the water environment and is thus an important indicator of water quality<sup>32,33</sup>. Birds can move long distances, however their diversity and community traits are indicators of local habitat conditions<sup>34</sup>. In the Yangtze River basin, many waterbodies are important habitats for migratory waterbirds along the East Asia-Australasian Flyway<sup>35</sup>.

At each site, we conducted surveys in three areas: the photovoltaic area (PA), the area near the photovoltaic area (NPA) within the same waterbody, area in a different waterbody without photovoltaic panels (CA). WSPV systems can be floating photovoltaic systems (FPVs, PV panels are installed on floating materials on the water surface) or pile-mounted photovoltaic systems (PMPVs, PV panels are fixed on top of piles instead of floating on the water surface). FPV and PMPV systems cover the water surface in different ways<sup>36</sup>, so their impacts on aquatic ecosystems can differ. We compared the ecological impacts of the FPV and PMPV systems on the physical and chemical properties and biodiversity of the waterbodies. We hypothesise that WSPV systems impact on the physical and chemical properties of waterbodies, alter species diversity and community composition of plankton and birds in the region, and that the impacts differ between the FPV and PMPV systems. To our knowledge, this is the most comprehensive study to date on the impacts of WSPV systems on the aquatic environment and biodiversity. Thus, our work makes a substantial contribution to the scientific understanding of the ecological consequences of WSPV systems, which have been largely ignored.

## Results

We surveyed 26 WSPV systems in the Yangtze River basin in China during the winter (January) and summer (July) of 2022 (Fig. 1). At each site, we collected water and plankton samples at three areas of PA, NPA and CA. Because the areas of PA and NPA were in the same waterbody and birds have many activities, we merged the bird records from the PA and NPA (PA + NPA) within each waterbody. We explored the impacts of WSPV systems on water physical and chemical properties, plankton, and birds.

## WSPV systems decreased water temperature and dissolved oxygen saturation

We first detected how the presence of WSPV panels altered water physical and chemical properties by comparing water samples collected in the PAs, NPAs, and CAs. Analysis of variance (ANOVA) indicated that water temperature (T) and dissolved oxygen saturation (DO%) were significantly higher in the CAs than in the PAs in both seasons of the WSPV system (for FPV and PMPV systems combined) ( $p < 0.05$ , Fig. 2, supplementary Table 3). T and DO% were also higher in the CAs than in the NPAs, but the difference was not significant ( $p > 0.05$  for both, Fig. 2). There was no significant difference in pH or the concentrations of total nitrogen (TN), total phosphorus (TP), and ammonia nitrogen ( $\text{NH}_3\text{-N}$ ) among the three areas, except that TP ( $p = 0.02$ ) and  $\text{NH}_3\text{-N}$  ( $p = 0.04$ ) were significantly higher in the CAs than in the PAs in winter (Fig. 2, supplementary Table 2). The trends were similar in the three types of areas for the FPV and PMPV systems separately in summer and winter (supplementary Table 2). There was no significant difference in water physical and chemical properties between the FPV and PMPV systems in the PAs in both seasons ( $p > 0.05$  for all), except that T ( $p = 0.003$ ) and DO% ( $p < 0.001$ ) were significantly higher in the PMPV systems in winter (supplementary Table 4).

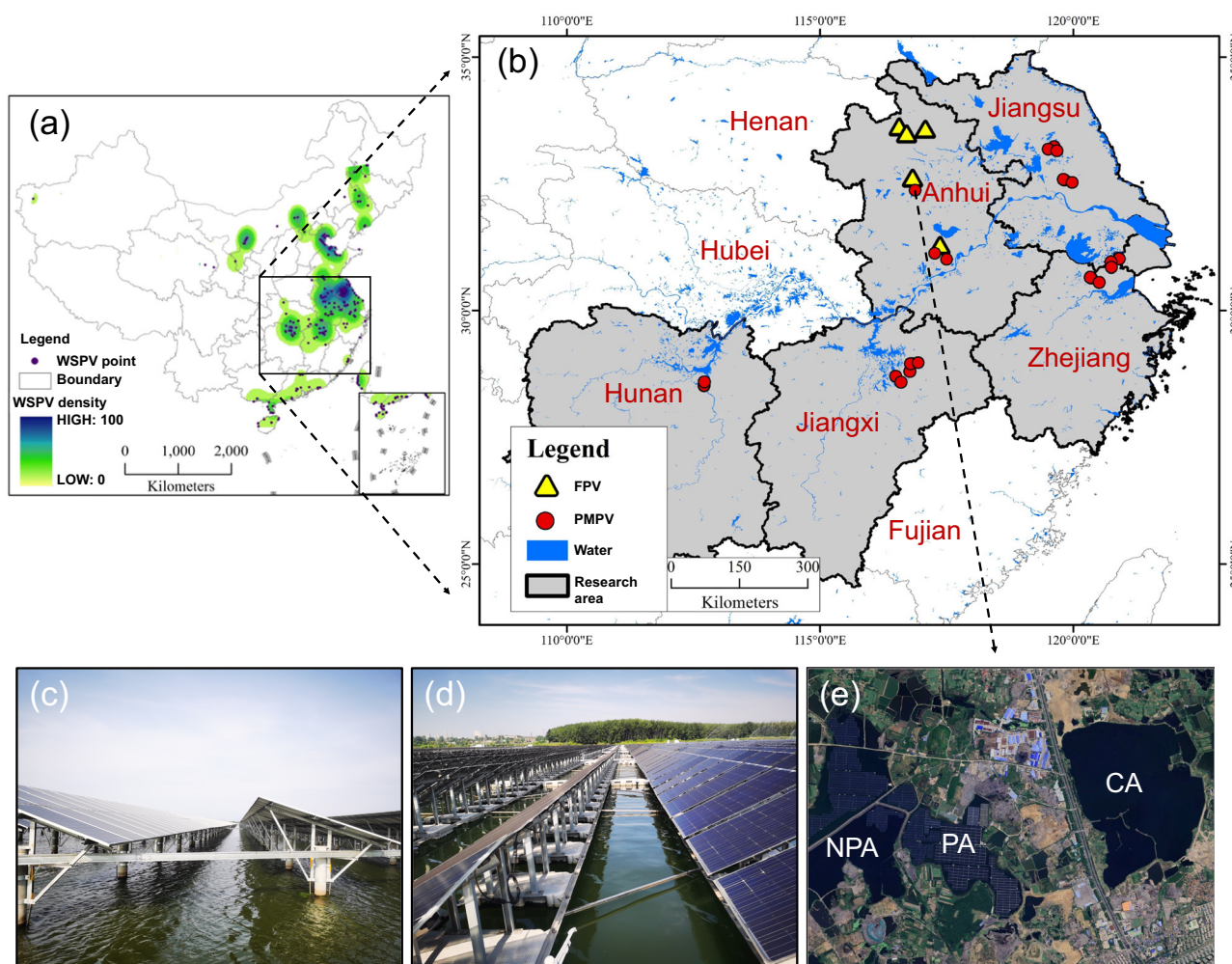
The average uncovered area of the water surface (UCA), in terms of the proportion of water surface that was not covered by PV panels, was  $38 \pm 4\%$  (ranging from 1% to 78%, supplementary Table 1) in the PAs. The UCA was significantly lower for the FPV systems ( $17 \pm 10\%$ ) than for the PMPV systems ( $43 \pm 4\%$ ) ( $p = 0.04$ ).

## WSPV systems altered the community composition of plankton

We detected the impacts of WSPV systems on plankton communities by examining three plankton types (phytoplankton, microzooplankton, and macrozooplankton) in the PAs, NPAs, and CAs. A total of 117 taxa from three types of plankton, including 71 phytoplankton genera from seven phyla (supplementary Table 5), 30 microzooplankton species from nine families and 17 genera (supplementary Table 6), and 16 macrozooplankton species from eight families and 12 genera (supplementary Table 7), were identified. *Microcystis* spp. was the most abundant taxa of phytoplankton in both seasons; *Diurella rousseleti* was the most abundant microzooplankton in summer and *Brachionus budapestiensis* in winter; and *Daphnia pulex* and *Mesocyclops leuckarti* were the most abundant macrozooplankton in summer and *Mesocyclops leuckarti* in winter.

Species richness and the individual density for each of the three plankton types were significantly lower in the PAs than in the CAs in both seasons ( $p < 0.05$  for all), except for the difference in species richness of phytoplankton in summer, which was marginally significantly ( $p = 0.07$ ) lower in the PAs than in the CAs (Fig. 3a, b, e, f, i, j; supplementary table 3). The individual density of the three plankton types also tended to be lower in the NPAs than in the CAs in the same season (Fig. 3b, f, j). Moreover, the individual densities of abundant phytoplankton genera (>5% of the total individuals) were significantly lower in the PAs than in the NPAs or CAs in either season ( $p < 0.05$  for all), except for *Oscillatoria* ( $p = 0.20$ ) and *Merismopedia* ( $p = 0.30$ ) in summer, and *Pseudanabaena* ( $p = 0.23$ ) in winter (supplementary Fig. 1). The phytoplankton and microzooplankton species richness and individual densities in winter and the phytoplankton individual densities in summer in PAs were significantly higher in the PMPV than FPV systems ( $p < 0.05$  for all), while macrozooplankton were not significantly different between the two systems in both seasons (supplementary table 4).

The Shannon–Wiener and Pielou evenness indices for each of the three plankton communities were significantly higher or tended to be higher in the PAs than in the NPAs and CAs in summer, while they tended to be lower or not significantly different among the three areas in winter (Fig. 3c, d, g, h, k, l). The values of these indices were consistent between the FPV and PMPV systems in both seasons. However, the species richness and individual densities of the three plankton types tended to be higher in the PMPV than



**Fig. 1 | The surveyed region and the distribution of water-surface photovoltaic (WSPV) systems in China and the sampling sites in the middle and lower reaches of the Yangtze River.** **a** Density of water-surface photovoltaic (WSPV) systems in China (data from Zhang et al. 2022). **b** Locations of the 26 waterbodies with WSPV systems sampled in this study, including five floating photovoltaic (FPV) systems

and 21 pile-mounted photovoltaic (PMPV) systems. **c, d** Photograph of a pile-mounted photovoltaic system and floating photovoltaic system. **e** Image (earth.-google.com, image taken in January 2021) showing the three types of areas sampled taken in Liugangtang, Huainan, Anhui Province (PA: photovoltaic area, NPA: near the photovoltaic area, CA: control area).

in the FPV systems (supplementary Table 4). There was no significant difference in the Shannon–Wiener and Pielou evenness indices for each of the three plankton communities between the FPV and PMPV systems in both seasons ( $p > 0.05$ ), except for phytoplankton indices were significantly higher in the PMPV than FPV systems in winter ( $p < 0.05$ , supplementary Table 4).

Nonmetric multidimensional scaling (NMDS) analysis indicated that each of the three plankton communities differed significantly between the PAs, NPAs, and CAs in both seasons (stress = 0.087 ~ 0.182, Fig. 4). Analysis of similarity (ANOSIM) further indicated that the community composition of the three plankton communities differed significantly between the PAs and CAs in both seasons ( $p < 0.05$  for all; supplementary Table 9). The three plankton communities in summer and the phytoplankton community in winter also differed significantly between the PAs and the NPAs ( $p < 0.05$  for all; supplementary Table 9). The community composition of the three plankton differed significantly between the FPV and PMPV systems in both seasons ( $p < 0.05$  for all; supplementary Fig. 2, supplementary Table 9).

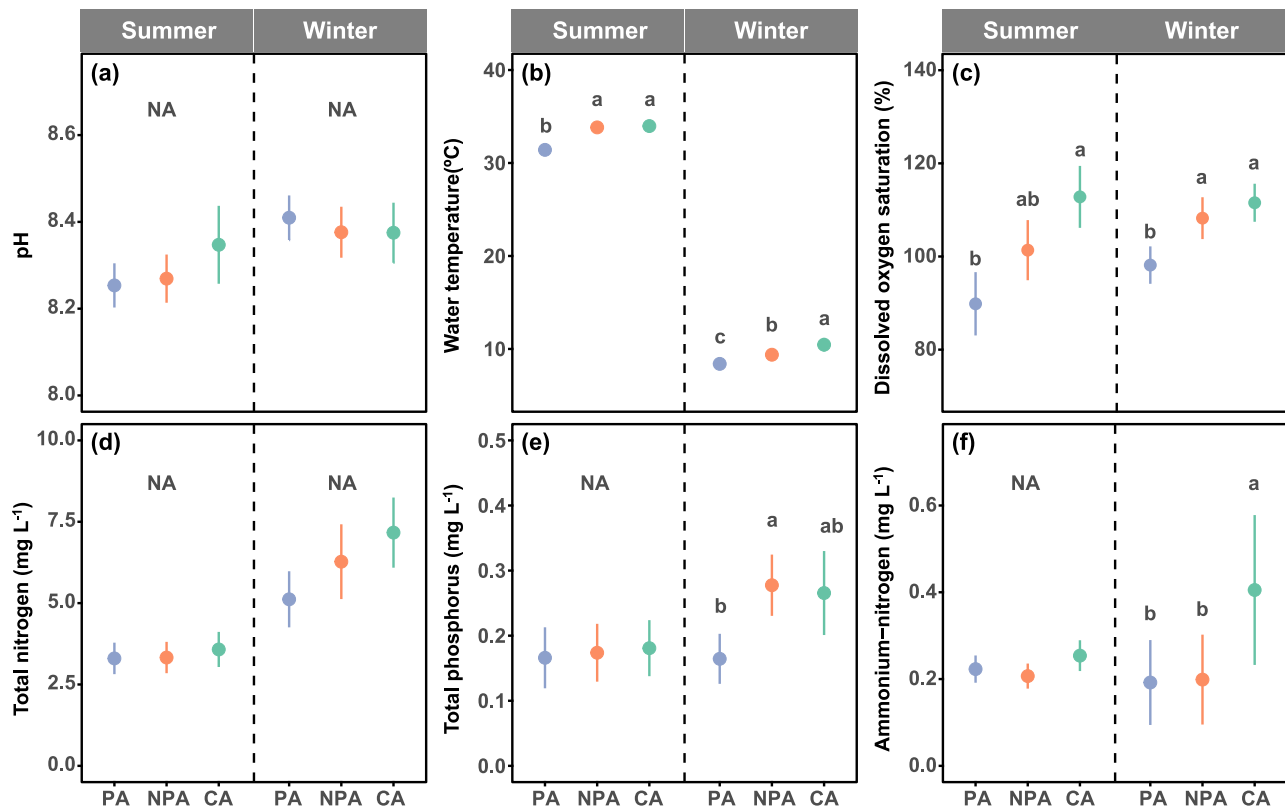
Redundancy analysis (RDA) indicated that the species richness, individual density, and Shannon–Wiener diversity index of the three plankton communities were closely related to the physical and chemical properties of the waterbody in both seasons (Fig. 5a–f, supplementary Table 10). Spearman correlation analysis also showed that generally, the species richness and

individual density of the three plankton groups were positively related to the physical and chemical properties of the waterbody (Fig. 5g, h). However, linear regression indicated that the differences in T, DO%, and plankton community indices between the PAs and CAs at each site were not significantly correlated with the UCA of the waterbody in either season, except for macrozooplankton species richness which was positively correlated with UCA in winter ( $R^2 = 0.11$ ,  $p = 0.02$ ) (supplementary Fig. 3). We found that the concentration of nutrients (TN, TP and  $\text{NH}_3\text{-N}$ ) and pH was less strongly correlated to the plankton community indices than other water physical and chemical properties, especially in winter (Fig. 5g, h). Moreover, the species richness and individual density of phytoplankton were significantly correlated with that of microzooplankton in both seasons, and they both were significantly correlated with the species richness and individual density of macrozooplankton in summer (Fig. 5g, h).

### WSPV systems decreased the diversity and altered the composition of bird communities

We detected the effects of WSPV systems on bird communities by conducting bird surveys in the PA+NPAs and CAs. A total of 5964 individuals belonging to 42 species were recorded, including 1407 individuals belonging to 22 species in summer and 4557 individuals belonging to 34 species in winter (supplementary Table 11). In both seasons, fewer species and individuals were recorded in the PA+NPAs (1089 individuals in 26 species)





**Fig. 2 | Variation in water physical and chemical properties in the three types of areas sampled in summer ( $n = 25$ ) and winter ( $n = 26$ ) in WSPV systems. a pH. b Water temperature. c Dissolved oxygen saturation. d Total nitrogen. e Total phosphorus. f Ammonium-nitrogen. In the same season, different letters show**

significant differences among the three areas (Wilcoxon test;  $p < 0.05$ ), NA: not significant. PA: photovoltaic area, NPA: near the photovoltaic area, CA: control area. Points with error bars are means and standard errors. The blue, orange, and green dots represent the values in the PAs, NPAs, and CAs, respectively.

than in the CAs (4875 individuals in 35 species). In the CAs, waterbirds were the overwhelming majority, accounting for 94% of the total species (33 of 35) and 98% of the total individuals (4780 of 4875); while only 2 species of land birds (*Cecropis daurica* and *Hirundo rustica*, 95 individuals) were recorded. In the PA+NPAs, 23% of the total species (6 of 26) and 13% of the total individuals (140 of 1089) were land birds (supplementary Fig. 4); all were recorded resting or foraging on PV modules. In summer, five waterbird species (*Podiceps cristatus*, *Tachybaptus ruficollis*, *Gallinula chloropus*, *Chlidonias hybrida*, and *Hydrophasianus chirurgus*) were recorded nesting in eight CAs, while no waterbirds nested in the PA+NPAs.

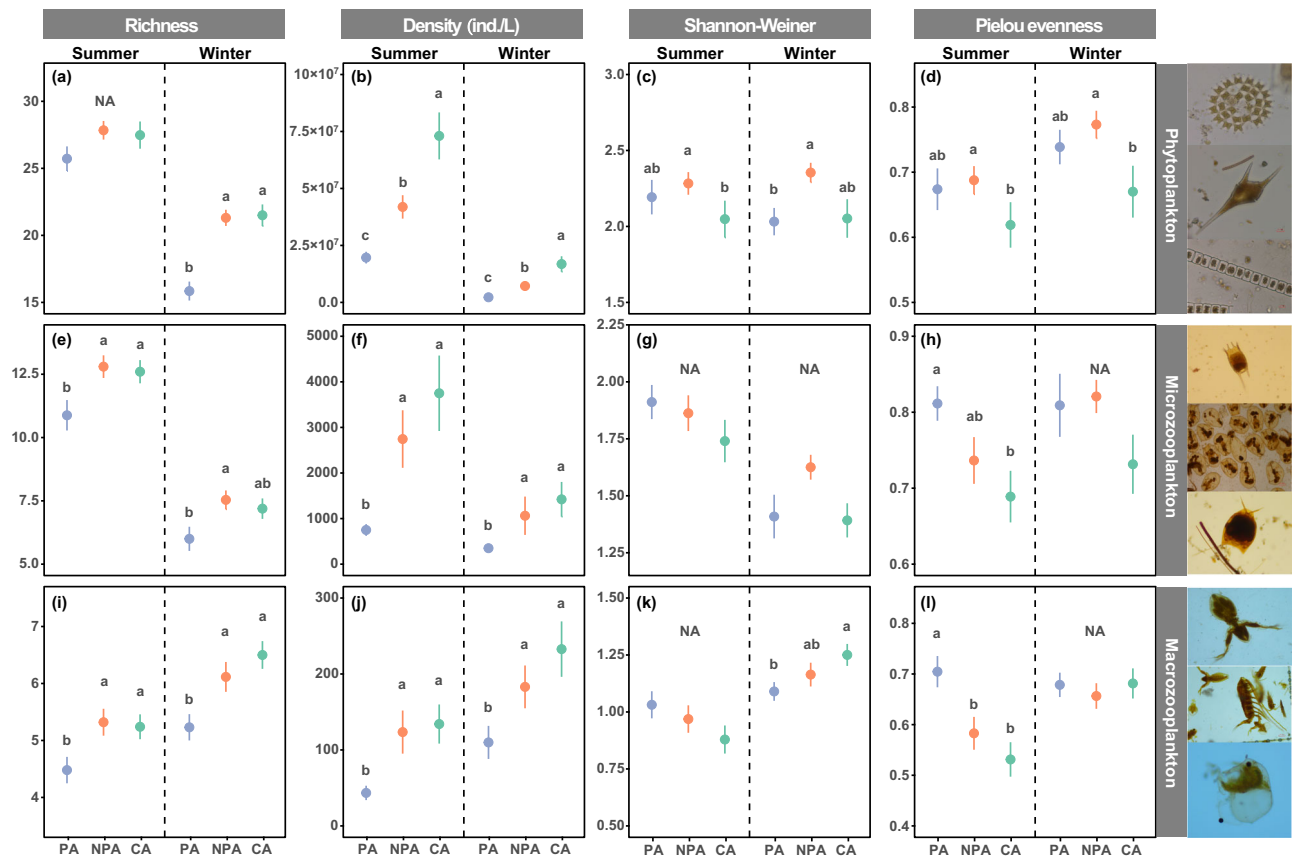
Bird species richness, individual density, and the Shannon–Wiener diversity index were significantly lower in the PA+NPAs than in the CAs in both seasons ( $p < 0.05$  for all; supplementary Table 3), except for the difference in Shannon–Wiener diversity index in winter ( $p = 0.12$ ), while there was no significant difference in the Pielou evenness index between the PA+NPAs and the CAs ( $p = 0.45$  in summer and  $0.39$  in winter) (Fig. 6a–d). The same trends in bird community traits between the PA+NPAs and the CAs were observed for both the FPV and PMPV systems (supplementary Table 12). There was no significant difference in bird community indices between the FPV and PMPV systems in both seasons ( $p > 0.05$  for all; supplementary Table 4).

NMDS indicated that bird community structures differed significantly between the PA+NPAs and CAs in both seasons (stress = 0.133 in summer and 0.116 in winter, Fig. 6e, f). ANOSIM also indicated that there was a significant difference in the species composition of bird communities between the two areas ( $R = 0.27$  in summer and  $0.10$  in winter,  $p < 0.05$  for both). All these indicated that WSPV systems decreased the diversity and altered the composition of bird communities.

## Discussion and conclusion

Because WSPV systems are an important avenue for future clean energy use<sup>16</sup>, it is essential to understand their potential impacts on ecology and biodiversity. Our surveys on 26 WSPV systems in the Yangtze River basin in China indicated that WSPV systems led to decreases in the UCA, T, DO%, and in the diversity of plankton and waterbirds. The overall species richness and individual densities of birds were lower in the PA+NPAs than in the CAs, and waterbirds were not seen nesting in waterbodies with WSPV systems. Moreover, the plankton and bird communities in the waterbodies with WSPV systems differed significantly from those in the CAs. FPV systems exhibited lower T, DO%, phytoplankton and microzooplankton community indices than the PMPV systems. These results suggest that WSPV systems have impacts on the aquatic environment and biodiversity and that the impacts were not limited to the area covered by the PV panels but extended to surrounding areas in the same waterbody.

We found that WSPV systems led to decreases in the T and DO% of waterbodies in both seasons, which is consistent with previous experimental studies and model predictions<sup>17,23</sup>. The decreased light radiation due to shading from the PV modules<sup>37</sup> might be the main cause of decreased T around WSPV systems. Temperature impacts the growth and reproduction of plankton, and we found a significant relationship between T and the plankton densities in this study. DO% in water originates from the diffusion of oxygen in the air and photosynthesis by aquatic plants and phytoplankton<sup>38</sup>. PV modules in FPV or PMPV systems can attenuate the turbulence of wind moving across water, and FPV modules can also reduce the contact area between air and water; both of these phenomena reduce the transfer of oxygen from the air into the water. The shading created by PV modules also reduces the oxygen produced by photosynthesis in aquatic



**Fig. 3 | Variation in phytoplankton, microzooplankton and macrozooplankton community indices and individual density in the three types of areas sampled in summer ( $n = 25$ ) and winter ( $n = 26$ ) in WSPV systems (FPV and PMPV systems). a, e, i Species richness. b, f, j Individual density. c, g, k Shannon–Wiener**

diversity index. d, h, l Pielou evenness index. In the same season, different letters indicate significant differences among the three types of areas sampled (Wilcoxon test;  $p < 0.05$ ), NA: not significant. PA: photovoltaic area, NPA: near the photovoltaic area, CA: control area. Points with error bars are means and standard errors.

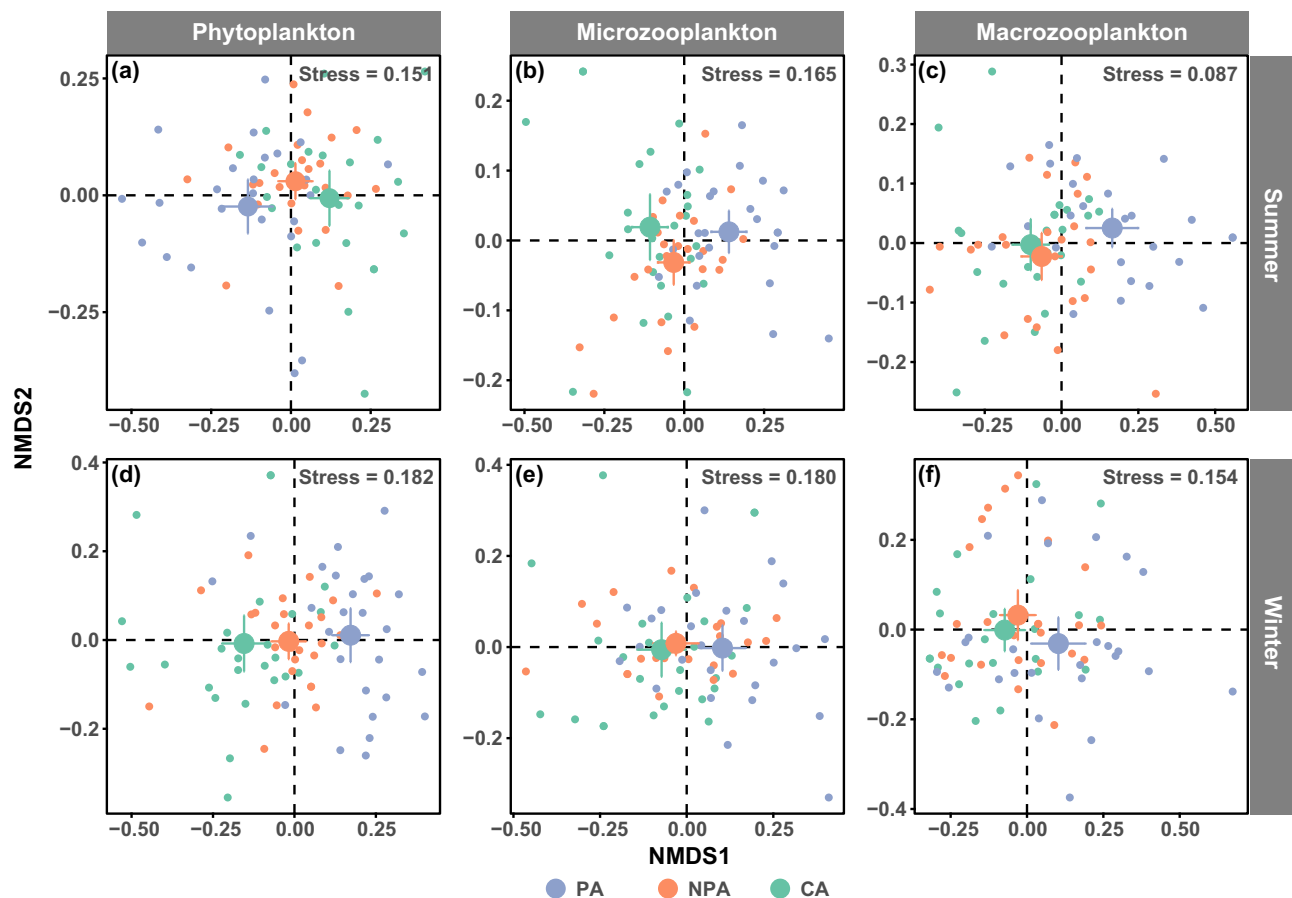
plants and phytoplankton<sup>22</sup>. Many waterbodies in the Yangtze River Basin were used for aquaculture<sup>19</sup>. We found that TP and  $\text{NH}_3\text{-N}$  were significantly higher in the CAs than in the PAs in winter. This may be because of the feed input for aquaculture can increase the nutrient content of waterbodies. WSPV facilities are inconvenient for aquaculture management, which might decrease the amount of feed input in the waterbodies with WSPV systems.

Our results indicated that the species richness and densities of phytoplankton, microzooplankton, and macrozooplankton decreased in the PAs, and these decreases were closely related to the environmental changes induced by the WSPV systems, including decreased UCA, T and DO%. All of these changes could affect the growth and reproduction of plankton<sup>39,40</sup>. We found that UCA was generally positively related to the phytoplankton densities, but not all phytoplankton taxa had reduced in the PAs with low UCA. This may be related to the different optimum light demands between phytoplankton groups, which closely related to their ecological habits and adaptive capacity to environmental changes<sup>41,42</sup>. In general, when environmental factors lead to a decrease in light radiation in waterbodies, phytoplankton growth is limited, and lower light availability corresponds to lower phytoplankton biomass<sup>43,44</sup>. However, this is not the case for all phytoplankton taxa, and phytoplankton with low light demand may be less affected when light decreases, and may even be more viable due to the declining biomass of high light-demanding phytoplankton<sup>41,44</sup>. The abundant phytoplankton taxa with significantly lower density in the PAs than CAs (e.g. *Microcystis*, *Cryptomonas*, and *Coelastrum*), were those with high light demands, while the groups with non-significant differences in density between the PAs and CAs (*Pseudanabaena*, and *Oscillatoria*) were those with low light demands (supplementary Fig. 1)<sup>41,45</sup>. Moreover, changes in phytoplankton communities can also be transferred along food chains,

impacting microzooplankton and macrozooplankton at higher trophic levels.

In our study area, nutrient concentration had relatively weaker impacts on plankton diversity than other water physical and chemical properties (DO%, UCA, and T). This may be because of the nutrient enrichment of the waterbodies from the well-developed agriculture and aquaculture in the study area<sup>18,46</sup>, thus nutrients were not the main limiting factor for the growth and reproduction of plankton. Although the species richness and individual densities of all three plankton groups were low in the PAs, the Shannon–Wiener diversity and Pielou evenness indices were generally higher in the PAs than in the NPAs or CAs in summer. This may be attributed to the fact that adverse water conditions created by WSPV systems suppress the population growth of abundant groups (e.g. *Microcystis* spp. in Cyanobacteria)<sup>22,47</sup>, thus resulting in higher abundance-based Shannon–Wiener diversity and Pielou evenness indices in the PAs. In the three areas of both WSPV systems, the abundant species and groups in the three plankton communities (e.g. *Microcystis* spp., *Diurella rousseleti*, and *Daphnia pulex*) were all indicators of eutrophic conditions<sup>48</sup>, which is associated with the nutrient enrichment of the waterbodies in the study area<sup>49</sup>. Although WSPV systems have the potential to mitigate the risk of bloom outbreaks to some extent<sup>29</sup>, WSPV systems do not decrease the nutrient concentrations in waterbodies, therefore cannot solve the problem of eutrophication.

We found that both FPV and PMPV systems caused a decrease in T, DO%, UCA, and plankton diversity of waterbodies, with a sharper decrease than in the FPV than PMPV systems. This could be because the pontoon and mooring components of the FPV system are placed on the water surface, which impedes contact between the air and water and thereby reduces the effect of wind turbulence on the water, thus reducing the transfer of



**Fig. 4 | Nonmetric multidimensional scaling (NMDS) plot of the phytoplankton, microzooplankton and macrozooplankton communities among the three areas based on their community structures in summer ( $n = 25$ ) and winter ( $n = 26$ ). a, d Phytoplankton. b, e Microzooplankton. c, f Macrozooplankton. The light points**

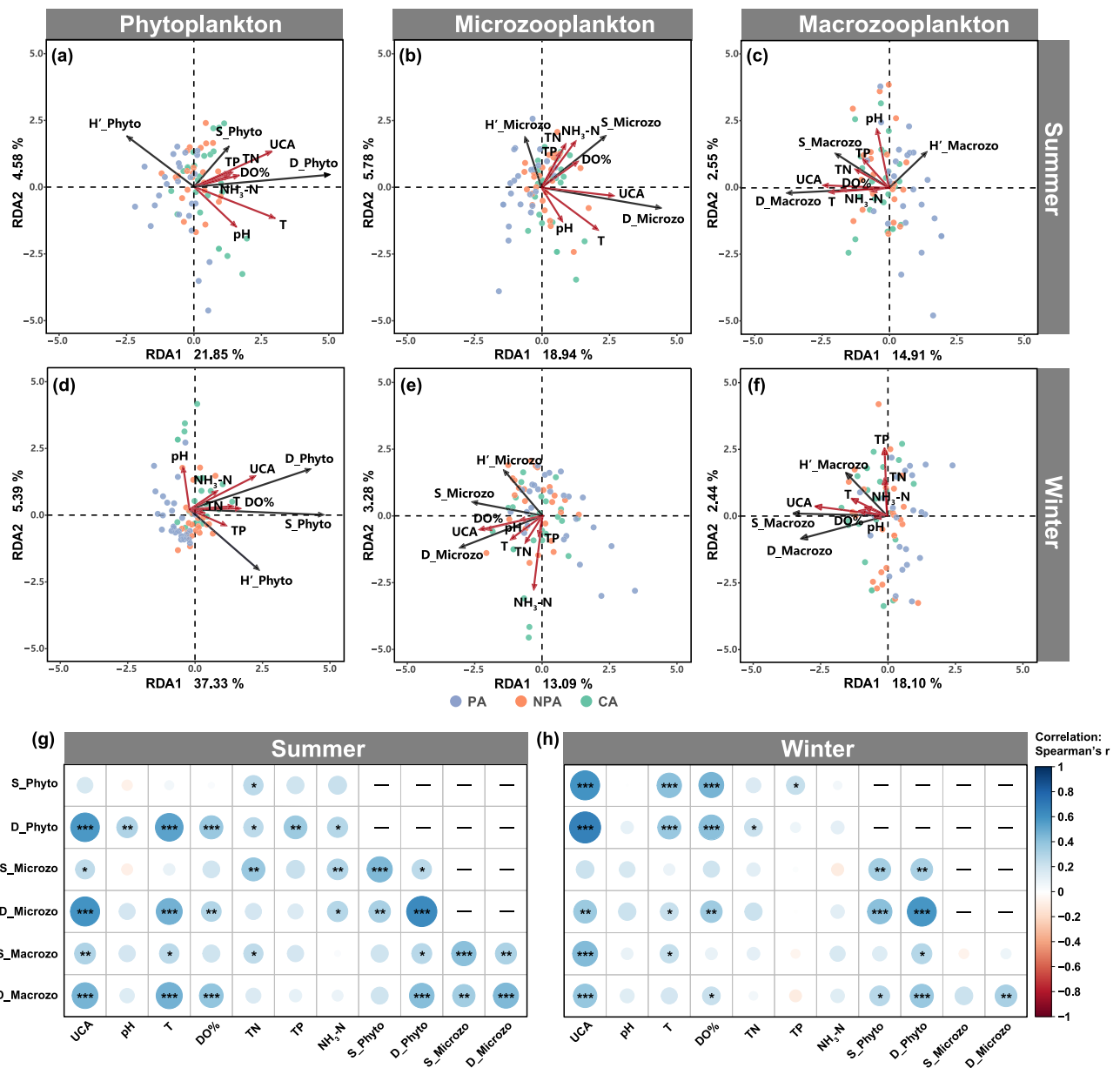
exhibit the raw data. Points with error bars are means and associated 95% confidence intervals of the data. The blue, orange, and green dots represent the photovoltaic areas (PAs), near the photovoltaic areas (NPAs) and control areas (CAs), respectively.

oxygen and heat from the air into the water<sup>14,38</sup>. In addition, compared with PMPV systems, FPV systems have additional components, including pontoons, floats, mooring systems and connectors, and thus have higher coverage, further reducing the amount of light radiation that enters the water<sup>24</sup>. The T, DO% and UCA in the water largely affect the reproduction and growth of aquatic organisms, and thus affect the diversity and composition of aquatic communities. Actually, FPV were not a common WSPV system in the study region. All the five FPV systems were located in Anhui province (supplementary Table 1). We found that the plankton individual densities at the NPAs and CAs of the FPV systems were also less abundant than those of the PMPV systems in both seasons (supplementary Table 8). Thus, the higher plankton individual densities in PMPV than FPV systems might be due to different waterbody conditions among sites.

Earlier model simulations have predicted that the impacts of WSPV systems can be limited when PV panel coverage is low<sup>17,22</sup>. However, we found the differences in water physical and chemical properties and plankton community indices in the PAs and CAs were not related to the UCA in both seasons, suggesting that even high UCA can significantly affect waterbodies (supplementary Fig. 3). This could be because most PV panels are not arranged flat but with a southward inclination angle to maximize solar radiation conversion and power generation per unit area of the PV system; thus, PV panels can be illuminated perpendicularly<sup>50</sup>. This arrangement greatly increases the shading by PV panels, resulting in the sunlight shining area on waterbodies being much smaller than the UCA. This suggests that the UCA largely underestimates the effects of WSPV systems on waterbodies. The shading area of the PV panels on water surfaces is the most suitable metric to measure the effects of WSPV systems.

Waterbirds are highly dependent on wetlands for nesting, feeding, and resting<sup>35</sup> and thus are susceptible to wetland habitat changes by the introduction of WSPV systems<sup>20</sup>. In the PV areas, we found decreased species richness and individual densities of waterbirds, no nesting waterbirds, and altered community composition. These changes may be related to habitat occupation and landscape changes due to the presence of PV modules and disturbances from routine PV management. The increased land bird abundance in the PV areas may be attributed to the attractiveness of the dark-coloured solar panels to insects<sup>51</sup>, providing prey for insectivorous land birds. This is consistent with the foraging behaviour of birds on PV panels. The decreased waterbird diversity suggests that WSPV systems largely impact this community. Because both FPV and PMPV systems had similar impacts on bird communities, we suggest that regardless of the PV system types, WSPV systems should be installed at suitable sites and scales, and avoiding critical habitats for waterbirds.

The changed water physical and chemical properties and plankton and bird communities can further impact ecosystem stability and resiliency. WSPV systems are often situated in waterbodies with limited flow, such as lakes, reservoirs, and coal mining subsidence wetlands<sup>24,52</sup>, making it difficult to mitigate the impacts of WSPV systems through water exchange. Therefore, the cumulative effects of these impacts are likely to intensify over time. While flowing waterbodies, such as rivers, may mitigate the cumulative effects of WSPV systems, they are often unsuitable for WSPV system installation due to their size or management requirements (e.g. flooding). Additionally, waterbodies serve various functions, such as water supply, aquaculture, recreation, and flood control. Although WSPV systems can spatially coexist with other functions,



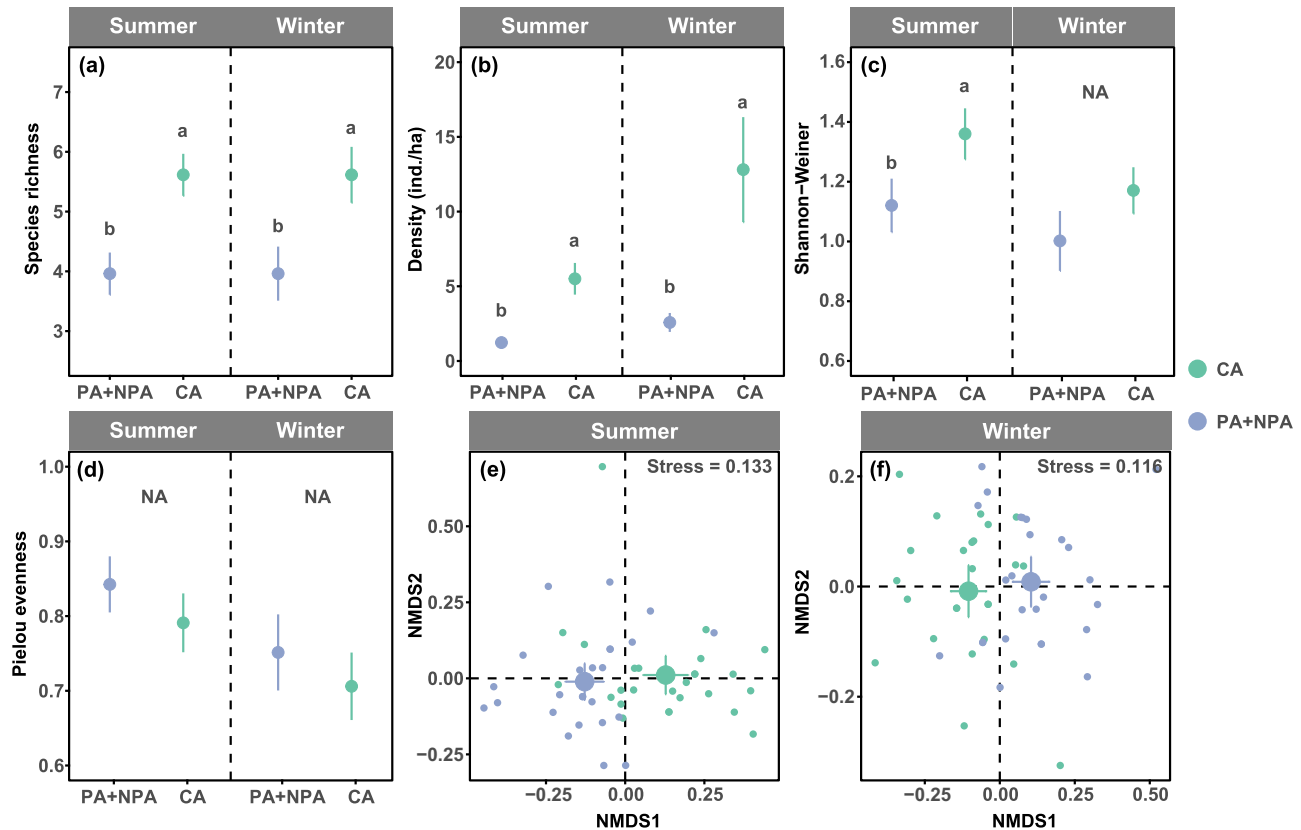
**Fig. 5 | Effect of water physical and chemical properties on the plankton community indices.** Redundancy analysis (RDA) of the relationship between water physical and chemical properties (UCA, T, pH, DO%, TN, TP, and NH<sub>3</sub>-N) and plankton (phytoplankton, microzooplankton, and macrozooplankton) community indices (species richness, individual density, and Shannon–Wiener diversity index) in summer (a, b, c) and winter (d, e, f). The red arrows indicate water physical and chemical properties, and the black arrows indicate plankton community indices. The length of the arrows represents the strength of impact of the water physical and chemical property on the plankton community index. The longer the arrow, the stronger the effect, and vice versa. The angle between the arrow of the plankton community index and the water physical and chemical property indicates the correlation, the angle of <90° indicates a positive correlation while the angle of >90°

indicates a negative correlation. The blue, orange, and green dots represent the photovoltaic areas (PAs), near the photovoltaic areas (NPAs) and control areas (CAs), respectively. **g, h** Spearman correlation analysis of water physical and chemical properties (UCA, T, pH, DO%, TN, TP, NH<sub>3</sub>-N) and plankton community indices (D\_Phyto, S\_Phyto, D\_Microzo, and S\_Microzo) with plankton community indices (D\_Phyto, S\_Phyto, D\_Microzo, S\_Microzo, D\_Macrozo, and S\_Macrozo). Colour depth and the size of the dots indicate the correlation strength. Phyto: phytoplankton; Microzo: microzooplankton; Macrozo: macrozooplankton; H': Shannon–Wiener diversity index; D: individual density; S: species richness. The *p*-value of the significant predictor is given as: \*\*\* *p* < 0.001, \*\* *p* < 0.01, \* *p* < 0.05. —: no comparison.

such as aquaculture<sup>17,53</sup>, our study showed that WSPV systems impact the physical and chemical properties and biological communities of waterbodies, which may weaken their suitability for other functions. For instance, WSPV systems reduced the DO of waterbodies, which is detrimental to aquaculture. Moreover, the electromagnetic fields produced by PV cabling and the potential diffusion of pollutants (e.g. microplastics) from PV modules into water may have long-term effects on aquatic environments<sup>10,54</sup>, which are still unknown and require further

studies. Therefore, the compatibility of WSPV systems with other functions should be considered.

As an emerging mode of solar energy utilization, WSPV systems have developed in a short period of about 10 years<sup>8</sup>. The WSPV systems in the study have only operated for 3–5 years, and there is some uncertainty for a single survey at each site, thus long-term monitoring with more surveys at each area will help elucidate the ecological and environmental impacts of WSPV systems. Moreover, the region of this study is located in the



**Fig. 6 | Comparison of bird community indices and nonmetric multidimensional scaling (NMDS) plot between the PA + NPAs and CAs in summer and winter ( $n = 26$ ).** Bird community indices (a: species richness, b: individual density, c: Shannon-Weiner diversity index, d: Pielou evenness index) between the PA+NPA and CAs in summer and winter. Different letters show significant differences between the two types of waterbodies in the same season (Wilcoxon test;  $p < 0.05$ ),

NA: not significant. PA + NPA: photovoltaic area and near the photovoltaic area, CA: control area. Points with error bars are means and standard errors. e, f NMDS plot of the bird communities across the PA+NPA and CAs based on their community structures in summer and winter. The light points exhibit the raw data. Points with error bars represent the means and associated 95% confidence intervals of the data. The blue and green dots represent the PA+NPA and CAs, respectively.

subtropics, the extent of impacts of WSPV systems may vary between regions with different environmental background (e.g. nutrient levels) and meteorological conditions (e.g. rainfall, temperature, light radiations, and evaporation)<sup>55</sup>. Comprehensive understanding detecting the different impacts of WSPV systems can help predict the ecological and environmental consequences of WSPV systems in the future. In addition, the areas of waterbodies covered and the coverage proportion of WSPV systems can be key factors in the degree of photovoltaic impacts, on which further research is required.

Expanding the scope of light energy use, WSPV systems have broad development prospects in the future from the perspective of water resource availability<sup>13</sup>. However, this study reveals that WSPV systems have significant impacts on the aquatic environment and biodiversity that could be long-lived. Since the cover created by the PV modules is the cause of the series of effects we observed, we suggest that WSPV systems should be installed at suitable sites and scales. It is also necessary to conduct long-term monitoring to understand the impacts of WSPV systems on ecological and environmental conditions; such monitoring is currently lacking but critical for targeted measures to mitigate adverse impacts. Our study provides important insights into the ecological and environmental consequences of WSPV systems and addresses the implications of the development of WSPV systems as part of the sustainable use of water resources.

## Materials and methods

### Survey area and sampling sites

The Yangtze River Basin is located in the middle part of China, with a large area of waterbodies including rivers, lakes, and ponds, and rich biodiversity, especially waterbirds. This region has a dense human population and well-

developed agriculture and aquaculture industries<sup>19</sup>. We focused on waterbodies with WSPV systems in the middle and lower reaches of the Yangtze River, which is the main distribution region of WSPV systems in China (Fig. 1a)<sup>28</sup>. Waterbodies with WSPV systems were identified based on information from the China Photovoltaic Website (guangfu.bjx.com.cn) and the image acquisition platform Google Earth (earth.google.com), the images between May 2017 and November 2021). A waterbody with a WSPV system was selected as a study site if it met the following criteria: (1) it was established on an independent waterbody that was separate from rivers or other flowing waterbodies; (2) the area of the waterbody was larger than 10 ha; (3) there was a similar waterbody (in terms of size and hydrogeologic features) without a WSPV system within 2 km of the WSPV system that could serve as a control; and (4) the WSPV system had been in operation for at least 3 years (to exclude short-term impacts associated with system installation). Eventually, we selected 26 waterbodies with WSPV systems (including 5 waterbodies with FPV systems and 21 with PMPV systems), with an average area of 121 ha and 26 control areas, covering a range of 550 km from north to south and 800 km from east to west (Fig. 1, supplementary Table 1). All the waterbodies in this study were used for extensive aquaculture.

### Data collection

Due to large seasonal differences in environmental conditions, field sampling and surveys were conducted twice: in winter (January) and in summer (July) in 2022. Each study site was classified into three areas: (1) photovoltaic area (PA), the area covered by photovoltaic modules; (2) NPA, the area adjacent to the PA in the same waterbody, and (3) control area (CA), a nearby waterbody with similar size but not connected with the waterbody of



PA. To avoid edge effects, sampling sites were located at least 20 m from the edge of each area. Physical and chemical properties measurement and plankton sampling were conducted at each of the three areas at each site. Since the area of PA and NPA were in the same water body at each site and birds have many activities, PAs and NPAs were combined as PA+NPAs in the bird surveys. The PA in one waterbody with a PMPV system in Guanhu, Jiangxi Province was inaccessible for sampling in summer because the area was closed. Thus, the total sample size was 25 for physical and chemical properties and plankton surveys in summer.

**Determination of the uncovered area of the water surface measurement.** Light radiation largely impacts the physical and chemical properties and organisms of a waterbody. To understand the effects of WSPV systems on the light radiation of waterbodies, we extracted the uncovered area of the water surface in the photovoltaic area (UCA), i.e. the areal percentage of the water surface exposed to direct light radiation in the photovoltaic area, for each sampling site based on image acquisition platform Google Earth (supplementary Fig. 5). The image source was CNES/Airbus and Maxar Technologies at a resolution of 1.5 m. We visually interpreted the regions covered by PV modules using Photoshop software (Adobe, San Jose, 2021) and measured the area of the regions by using the “selection” function to calculate the UCA<sup>56</sup> as  $UCA = (1 - \text{area of the waterbody covered by the PV modules} / \text{total area of the WSPV region}) \times 100\%$ . NPAs and CAs were not covered by PV modules and thus received UCA values of 100%. In three sites with WSPV systems, the extracted UCA was 0 due to the close proximity of the PV modules. We adjusted the UCA to 1% for these sites, as there were narrow gaps between adjacent PV panels according to field surveys (supplementary Table 1).

**Measurement of water physical and chemical properties.** A total of six physical and chemical indicators were measured: pH, water temperature (T), dissolved oxygen (DO), total nitrogen (TN), total phosphorus (TP), and ammonia-nitrogen ( $\text{NH}_3\text{-N}$ ). We measured the DO, pH and T using a portable multifunctional water quality detector (AZ86031, AZ Instrument Corporation, Beijing) in triplicate within each area (PA, NPA, and CA), at a distance of at least 20 m from each other. The mean values of the three measurements within each area were used for further analysis. Sampling jars (1 L) were used to collect three water samples (0–50 cm depth) at each of the three sampling sites. The water samples collected in each area were mixed and left to stand until settling had occurred, and then the supernatant liquid (0.5 L) was transferred into clean opaque polyethylene plastic bottles and mixed with 8 mL of 20%  $\text{H}_2\text{SO}_4$  to normalize the pH of the water samples <2. To avoid the impacts of survey time on the physical and chemical features of waterbody, all the measurements and samplings in each area were completed within 1 h on the same days between 9:00 and 16:00 on a sunny day. The sampling order was random in the three areas. The water samples were transferred to the laboratory in an insulated box with ice bags and stored at  $-20^\circ\text{C}$  for testing for TN, TP, and  $\text{NH}_3\text{-N}$  using a UV-visible spectrophotometer (Cary 50, Agilent, America)<sup>33,57,58</sup> within 2 weeks. Since dissolved oxygen concentration can be affected by water temperature, we exhibited the percentage saturation of dissolved oxygen instead. We used the water temperature measured at each area to query the saturated dissolved oxygen in the waterbody, and then calculated the percentage saturation of dissolved oxygen (DO%) based on the dissolved oxygen concentration measured at the area (percentage saturation of dissolved oxygen (%) = dissolved oxygen concentration/dissolved oxygen saturation at the water temperature  $\times 100\%$ ).

**Plankton surveys.** Samples of plankton (phytoplankton, microzooplankton (including rotifers and protozoa), and macrozooplankton (including cladocera and copepods)) were collected at the same sites where the measurements of the physical and chemical properties of water were taken. To survey phytoplankton and microzooplankton, we used sampling jars (1 L) to collect water samples three times, obtaining a total

of 3 L of water, at a depth of 0–50 cm at each of the three sampling sites. We mixed the 3 L of water at each site, placed 1 L of the water samples into a plastic bottle, and added 15 mL of Lugol's iodine solution. In the laboratory, each sample was precipitated using a pear-shaped funnel for 48 h. The supernatant liquid was removed to condense the sample to 50 mL, and the phytoplankton and microzooplankton in the resulting liquid were counted.

To survey the macrozooplankton, we collected 2 L water samples at a depth of 0–50 cm at each sampling site. The 2 L of water samples were filtered using a plankton net (13#; pore size: 0.112 mm). The samples from the header of the net were transferred into 50 mL polyethylene bottles and fixed with 1 mL of Lugol's iodine solution. Water samples used for plankton analysis were stored at  $4^\circ\text{C}$ .

Phytoplankton were observed and counted using an optical microscope ( $\times 400$ , Eclipse E200, Nikon, Tokyo). Samples of 0.1 mL of the mixed concentrated solution were collected and placed in a 0.1 mL Sedgwick–Rafter cell counting chamber (20 mm  $\times$  20 mm). A total of 20 views were observed for each counting chamber. We repeated this process for a total of five counting chambers for each solution<sup>59</sup>. Phytoplankton were identified to the genus level, and the numbers of individuals belonging to each genus were counted. Phytoplankton counts were converted to density ( $\text{ind. L}^{-1}$ ) according to the view area (diameter of 0.55 mm).

To count microzooplankton, 1 mL of the mixed concentrated solution was placed in a 1 mL Sedgwick–Rafter cell counting chamber. The species and number of microzooplankton were recorded. We repeated this process for five counting chambers for each solution. Individual numbers were converted to density ( $\text{ind. L}^{-1}$ ) for each species. The same methods were used for counting macrozooplankton except that 5 mL of concentrated sample and 5 mL Bogorov counting chambers were used.

**Bird surveys.** Bird surveys were conducted using binoculars (8 $\times$  magnification) and spotting telescopes (20–60 $\times$  magnification) in the early morning (5:00–8:30) and late afternoon (16:00–18:30). We walked around the perimeters of the waterbodies and used boats to traverse the waterbodies to record the species, numbers, and locations of birds (in the waterbody or on the PV modules including solar panels, mounts, and floating materials) in the entire region. The same route was followed for each subsequent survey in the same area, and the characteristics of these routes were consistent between areas. Generally, bird surveys lasted for half an hour to one hour at each area. Aerial foraging birds were recorded because they rely on waterbodies for food while other flying birds were excluded. We also recorded the species that nested at each site in summer. Birds were classified into three ecological groups: land birds, wading birds and swimming birds<sup>60</sup>. Both wading and swimming birds are waterbirds that are highly dependent on waterbodies; wading birds generally use shallow water areas, and swimming birds use deep water areas. Individual densities of each species were calculated based on the area of each site.

### Statistical analysis

We calculated the species richness, individual density, Shannon–Wiener diversity index and Pielou evenness index of phytoplankton, microzooplankton, macrozooplankton and all birds at each site in each season<sup>61,62</sup>. Shapiro–Wilk tests indicated that not all the data fit a normal distribution; thus, Wilcoxon nonparametric ANOVAs followed by rank tests were used to compare the physical and chemical properties of water (UCA, T, pH, DO %, TN, TP,  $\text{NH}_3\text{-N}$ ) and biological community indices (species richness, individual density, Shannon–Wiener diversity index and Pielou evenness index) of each biological group among the three areas of WSPV systems (PA, NPA and CA; two areas (PA + NPA and CA) for birds) in each season. We further compared the differences in physical and chemical properties and diversity indexes of each biological group among the three areas of the FPV and PMPV systems. Taxa were defined as abundant when the number of individuals exceeded 5% of the total. We used the Wilcoxon test to compare the individual densities of those abundant phytoplankton taxa

(>5% of the total) between the three areas in each season. In addition, we used the Wilcoxon test to compare water physical and chemical properties and biological community indices of the FPA and PMPV systems in the PAs.

NMDS and RDA were performed using the package “vegan” in R software ([www.r-project.org](http://www.r-project.org)). NMDS was used to detect the species and group composition of plankton and bird communities in different waterbodies in each season. A species community similarity matrix was constructed for each season based on Bray–Curtis distance according to individual density<sup>63</sup>. Analysis of similarity (ANOSIM) was used to test for differences among the three waterbody types (three areas (PA, NPA and CA) for plankton; two areas (PA + NPA and CA) for birds)<sup>64</sup>. We used NMDS and ANOSIM to analyse the composition of plankton communities of the FPV and PMPV systems. Considering the species differences among regions, bird communities were analysed based on individual densities of three ecological groups (land birds, wading birds and swimming birds, supplementary Table 11). The model of detrended correspondence analysis showed that all the axis lengths of gradient were less than 4.0, indicating a homogeneous or short gradient, making the linear response model appropriate to apply. Thus, we proceeded with modelling through an RDA for describing species composition. RDA was also used to detect the relationship between environmental conditions and density and diversity indices of the plankton communities. Plankton individual densities were log10 transformed prior to RDA analysis. All the variance inflation factor values were no more than 2.2 in winter and 5.4 in summer, suggesting the absence of multicollinearity among all the variables. We further used Spearman correlation analysis to determine the relationship between environmental conditions and plankton community indices (species richness and individual density). Considering the predator/prey relationships among phytoplankton, microzooplankton and macrozooplankton<sup>30,31</sup>, the species richness and individual density of phytoplankton were included as potential factors affecting microzooplankton, and the species richness and individual densities of phytoplankton and microzooplankton were included as potential factors affecting macrozooplankton.

To investigate the impacts of different UCA levels on water physical and chemical properties and plankton community indices in WSPV systems, we calculated the differences in T, DO%, and plankton community indices (species richness and individual density) between the PAs and CAs, which indicators were significantly affected by the WSPV system. Linear regression analyses were used to detect the effects of UCA on the differences in T, DO%, and plankton community indices in each season.

All statistical analyses were performed with R version 4.2.2 (R Development Core Team, 2022). The results are shown as the mean ± standard error (SE).

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

Additional material is available in supplemental information. The datasets used for our analyses and Supplementary Tables 1–12 are available at <https://figshare.com/s/23e70e6131e9d4dc7f0f>.

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## Author contributions

Sen Yang conducted field and laboratory work and collected data, designed and contributed to research design, sample and data analysis, data interpretation, and manuscript writing and editing. Youzheng Zhang contributed to manuscript writing. Defeng Tian contributed to sample and data analysis, and manuscript editing. Zekang Liu contributed to sample and

data analysis, and manuscript editing. Zhijun Ma led the project, conceived the research, designed and contributed to research design, and manuscript writing and editing. All authors contributed to the design and writing of the manuscript, adding to their respective area of expertise.

### Competing interests

The authors declare no competing interests.

### Additional information

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