

Wetland productivity and stability increase more with average plant size than with plant functional diversity

Received: 7 August 2024

Accepted: 24 October 2025

Published online: 28 November 2025

 Check for updates

Hao Liu¹, Jianjun Xu¹, Xinyue Qi¹, Xiao Xu², Jihua Wu^{1,3}, Bo Li^{1,2} & Ming Nie¹ ✉

The functional trait diversity of plant communities regulates the effects of biodiversity on ecosystem functioning and stability. However, the role of functional trait diversity in explaining ecosystem productivity and stability in natural wetlands remains unclear. Using vegetation data from 1139 sites across U.S. wetlands, we examine the associations of functional diversity (trait dispersion within a community) and functional identity (community-level trait values) of plant size traits and resource economics traits with satellite-derived productivity and temporal stability at continental scales. Community-level plant size shows the strongest association with productivity and stability, which is consistent across different wetland types and levels of anthropogenic disturbance. While functional diversity is generally positively correlated with productivity and stability, these relationships vary substantially across environmental contexts. Notably, weaker correlations are observed under higher levels of anthropogenic disturbances. These findings suggest that wetland conservation and restoration efforts should focus on increasing functional diversity and prioritizing large dominant species to increase productivity and stability.

Despite covering only 6% of Earth's land surface, wetland ecosystems are globally important because of the multiple benefits they provide to humanity, known as ecosystem services, such as water quality improvements, biodiversity support, nutrient cycling, and climate change mitigation^{1,2}. Plant diversity can safeguard multiple aspects of ecosystem functioning, including primary production and carbon burial, thereby ensuring the delivery of ecosystem services³. However, ongoing anthropogenic and climate stresses have rendered wetlands among the most threatened ecosystems globally in terms of biodiversity⁴. Identification of the mechanisms through which biodiversity drives and stabilizes ecosystem functioning is pivotal for

managing and restoring ecosystems⁵. Trait-based functional diversity, or the value and range of species traits, is increasingly recognized as more critical than taxonomic diversity in underlying the relationships between biodiversity and ecosystem functioning, as functional traits are essential for elucidating how species utilize resources and assemble within communities^{6–8}. However, our understanding of how functional trait diversity drives and stabilizes ecosystem productivity in wetlands significantly lags behind that in terrestrial forests and grasslands⁹.

Biodiversity primarily enhances ecosystem productivity through complementarity effects and selection effects^{3,6}. These mechanisms

¹State Key Laboratory of Wetland Conservation and Restoration, National Observations and Research Station for Wetland Ecosystems of the Yangtze Estuary, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, and Institute of Eco-Chongming, School of Life Sciences, Fudan University, Shanghai, China. ²State Key Laboratory for Vegetation Structure, Functions and Construction (VegLab), Ministry of Education Key Laboratory for Transboundary Ecosystem Security of Southwest China, Institute of Biodiversity, School of Ecology and Environmental Science, and Southwest United Graduate School, Yunnan University, Kunming, China. ³State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems, College of Ecology, Lanzhou University, Lanzhou, China. ✉e-mail: mnie@fudan.edu.cn

can be evaluated by examining how functional diversity and functional identity influence ecosystem functioning^{6,10}. Functional diversity characterizes the extent of differences in functional traits among species within a community⁶. Functional diversity captures variations in resource use and environmental interactions that extend beyond the species presence and abundance information associated with taxonomic diversity¹¹. According to the niche complementarity hypothesis, high functional diversity enhances ecosystem productivity by promoting complementary resource use and facilitation in communities¹². Alternatively, the mass ratio hypothesis posits that ecosystem productivity is overwhelmingly determined by the characteristics of dominant species^{10,13}. Functional identity, also known as functional composition, refers to the aggregate expression of certain functional traits within a community, is shaped primarily by the dominance of species with particular traits^{6,10}, and serves as a key metric for assessing the role of selection effects in ecosystem processes^{14,15}. Functional identity is typically quantified by the community-weighted mean (CWM) of traits, where trait values are weighted by the relative abundance of each species in the community^{10,16}. For example, a recent global study revealed that grassland productivity was driven by the CWM of traits rather than functional diversity, suggesting the prevalence of selection effects¹⁵. Moreover, functional identity can indirectly affect ecosystem stability by shaping community resistance and resilience¹⁷, while functional diversity can increase ecosystem stability by increasing species asynchrony¹⁸. Experimental studies in terrestrial systems have generally shown that complementarity effects and species asynchrony, driven by functional diversity, are the major processes underlying positive relationships between biodiversity and ecosystem functioning and stability^{19,20}, and the effects strengthen over time^{21,22}. Wetland ecosystems, located at the interface of land and water, are unique systems characterized by distinct hydrological and anoxic soil conditions⁹. The unique and strong environmental filter in wetlands may homogenize plant traits, which might decrease the importance of functional diversity because coexisting species are less functionally dissimilar¹². A few studies have reported that functional identity effects dominate over functional diversity effects in wetlands at local scales^{14,23}. For example, the CWM of the leaf area outweighs the effects of functional diversity in driving the productivity of mangrove forests¹⁴. However, these local-scale studies limit the ability to generalize the effects of functional trait diversity on ecosystem productivity and stability across diverse wetland habitats²⁴, and the extent to which functional diversity and identity impact the productivity and stability of natural wetland communities remains unknown at large biogeographical scales.

The role of biodiversity in driving ecosystem functioning is widely acknowledged to be context dependent and shaped by climate factors, community features, and anthropogenic disturbances^{25,26}. Wetland ecosystems are often characterized by a mixture of herbaceous and woody plant life forms, ranging from fens with few woody plants to forested swamps with understory herbaceous species²⁷. As succession progresses, woody-dominated systems may develop canopy and root structures that are more heterogeneous than those in herbaceous systems^{28,29}. On the basis of the biotope–space hypothesis, which theorizes an increase in the magnitude of positive biodiversity effects with increasing biotope space^{30,31}, functional diversity may therefore be more important in driving ecosystem productivity in woody wetlands²⁰. Moreover, environmental stress also mediates the relationships between biodiversity and ecosystem productivity³². Based on the stress gradient hypothesis, which states that the importance of competition reduction and facilitation increases in stressful environments, complementarity effects should be greater under harsh environmental conditions³³. Therefore, the effects of functional diversity may be strengthened in wetlands subjected to high environmental stress, such as coastal wetlands exposed to natural stressors such as

salinity and tidal fluctuations, as well as in wetlands experiencing high levels of anthropogenic disturbances. However, recent evidence suggests that disturbances can disrupt the relationships between biodiversity and ecosystem functions^{34,35}. Given these uncertainties, it is necessary to consider the specific context of wetland ecosystems when assessing the role of functional diversity in driving ecosystem functioning and stability.

In addition to the environmental background, the selection of functional traits significantly influences the relationships between functional characteristics and ecosystem functioning³⁶. Plant functional traits are highly diverse, yet many may covary, as they reflect the shared ecological strategies that plants employ to adapt to environments^{37,38}. Two major dimensions of global plant trait variation have been identified in a multidimensional trait space: the resource economics spectrum and the plant size spectrum³⁹. Resource economics describes a trade-off between resource conservation and resource acquisition that is consistent across plant organs^{37,40,41}, whereas plant size reflects a trade-off between smaller and larger organ sizes^{39,42}. The resource economics spectrum runs from the traits associated with conservative resource-use strategies (e.g., high leaf dry matter content (LDMC) and long tissue lifespan) to the contrasting traits associated with rapid resource capture (e.g., high specific leaf area (SLA) and high leaf nitrogen concentration (LNC))^{37,40}. Resource economics traits refer to the functional traits inherently related to the acquisition–conservation trade-off, such as SLA, LNC, and LDMC. The community-level means and diversity of resource economics traits have been widely used to predict ecosystem productivity and stability¹⁹. Moreover, recent studies have increasingly recognized the crucial role of the functional characteristics of plant size-related traits, such as plant height and leaf area, in assessing ecosystem productivity and stability, in both grassland and forest ecosystems^{43,44}. For example, canopy structural complexity is associated with high forest ecosystem productivity and stability globally through an increased light interception capacity⁴⁵. The effectiveness of the functional characteristics of different facets of trait variation in predicting ecosystem productivity and stability may depend on the specific resources that limit plant growth within ecosystems³⁶. Understanding how the functional diversity and identity of traits from different trait dimensions affect productivity and stability can enhance our knowledge of the mechanisms driving ecosystem dynamics in response to changing environmental conditions and resource availability.

Here, we use data from 1139 natural wetlands surveyed during the 2011 and 2016 National Wetland Condition Assessment (NWCA) across the conterminous United States (Fig. 1) to evaluate whether and how functional diversity and identity interact with local factors to affect wetland productivity and temporal stability at a continental scale. Remote sensing enables the detection of vegetation reflectance characteristics, offering large-scale and long-term estimates of vegetation productivity that are unobtainable by traditional field surveys⁴⁶. Spectral vegetation indicators have been widely employed to evaluate productivity and stability during the exploration of large-scale relationships between biodiversity and ecosystem functioning and stability^{45,47}.

In this study, we use the long-term (2006–2021) means of satellite-derived annual maximum normalized difference vegetation index (NDVI) data as site-level proxies of productivity (Supplementary Fig. 1). The temporal stability of productivity is evaluated via the mean-to-standard deviation (SD) ratio of the annual maximum NDVI from 2006 to 2021. Within each wetland site (a 40-m-radius circle, Supplementary Fig. 1), the abundance (cover) and plant height data for each plant species are recorded following standard protocols by the NWCA^{48,49}. In addition, leaf area and three resource economics trait datasets (i.e., SLA, LNC, and LDMC, Supplementary Table 1) were obtained from the TRY and BIEN databases to calculate functional diversity and identity, which represent the long-term average conditions of functional trait

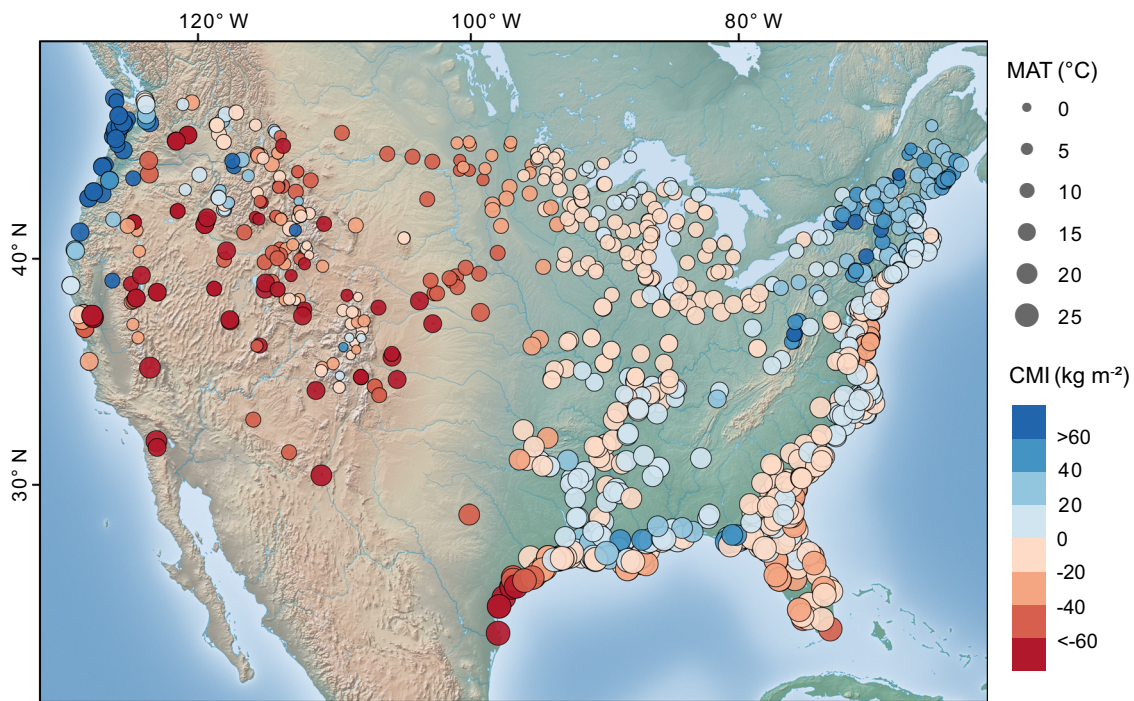


Fig. 1 | Spatial distribution of wetland sites with climatic information. Sites were surveyed as part of the 2011 and 2016 National Wetland Condition Assessment (NWCA) by the U.S. Environmental Protection Agency. The long-term averages of

the mean annual temperature (MAT) and monthly climate moisture index (CMI) are given. Source data are provided as a Source Data file.

diversity. We first explore the general effects of functional diversity and identity in terms of plant size traits and resource economics traits on the productivity and temporal stability of wetlands. We then evaluate whether the relationships between functional characteristics and productivity and stability vary across wetland types and under different intensities of anthropogenic disturbance. Furthermore, we compare the relative effects of functional diversity, functional identity, and environmental factors on productivity and stability via structural equation modeling.

We hypothesize that (1) high functional diversity enhances wetland productivity and stability; (2) functional identity surpasses functional diversity in explaining wetland productivity and stability; and (3) the role of functional diversity increases in woody wetlands and stressful environments. Our study underscores both the generality and context dependence of functional diversity and identity in shaping wetland productivity and temporal stability, with plant size emerging as the predominant contributor to higher and more stable productivity.

Results

Overall effects of functional diversity and identity

We derived two components from a principal component analysis (PCA) with the CWM of five traits (plant height, leaf area, SLA, LDMC, and LNC) to represent functional identity (CWM_{PC1} and CWM_{PC2}, Supplementary Fig. 2). The results of multiple linear regression models revealed that the functional diversity (indicated by functional dispersion, FD_{is}) of all the traits generally showed positive correlations with productivity and stability (Supplementary Table 2). The overall effects were further explored by disentangling functional diversity into two components: FD_{is} of plant size-related traits (leaf size and plant height) and FD_{is} of resource economics traits (SLA, LNC, and LDMC). The FD_{is} of resource economics traits positively influenced productivity but had no effect on stability (Fig. 2a, f and Supplementary Table 3), whereas the FD_{is} of plant size traits had a positive effect on both productivity and stability (Fig. 2b, g). We detected strong positive

effects of CWM_{PC2} (representing larger plant size, i.e., greater height and leaf area) on productivity and stability (Fig. 2d, i), whereas CWM_{PC1} (representing more acquisitive traits, i.e., higher LNC and SLA and lower LDMC) had significant but weaker positive effects on productivity and stability (Fig. 2c, e, h, j).

Context-dependent functional diversity and identity effects

We further investigated whether the impacts of functional identity and diversity on productivity and stability varied across different wetland types. The FD_{is} of resource economics traits and dominant vegetation type (herbaceous and woody wetlands) had a marginally significant interaction effect on productivity (Supplementary Table 4 and Supplementary Fig. 3a). The FD_{is} of resource economics traits had a positive effect on productivity in herbaceous wetlands but not in woody wetlands (Fig. 3e and Supplementary Fig. 3a). The FD_{is} of plant size also had a significant positive effect on stability in only herbaceous wetlands (Fig. 3j and Supplementary Fig. 3b). However, the effects of CWM_{PC1} and CWM_{PC2} on productivity and stability did not vary significantly between herbaceous wetlands and woody wetlands (Fig. 3c–e, h–j and Supplementary Table 4). In a comparison of inland and tidal wetlands, the effects of FD_{is} of resource economics traits and plant size traits on productivity and stability did not vary significantly between the two wetland types (Fig. 4a, b, f, g and Supplementary Table 5). The effect of CWM_{PC1} shifted from a negative impact on productivity and a neutral impact on stability in tidal wetlands to a positive impact on both productivity and stability in inland wetlands (Fig. 4c, e, h, j and Supplementary Fig. 3c, e). The positive effects of CWM_{PC2} on productivity and stability were stronger in inland wetlands than in tidal wetlands (Fig. 4d, e, i, j and Supplementary Fig. 3d, f).

Across wetlands with varying levels of anthropogenic disturbance, a positive effect of the FD_{is} of resource economics traits on productivity and stability was evident only in the least disturbed wetlands, whereas the effects shifted to neutral in the intermediate and most disturbed wetlands (Fig. 5a, e, f, j and Supplementary Fig. 3g, i). The effects of FD_{is} of plant size traits on productivity and stability did not

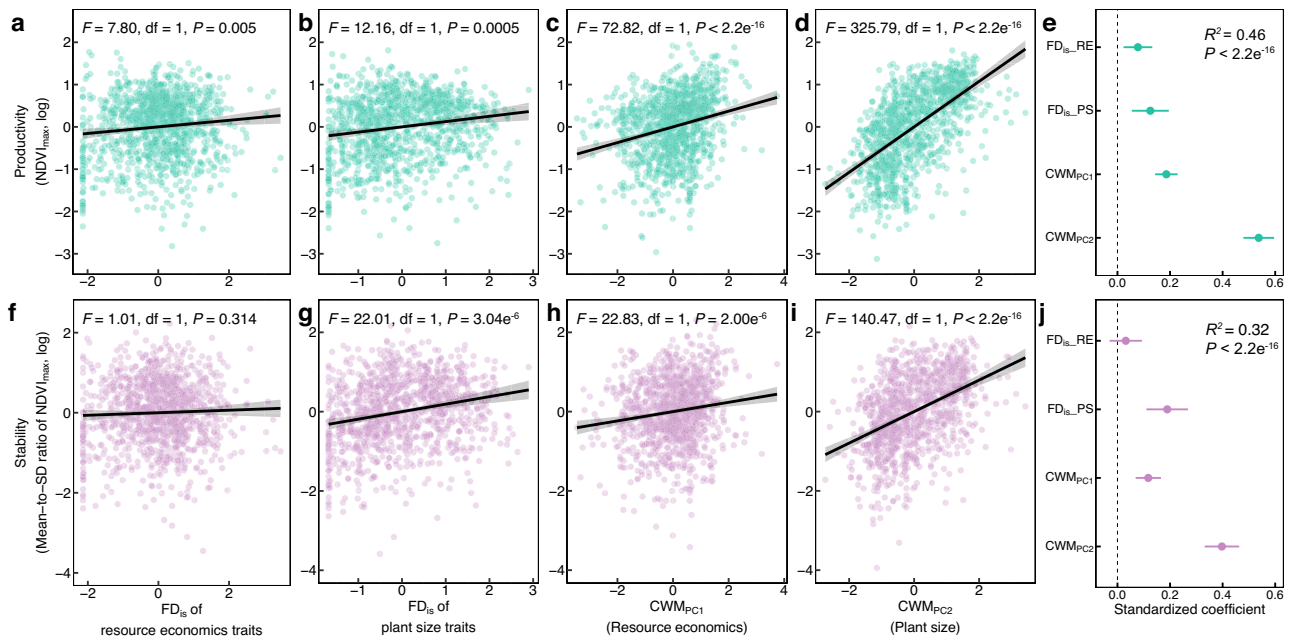


Fig. 2 | Effects of functional diversity and identity on productivity and stability in all wetlands. a–d, f–i Predicted productivity (a–d) and stability (f–i) as functions of functional dispersion (FD_{is}) of resource economic traits (a, f), FD_{is} of plant size traits (b, g), CWM_{PC1} (c, h), and CWM_{PC2} (d, i) based on multiple linear regression models ($n = 1139$). The black lines represent the mean predicted values, with non-focal predictors fixed at their means. The shaded areas indicate 95% confidence intervals. Points represent partial residuals for the focal functional indices in each panel. F and P -values (from type II ANOVA, two-sided F -tests) are shown in each panel. **e, j** Standardized regression coefficients ($n = 1139$) for predictors of

productivity (e) and stability (j). Points indicate coefficient estimates, with error bars showing 95% confidence intervals. The adjusted R^2 and P -values of the multiple linear regression models (two-sided F -tests) are given. Detailed ANOVA results of the multiple linear regression models and the most parsimonious models are given in Supplementary Table 3. High CWM_{PC1} values reflect more acquisitive traits, and high CWM_{PC2} values indicate larger plant size. FD_{is_RE} , functional dispersion of resource economics traits; FD_{is_PS} , functional dispersion of plant size traits. All variables were scaled. Source data are provided as a Source Data file.

vary across disturbance levels (Fig. 5b, g and Supplementary Table 6). In terms of functional identity, CWM_{PC2} consistently had positive effects on productivity and stability regardless of the level of disturbance (Fig. 5d, e, i, j). In contrast, CWM_{PC1} had positive effects on productivity and stability in the intermediate and most disturbed wetlands but had neutral effects on productivity and stability in the least disturbed wetlands (Fig. 5c, e, h, j and Supplementary Fig. 3h, j). Despite these differences across different wetland types and disturbance levels, CWM_{PC2} , which represents plant size, consistently explained productivity and stability more strongly than the other functional indices (Figs. 3–5 and Supplementary Tables 4–6).

Direct and indirect effects of environmental factors

We constructed structural equation models (SEMs, see the a priori model in Supplementary Fig. 4) to investigate the direct and indirect influences of climatic factors, soil pH, water table depth, and anthropogenic disturbance on productivity and stability, as mediated by functional diversity and identity. The SEMs revealed that CWM_{PC2} , which was affected primarily by a high mean annual temperature and climate moisture index, had direct positive effects on productivity and stability and emerged as the most important predictor of productivity and stability (Fig. 6 and Supplementary Fig. 5). In addition, CWM_{PC1} , which increased with low mean annual temperature, high soil pH, and disturbances, positively affected productivity and stability (Fig. 6 and Supplementary Fig. 5). The FD_{is} of plant size traits, largely affected by the climate moisture index, also positively influenced productivity and stability (Fig. 6 and Supplementary Fig. 5). The SEMs for the different wetland types and disturbance levels further underscored the consistent importance of CWM_{PC2} in affecting productivity and stability (Fig. 7). Climate factors had more profound effects than the other environmental factors on productivity and stability (Fig. 6b, d).

Specifically, the climate moisture index consistently exhibited a strong positive effect, whereas the mean annual temperature generally had a negative impact (Fig. 6b, d), although this effect was context dependent (Fig. 7).

Discussion

Our findings provide empirical evidence concerning the importance of the functional diversity and identity of vegetation communities in explaining productivity and stability across 1139 wetland sites in the United States. Although the influences of functional diversity and identity of plant size traits and resource economics traits appeared to be context dependent, varying across different wetland types and levels of anthropogenic disturbance, plant size was consistently the most critical functional attribute associated with productivity and stability. The results highlight that functional identity may be more closely linked to productivity and stability than functional diversity in real-world wetland ecosystems.

Although it is well established that functional diversity increases ecosystem productivity and stability⁷, the positive effects of functional diversity on wetland productivity and stability remain unexplored at large scales. Our results revealed that wetlands with high functional diversity generally exhibited high productivity and stability (Supplementary Table 2), demonstrating that niche complementarity contributes significantly to the productivity and stability of wetland ecosystems at large scales¹². Both of the functional diversity of resource economics traits and plant size traits contributed to productivity (Fig. 2). Resource economics traits are closely related to resource acquisition and resource use efficiency; for example, high SLA and low LDMC are associated with fast resource acquisition and fast growth, whereas low SLA and high LDMC increase the conservation of acquired resources and slow growth³⁹. In wetlands, where

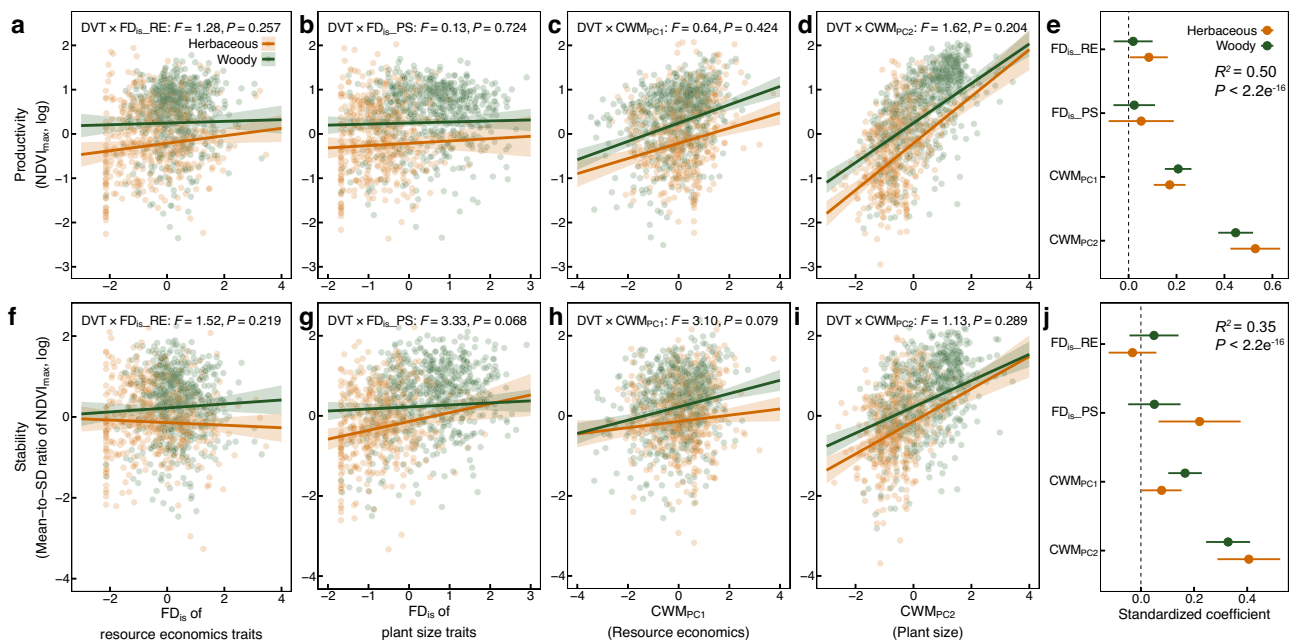


Fig. 3 | Effects of functional diversity and identity on productivity and stability in herbaceous and woody wetlands. **a–d**, **f–i** Predicted productivity (**a–d**) and stability (**f–i**) as functions of FD_{is} of resource economic traits (**a**, **f**), FD_{is} of plant size traits (**b**, **g**), CWM_{PC1} (**c**, **h**), and CWM_{PC2} (**d**, **i**) across dominant vegetation types (DVT; herbaceous ($n = 502$) and woody ($n = 637$) wetlands). The predictions are based on multiple linear regression models ($n = 1139$) with interactions between functional indices and DVT. Lines represent mean predicted values, with nonfocal predictors fixed at their means. The shaded areas represent 95% confidence intervals. Points represent partial residuals for the focal functional indices in each panel. The F and P -values of the interaction terms (from type II ANOVAs of the multiple linear regression models, two-sided F -tests) are shown in each panel. **e**, **j** Standardized regression coefficients for productivity (**e**) and stability (**j**) for

each predictor across DVT levels, derived from the same models ($n = 1139$). Points indicate coefficient estimates, with error bars showing 95% confidence intervals. The dashed line at zero denotes no effect; error bars crossing this line indicate that the coefficient is not statistically significant (at $P < 0.05$). The adjusted R^2 and P -values of the multiple linear regression models (two-sided F -tests) are given. Detailed ANOVA results of the multiple linear regression models and the most parsimonious models are given in Supplementary Table 4. High CWM_{PC1} values reflect more acquisitive traits, and high CWM_{PC2} values indicate larger plant size. FD_{is}RE, functional dispersion of resource economics traits; FD_{is}PS, functional dispersion of plant size traits. All variables were scaled. Source data are provided as a Source Data file.

resource availability fluctuates spatially and temporally, the coexistence of species with acquisitive traits and species with conservative traits can promote complementary nutrient utilization, enhancing overall ecosystem productivity⁵⁰. However, the functional diversity of plant size traits was more important than the functional diversity of resource economics traits in explaining productivity and stability (Figs. 2 and 6). Higher diversity in plant size (i.e., plant height and leaf area) can foster a complex vertical canopy structure that optimizes light interception⁵¹. Tall plants dominate the upper layers, intercepting direct sunlight, whereas short plants thrive in shaded understories, utilizing diffuse light. This stratified light use strategy enhances overall resource use and resilience to resource scarcity⁴⁵. Moreover, high diversity in terms of plant size may promote the asynchronous response of species to environmental fluctuations in wetlands, ultimately increasing stability⁵². Owing to their greater structural stability, large species can better withstand physical stresses such as flooding, wind, and heatwaves⁵³. Conversely, small species are often more agile in their response and resilient to hydraulic stress, such as drought, owing to their relatively low resource demands and faster recovery rates⁵⁴.

While functional diversity positively affects wetland productivity and stability, functional identity has an even stronger influence on these properties. CWM_{PC2} had stronger effects than the other functional indices on productivity and stability (Fig. 2). Further SEM analyses confirmed that CWM_{PC2} was the most important predictor of productivity and stability (Fig. 6), a pattern that was consistent across wetland types and disturbance levels (Fig. 7). These findings suggest that the selection effects of the dominant traits, aligned with the mass-ratio hypothesis, are stronger than the complementarity effects

associated with functional diversity in their relationships with wetland productivity and stability. Tall species are characterized by extensive canopy cover and high light interception for photosynthesis⁵⁵. These advantages in terms of light use allow tall species to benefit disproportionately from increased resource availability compared with short species⁵⁶. As plant height increases at the community level, wide leaves promote light capture by increasing the effective photosynthetic area, particularly benefiting understory plants at low irradiance levels^{43,44}. Thus, in natural wetlands, competition for light likely serves as a key mechanism underlying the association between selection processes and productivity. Moreover, larger species, with relatively low inherent mortality rates and high resistance to extreme or frequent environmental fluctuations^{53,57}, may play a crucial role in maintaining stability. Despite the strong effects of plant size on productivity and stability, importantly, CWM_{PC2} was highly correlated with the functional diversity of plant size (Fig. 6). These findings suggest that a strong selection effect of tall species is associated with not only increased canopy size but also increased vertical heterogeneity in communities. This covariation between selection and complementarity effects does not lead to an antagonistic outcome (i.e., increasing productivity but decreasing stability)⁵⁰ but instead synergistically enhances both productivity and stability in wetland ecosystems (Supplementary Fig. 9). Therefore, we highlight that strong selection effects, which are synergistically tied to niche complementarity, are the predominant influencers of the productivity and stability of wetland ecosystems.

CWM_{PC1} (resource economics) had a positive effect on productivity, yet its effect size was substantially smaller than that of plant size (Fig. 2). Nutrient competition seems to be less important

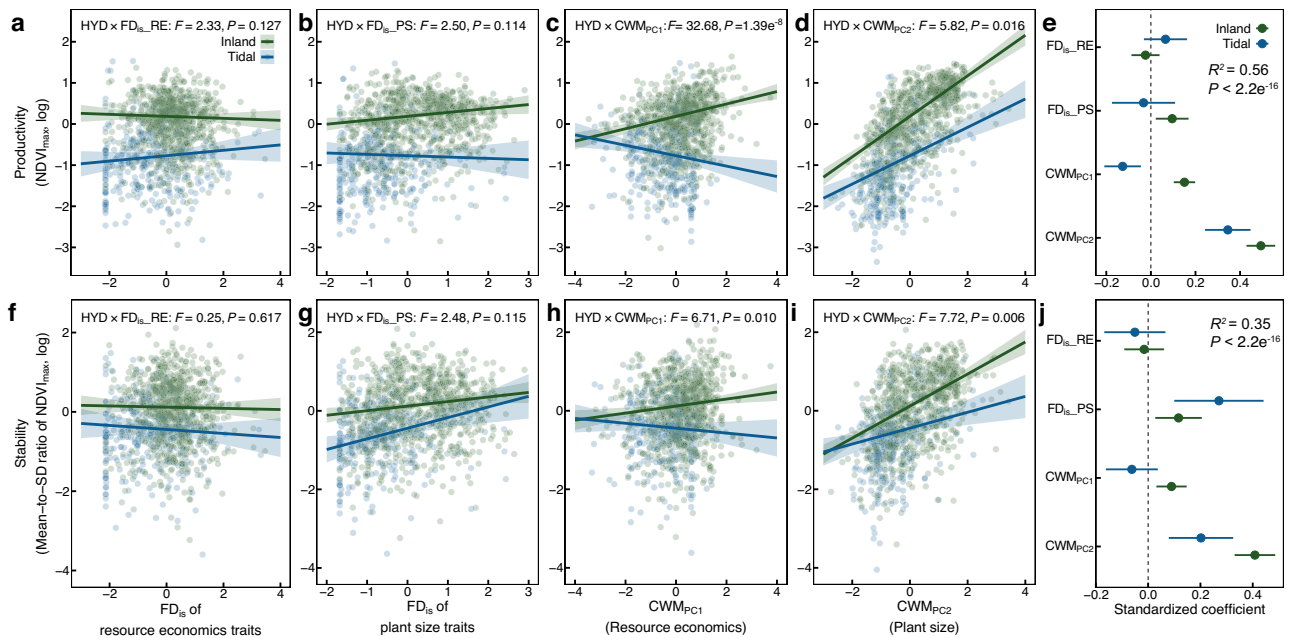


Fig. 4 | Effects of functional diversity and identity on productivity and stability in tidal and inland wetlands. a–d, f–i Predicted productivity (a–d) and stability (f–i) as functions of FD_{is} of resource economic traits (a, f), FD_{is} of plant size traits (b, g), CWM_{PC1} (c, h), and CWM_{PC2} (d, i) across hydrological classes (HYD; inland ($n = 835$) and tidal ($n = 304$) wetlands). The predictions are based on multiple linear regression models ($n = 1139$) with interactions between functional indices and HYD. Lines represent the mean predicted values, with nonfocal predictors fixed at their means. The shaded areas represent 95% confidence intervals. Points represent partial residuals for the focal functional indices in each panel. The F and P -values of the interaction terms (from type II ANOVAs of the multiple linear regression models, two-sided F -tests) are shown in each panel. **e, j** Standardized regression

coefficients for productivity (e) and stability (j) for each predictor across HYD levels, derived from the same models ($n = 1139$). Points indicate coefficient estimates, with error bars showing 95% confidence intervals. The dashed line at zero denotes no effect; error bars crossing this line indicate that the coefficient is not statistically significant (at $P < 0.05$). The adjusted R^2 and P -values of the multiple linear regression models (two-sided F -tests) are given. Detailed ANOVA results of the multiple linear regression models and the most parsimonious models are given in Supplementary Table 5. High CWM_{PC1} values reflect more acquisitive traits, and high CWM_{PC2} values indicate larger plant size. FD_{is} RE, functional dispersion of resource economics traits; FD_{is} PS, functional dispersion of plant size traits. All variables were scaled. Source data are provided as a Source Data file.

than light competition in competitive exclusion among species in mixed woody–herbaceous plant systems. Light availability was found to strongly mediate the effects of nutrient availability on species diversity and productivity in natural systems⁵⁸. Moreover, the effects of resource economics on stability were much weaker than those of plant size when estimated across all the sites (Fig. 2h). The relationship between plant resource economics and ecosystem stability has been demonstrated in many local-scale studies but is heavily dependent on the environmental context¹⁹. Acquisitive traits promote ecosystem stability at sites subjected to disturbances because of their ability to support fast recovery⁵⁹, whereas conservative traits may support ecosystem stability in the face of chronic environmental stresses, such as poor nutrient availability and drought^{17,60}. Our results also revealed contrasting effects, as indicated by the differing impacts of resource economics on stability between inland and tidal wetlands (Fig. 4h), as well as across wetlands under different disturbance levels (Fig. 5h). Thus, the weak overall effect of resource economics on stability likely stems from the opposing influences of acquisitive communities, which are generally more resilient, and conservative communities, which are generally more resistant, potentially canceling each other out¹⁹. Notably, the plant height data in this study were field-estimated, capturing intraspecific variation and offering greater accuracy and validity than other traits derived from public trait databases. However, the high accuracy does not amplify the explanatory power of plant size traits relative to resource economics traits, as the FD_{is} and CWM values calculated from database-derived and field-measured plant height data exerted comparable effects on productivity and stability (Supplementary Fig. 10). This consistency may stem from the limited impact of intraspecific trait variation on functional

composition across communities at large spatial scales, as predominantly driven by species turnover⁶¹.

Furthermore, our findings indicate that the effects of functional diversity and identity on productivity and stability vary substantially among different wetland plant types. We hypothesized that woody wetlands exhibit stronger complementarity effects than herbaceous wetlands due to increased biotope spaces (the physical aboveground and belowground space associated with a species' niche) in woody systems, which reduces niche overlap³⁰. Specifically, deeper soil and root growth zones allow species with more distinct root architecture to exploit more nutrients belowground³⁰, whereas a large vertical light gradient enables the coexistence of species with more distinct light-use strategies aboveground³¹, collectively promoting complementarity effects. A recent meta-analysis also revealed stronger complementarity effects in woody ecosystems²⁰. However, in contrast to our hypothesis, FD_{is} in resource economics traits increased productivity, whereas FD_{is} in plant size traits improved stability in herbaceous wetlands; neither of these showed significant effects in woody wetlands (Fig. 3 and Supplementary Fig. 3a, b). Although the functional diversity of woody wetlands was higher than that of herbaceous wetlands (Supplementary Fig. 11), complementarity effects tended to be stronger in herbaceous wetlands. This finding may be because herbaceous wetlands across the conterminous United States have greater nutrient inputs than woody wetlands⁶²; thus, increased nutrient availability may increase the complementary use of soil nutrients in decomposition-limiting systems⁶³. Moreover, the smaller stature of herbaceous plants than woody species increases their vulnerability to flooding, making high diversity in plant size crucial for flooding resistance⁶⁴.

Based on the stress gradient hypothesis, namely, that complementarity effects should be greater under harsh environmental

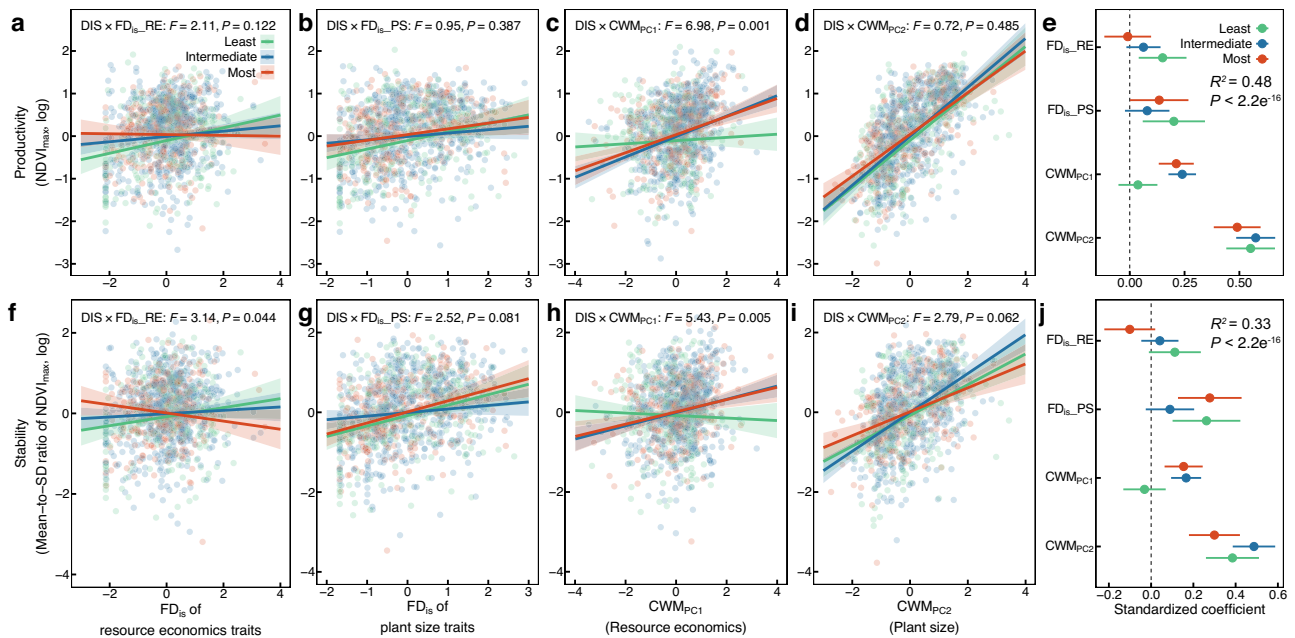


Fig. 5 | Effects of functional diversity and identity on productivity and stability in wetlands under different levels of anthropogenic disturbance.

a–d, f–i Predicted productivity (**a–d**) and stability (**f–i**) as functions of FD_{is} of resource economic traits (**a, f**), FD_{is} of plant size traits (**b, g**), CWM_{PC1} (**c, h**), and CWM_{PC2} (**d, i**) across anthropogenic disturbance levels (DIS; least ($n = 269$), intermediate ($n = 573$), and most ($n = 293$) disturbed wetlands). The predictions are based on multiple linear regression models with interactions between functional indices and DIS ($n = 1135$). Lines represent mean predicted values, with nonfocal predictors fixed at their means. The shaded areas represent 95% confidence intervals. Points represent partial residuals for the focal functional indices in each panel. The F and P -values of the interaction terms (from ANOVAs of the multiple linear regression models, two-sided F -tests) are shown in each panel.

e, j Standardized regression coefficients for productivity (**e**) and stability (**j**) for each predictor across DIS levels, derived from the same models ($n = 1135$). Points indicate coefficient estimates, with error bars showing 95% confidence intervals. The dashed line at zero denotes no effect; error bars crossing this line indicate that the coefficient is not statistically significant (at $P < 0.05$). The adjusted R^2 and P -values of the multiple linear regression models (two-sided F -tests) are given. Detailed ANOVA results of the multiple linear regression models and the most parsimonious models are given in Supplementary Table 6. High CWM_{PC1} values reflect more acquisitive traits, and high CWM_{PC2} values indicate larger plant size. FD_{is}RE, functional dispersion of resource economics traits; FD_{is}PS, functional dispersion of plant size traits. All variables were scaled. Source data are provided as a Source Data file.

conditions³³, we expected stronger effects of functional diversity in tidal wetlands that face strong environmental stress, such as tidal flooding and salinity. However, the results revealed that the effects of functional diversity on productivity and stability did not vary significantly between inland and tidal wetlands (Fig. 4). In contrast, the effects of functional identity differed significantly between inland and tidal wetlands. Unlike inland wetlands, where acquisitive traits were associated with high productivity and stability, conservative traits were linked to higher productivity in tidal wetlands (Fig. 4c, e). Conservative species with low SLA and high LDMC are important for tolerating high salinity and waterlogging in tidal wetlands⁶⁵ and thus play an important role in explaining biomass production⁶⁶. A recent study revealed that planted mangrove stands with slow-growing species tended to accumulate more plant and soil carbon stocks than fast-growing stands in the long term⁶⁷. The influence of conservative traits on productivity may constrain the impact of large plant size, as many conservative species in tidal wetlands tend to be relatively short^{68,69}. This phenomenon could explain the weaker effect of plant size on productivity observed in tidal wetlands than in inland wetlands (Fig. 4d, i).

Our results showed that anthropogenic disturbances significantly mediated the effects of functional diversity on productivity and stability. In contrast to the stress gradient hypothesis, the positive effects of the FD_{is} of resource economics traits on productivity and stability were observed only at the least disturbance intensity (Fig. 5e, j and Supplementary Fig. 3g, i), suggesting that anthropogenic disturbances diminished the effects of complementary resource use on productivity and stability. The disturbance level in this study was assessed based on human-induced abiotic

disturbances (physical alterations and heavy metal contamination) and biotic disturbances (plant invasion). Physical alterations, such as vegetation removal and surface modification, often arise from human land use changes and can directly decrease wetland plant diversity⁷⁰. However, frequent and intense disturbances also increase the relative abundance of species with acquisitive traits in plant communities⁷¹. The enrichment of heavy metals also leads to the loss of plant diversity but an increase in acquisitive species in wetland ecosystems⁷². These acquisitive species increase primary productivity under disturbance conditions⁷¹, thereby disrupting the positive relationship between functional diversity and productivity; this was illustrated by the increased positive effects of acquisitive traits on productivity under high disturbance levels in our study (Fig. 5c and Supplementary Fig. 3h). On the other hand, plant invasion often reduces community diversity but increases overall productivity through increasing the dominance of invasive species⁷³. This process can also eliminate the positive diversity–productivity relationship, shifting it toward a neutral or negative relationship³⁵. Moreover, plant invasion also shifts communities toward a more acquisitive resource strategy⁷⁴. Therefore, both abiotic and biotic disturbances tend to weaken the complementarity effects on productivity but increase the selection effect driven by acquisitive species on productivity. Moreover, under relatively high disturbance levels, fast-growing acquisitive plants can rapidly recover from disruptive disturbances, increasing ecosystem resilience¹⁹ and thereby positively affecting stability (Fig. 5h and Supplementary Fig. 3j). In contrast, in naturally low-disturbance environments, excessive cover of acquisitive species may decrease resistance¹⁷, diminishing the positive effects on stability (Fig. 5h and Supplementary Fig. 3j). Our study

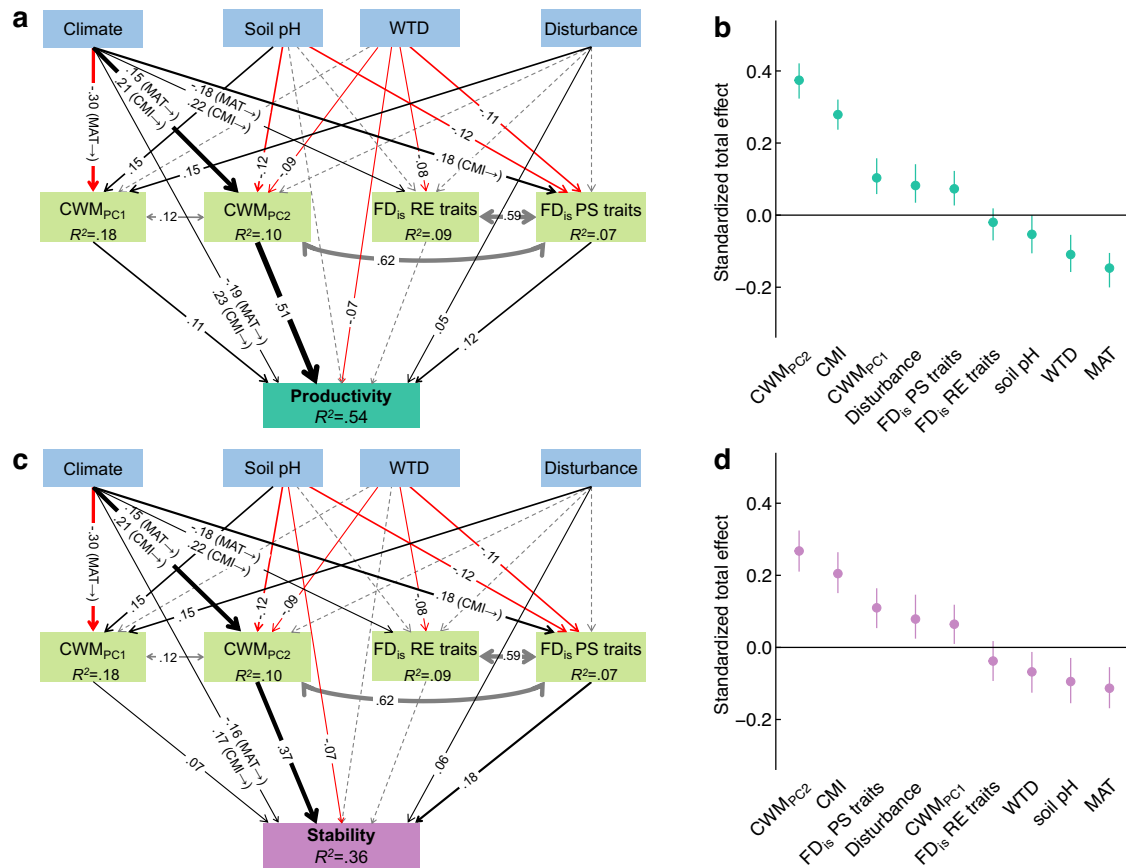


Fig. 6 | Structural equation models showing the effects of climate, soil factors, anthropogenic disturbances, functional identity, and functional diversity on primary productivity and stability. **a, c** Structural equation models (SEMs, $n = 868$) considering all plausible pathways influencing productivity (**a**) and stability (**c**). The black and red solid arrows indicate significant ($P < 0.05$, two-sided t test) positive and negative pathways, respectively, with numbers on the arrows representing standardized path coefficients. The dashed pathways denote the nonsignificant ($P > 0.05$) pathways. **b, d** Standardized total effects of each predictor on productivity (**b**) and stability (**d**). Standardized total effects, combining direct and indirect effects, were obtained from bootstrapped SEMs ($n = 868$). Points represent mean effect estimates, with error bars showing 95% confidence intervals

from 500 bootstrap iterations. The a priori model is provided in Supplementary Fig. 4, and the final models with only significant pathways are provided in Supplementary Fig. 5. The goodness-of-fit statistics for the final models were as follows: Fisher's $C = 14.67$, $P = 0.40$, and $df = 14$ (SEM for productivity) and Fisher's $C = 15.57$, $P = 0.34$, and $df = 14$ (SEM for stability), indicating a close fit of the models to the data. High CWM_{PC1} values indicate more acquisitive traits, and high CWM_{PC2} values indicate larger plant size. MAT mean annual temperature; CMI climate moisture index; WTD water table depth; Disturbance, anthropogenic disturbance; FD_{RE} RE traits, functional dispersion of resource economics traits; FD_{PS} PS traits, functional dispersion of plant size traits. Source data are provided as a Source Data file.

emphasizes the importance of mitigating human-induced land use change and pollution, as well as controlling plant invasion, as these pressures can undermine the role of biodiversity in sustaining wetland ecosystem functioning and stability.

Environmental conditions shape ecosystem productivity and stability both directly and indirectly through functional biodiversity. In this study, the climate moisture index emerged as the strongest environmental predictor of wetland productivity and stability, exerting both direct and indirect positive effects via its promotion on plant size and functional diversity (Fig. 6). In contrast, while the mean annual temperature was a potential key driver of productivity across terrestrial ecosystems, it had a pronounced net negative effect on wetland productivity and stability, as its direct detrimental impacts outweighed the indirect benefits mediated through increased plant size (Fig. 6). As a key hydrological factor that affects wetland physiochemical environments, water table depth directly reduced productivity and indirectly negatively impacted both productivity and stability by suppressing plant size and functional diversity (Fig. 6), highlighting the adverse effects of water saturation stress on productivity and stability in wetlands⁷⁵. Our results suggest that climate moisture is the primary abiotic factor associated with the productivity and stability of

wetlands, whereas high temperatures may impose water limitations or heat stress on wetland communities.

While NDVI-based metrics for productivity and stability are commonly used in terrestrial studies, their application in wetland ecosystems presents certain limitations. Wetlands are characterized by fluctuating water levels, diverse substrate types, and various plant growth forms, all of which influence their reflectance characteristics⁷⁶. For example, the presence of open water can obscure vegetation signals, potentially leading to the underestimation of productivity⁷⁶. In coastal wetlands, tidal inundation reduces near-infrared reflectance and shifts the red-edge position, reducing the efficacy of the NDVI for biomass estimation⁷⁷. Moreover, excessive litter can also attenuate the spectral signal of green vegetation⁷⁸. Furthermore, while canopy obstructions in woody wetlands may not be as severe as those in forest ecosystems, accurately capturing the productivity dynamics beneath the canopy remains challenging⁷⁹. These limitations may lead to overestimation of the stability of woody wetlands and underestimation of the productivity and stability of coastal wetlands, which may explain the patterns observed in this study, such as the higher stability of woody wetlands than herbaceous wetlands and the lower productivity and stability of tidal wetlands than inland wetlands (Supplementary

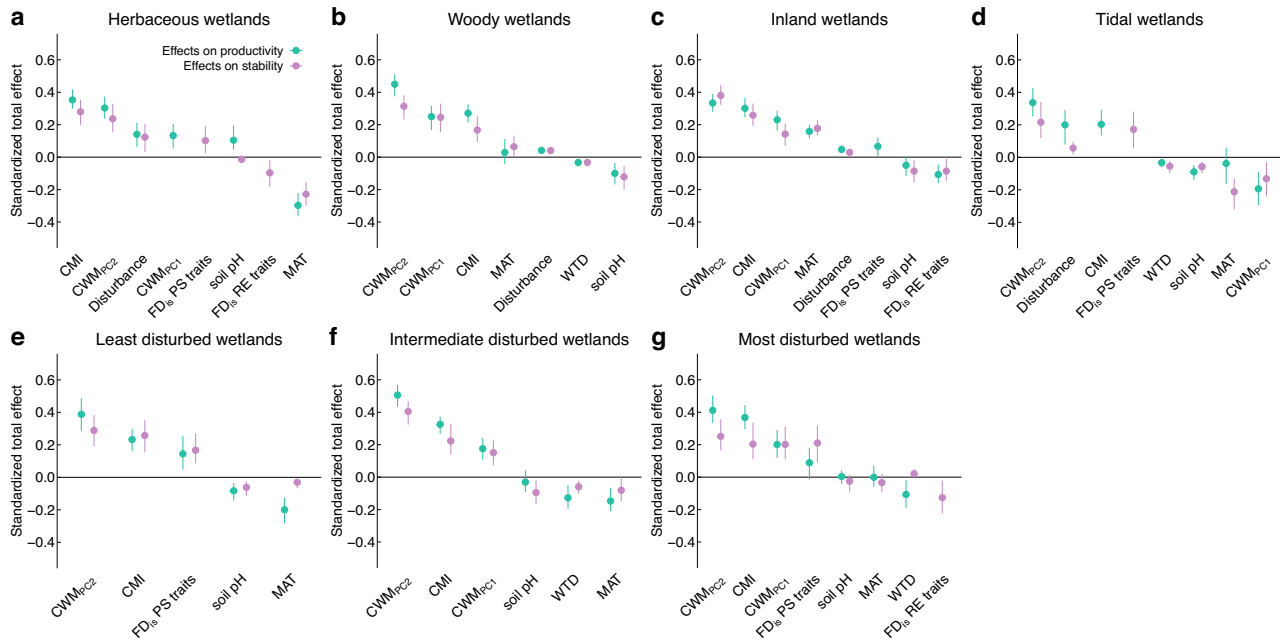


Fig. 7 | Standardized total effects of all significant factors in the final structural equation models on productivity and stability in different wetland types. **a** Herbaceous wetlands ($n = 417$). **b** Woody wetlands ($n = 451$). **c** Inland wetlands ($n = 604$). **d** Tidal wetlands ($n = 264$). **e** Least disturbed wetlands ($n = 212$). **f** Intermediate disturbed wetlands ($n = 416$). **g** Most disturbed wetlands ($n = 230$). The factors were ranked based on their combined effects on productivity and stability. The final structural equation models are given in Supplementary Figs. 6–8. Standardized total effects, combining direct and indirect effects, were obtained

from bootstrapped SEMs. Points represent mean effect estimates, with error bars showing 95% confidence intervals from 500 bootstrap iterations. High CWM_{PC1} values indicate more acquisitive traits, and high CWM_{PC2} values indicate larger plant size. *MAT* mean annual temperature; *CMI* climate moisture index; *WTD* water table depth; *Disturbance*, anthropogenic disturbance; FD_{is} RE traits, functional dispersion of resource economics traits; FD_{is} PS traits, functional dispersion of plant size traits. Source data are provided as a Source Data file.

Fig. 12). However, some noise, such as that associated with tidal inundation and litter, primarily affects continuous NDVI monitoring^{80,81}, and its impact on the annual maximum values used in this study was considered relatively minor. The restriction of water cover in NWCA wetlands, with water > 1 m deep covering less than 10% of the assessment area^{48,49}, also limits the influence of water and tidal conditions on remote sensing signals. Moreover, while canopy obstructions may amplify the apparent influence of plant size on productivity and stability in woody wetlands, we observed strong effects of plant size on productivity and stability in both woody wetlands and herbaceous wetlands (Fig. 3), suggesting that the interference of canopy obstruction was limited. Isolating these potential NDVI measurement errors from inherent ecosystem differences remains challenging; however, independent analyses of different wetland types allowed us to control for inherent differences among wetland types. Despite the limitations of the NDVI in assessing wetland productivity and stability, NDVI remains invaluable in large-scale studies because of its ability to provide consistent, comparable data with extensive spatial and temporal coverage. For research at the regional scale or in specific wetland types, the use of specific spectral vegetation indices that are sensitive to specific ground features could be explored in the future⁷⁶. We also advocate for the integration of more advanced remote sensing technologies, such as light detection and ranging (LiDAR) and solar-induced fluorescence (SIF), which provide detailed canopy structural and physiological data⁸², to increase the accuracy of large-scale productivity and stability assessments of wetland ecosystems.

Our study highlights the crucial roles of functional diversity and identity in vegetation communities in explaining variation in wetland productivity and stability across large geographic scales. We provide evidence of positive continental-scale relationships between functional diversity and productivity and stability in wetland ecosystems.

Moreover, community-level plant size was found to have the strongest association with productivity and stability, regardless of the environmental context of different wetland types and anthropogenic disturbance intensities. Our results also revealed that the relationships between specific functional characteristics and wetland productivity and stability are largely context dependent. Notably, anthropogenic disturbances diminished the positive influence of functional diversity on both productivity and stability. It is imperative to develop trait-based management and restoration policies for wetland ecosystems, focusing not only on the conservation and restoration of community functional diversity but also, more importantly, on large key plant species. This study advances our understanding of how functional trait diversity mediates the effects of biodiversity on ecosystem productivity and stability in natural wetland ecosystems. Further efforts should be made to enhance our understanding of the role of wetland-specific traits, such as aerenchyma formation and root porosity, in the unique ecosystem functioning and services provided by wetlands.

Methods

Wetland sites and vegetation diversity

This study focused on the wetlands of the U.S. surveyed by the National Wetland Condition Assessment (NWCA) conducted by the U.S. Environmental Protection Agency in 2011 and 2016^{48,49}. The target wetlands of the NWCA are currently unused for crop production; these wetlands included tidal and nontidal wetted areas with rooted vegetation and, when present, shallow open water less than 1 m in depth^{48,49}. Vegetation data were collected once or twice during the peak growing season when most plants were in the flowering or fruiting stage to optimize species identification and characterize species abundance^{48,49}. At each site, sampling was conducted via a consistent sampling and quality assurance approach to document the species composition and environmental characteristics of five 100 m²

(10 × 10 m) vegetation plots within an ~0.5 ha (40 m radius) assessment area (Supplementary Fig. 1)^{48,49}.

In this study, we used site-level (500 m² total sample area of five plots) estimates of species richness and the relative cover of each species (community composition) provided by the NWCA. For the sites that were repeatedly sampled in 2011 and 2016, we used the data from 2016. For some sites with two seasonal visits during one sampling year (<10% observations), we used the data from the first survey. Owing to the short life cycles and high turnover of annual species, their overabundance can lead to unpredictable and extreme interannual variability in community structure³³, diminishing the ability of community composition data to represent the long-term average state of local communities. Therefore, we selected sites where perennial species accounted for at least 90% of the relative cover. Moreover, to avoid excessive unvegetated areas, the percentage of water cover or exposed soil or sediment in the vegetation plots was restricted to less than 10%. Finally, vegetation data collected at 1139 sites in total in 2011 and 2016 were used for the analysis in this study.

Wetland classification

The NWCA developed distinct subpopulation groups for the survey sites to support accurate assessments of species composition and environmental conditions within relevant geographic contexts. These classifications serve as key tools for understanding how the effects of functional trait diversity on productivity and stability vary across different natural and anthropogenic environmental contexts. Specifically, wetlands were classified as herbaceous wetlands dominated by emergent herbaceous plants or woody wetlands dominated by trees and shrubs on the basis of their dominant vegetation and were classified as inland or tidal wetlands on the basis of their hydrology and location^{48,49}. Of the 1139 sites analyzed in this study, 502 were herbaceous wetlands and 637 were woody wetlands. In addition, 835 sites were classified as inland wetlands, whereas 304 were tidal wetlands.

Moreover, the NWCA developed a quantitative definition of anthropogenic disturbance based on physical alterations, soil chemistry, and biological data collected at wetland sites⁴⁹, which reflects a continuous gradient of anthropogenic disturbances ranging from no observable or measurable anthropogenic impacts to highly altered wetland sites⁴⁹. Wetland sites that fall along this continuous disturbance gradient were assigned to one of three disturbance classes: “least disturbed”, “intermediate disturbed”, or “most disturbed”. Six human-mediated physical alteration indices (vegetation removal, vegetation replacement, water addition/subtraction, water obstruction, soil hardening, and surface modification), two soil chemistry indices (heavy metal enrichment factor and heavy metal index), and one biological index (relative percent cover of nonnative plant species) were used to establish the disturbance gradient⁴⁹. Through a stepwise screening process, physical and chemical indices and metrics were used to define the least and most disturbed sites, and then a biological metric was used to further screen the least disturbed sites⁴⁹. First, thresholds for “least disturbed” and “most disturbed” were set for each of the physical and chemical indices and metrics. If any index or metric at a site exceeded the most disturbed thresholds, it was considered “most disturbed”. If any single physical or chemical “least disturbed” threshold was exceeded at a site, it was not considered “least disturbed”. Subsequently, sites identified as “least disturbed” were further screened via the biological metric: for a site to be considered “least disturbed”, the relative percent cover of nonnative species had to be less than 10%. Finally, sites not falling into either the least or most disturbed categories were classified into the “intermediate disturbed” category. In general, the “least disturbed” class describes sites that have the best available physical, chemical, and biological conditions in the current state of the landscape, whereas the “most disturbed” class describes sites that are defined as the most disturbed relative to the “least disturbed”, typically representing 20–30% of NWCA sites⁴⁹. This

stepwise screening method was used to determine a site’s overall disturbance level by prioritizing the most severe indicator among physical, chemical, and biological indices rather than relying on the collective level of all disturbances⁸⁴. This approach accounts for the potential asynchrony and randomness of different disturbance types in natural systems⁸⁵, effectively preventing masking of severe disturbances in specific aspects by less severe ones in others. For a more detailed information on the threshold setting and screening process, please refer to chapter 6 of the NWCA 2016 technical support document⁴⁹. Among the 1139 sites, 269 sites were classified as least disturbed, 573 sites were classified as intermediately disturbed, and 293 sites were classified as most disturbed.

Environmental characteristics

We collected climate data for all sites from CHELSA Version 2.1⁸⁶; these data included the mean annual temperature (MAT, °C) and mean monthly climate moisture index (CMI, kg m⁻² month⁻¹). The CMI is the difference between the precipitation amount and potential evapotranspiration. The soil pH and groundwater water table depth (WTD, from –130 to 0 cm) from NWCA field surveys^{48,49} were included to account for the potential effects of site conditions on the functional characteristics of vegetation, which could influence the magnitude and stability of primary productivity.

Trait data collection and imputation of missing traits

The plant height data were obtained from the NWCA surveys, where the species were categorized into seven height classes based on the observed height in the vegetation plots. The classes were defined as follows: Class 1 (<0.5 m), Class 2 (0.5–2 m), Class 3 (2–5 m), Class 4 (5–15 m), Class 5 (15–30 m), Class 6 (>30 m), and Class E (liana, vine, or epiphyte species). For analytical purposes, we assigned representative average heights to each class: 0.1 m for Class E, 0.25 m for Class 1, 1.25 m for Class 2, 3.5 m for Class 3, 10 m for Class 4, 22.5 m for Class 5, and 30 m for Class 6.

In addition to the available height data from the NWCA surveys, we obtained the mean trait values of four other traits of each species, namely, leaf area (mm²), LNC (mg g⁻¹), SLA (cm² g⁻¹), and LDMC (g g⁻¹), via all available measurements for each species from the TRY plant trait database⁸⁷ (version 6.1, <https://www.try-db.org>). We further improved the coverage of trait data via available mean trait values from the Botanical Information and Ecology Network (BIEN) database (<http://bien.nceas.ucsb.edu/bien/biendata/>)⁸⁸. Specifically, trait mean values from BIEN were used to supplement missing trait mean values in TRY; existing TRY records were retained and not replaced by BIEN entries when there is an overlap between TRY and BIEN. Of the four traits obtained from the trait database, leaf area was available for 1139 species, SLA for 1260 species, LNC for 1002 species, and LDMC for 880 species. Among the 2123 total species, 675 had data for all four traits, 371 had data for three traits, 170 had data for two, 128 had data for one, and 779 lacked data for all four traits. We additionally extracted the species mean height (available for 1491 species) from the TRY and BIEN databases to assess the reliability of calculating functional characteristics via trait data obtained from the database compared with field-observed data. We completed trait information by implementing a phylogenetically informed trait imputation procedure for the five traits at the same time via the ‘missForest’ R package⁸⁹, which is effective and widely used for the imputation of missing trait values^{90,91}. In this method, a random forest algorithm trained with the observed values in a data matrix was used to predict missing values⁸⁹; moreover, phylogenetic information can be included in the trait imputation process to improve the estimates of missing values⁹². We incorporated the evolutionary relationships among species into the imputation process by including the first ten phylogenetic eigenvectors in the matrix to be imputed⁹². To increase the size of the training sample set and reduce

the uncertainty regarding the imputed trait value, we selected an additional 13,038 species with data for at least three of the five traits from the TRY database, excluding the 2123 species in the NWCA, and further improved trait coverage with the BIEN database, resulting in a dataset that included 15,161 species for the imputation procedure. The phylogeny was obtained via the R package 'V.phylomaker'⁹³, with the GBOTB phylogeny serving as the backbone⁹⁴.

We used a hold-out method to assess the accuracy of the trait imputation procedure. We randomly selected 20% of the available values of specific traits of the 2123 wetland species as the validation set and then implemented an imputation procedure without these trait values. After the imputation procedure, we performed linear regression to test the correlation between the actual and imputed values. The predictive accuracy of each trait was sufficiently high ($R^2 > 0.5$), indicating the overall effectiveness of the imputation method employed in this study (Supplementary Fig. 13). Moreover, to estimate the reliability of assessing functional diversity via traits from public databases, we performed correlation analyses to test the correlation between the CWM calculated from the plant height field surveyed by NWCA and the database-derived plant height after imputation, as well as the correlation between the FD_{is} values calculated for the two sources (Supplementary Fig. 14). The results demonstrated a strong correlation between the CWM of the surveyed plant height and the plant height obtained from the imputation procedure ($r = 0.86$, $P < 0.001$), as well as between the FD_{is} values calculated from these two sources ($r = 0.88$, $P < 0.001$). Although the trait data extracted from the public trait database represent species-level means and require imputation to address data gaps, which differ from field-measured data in terms of completeness and the ability to capture intraspecific variation, our test indicates that the trait data extracted from public databases are effective for assessing functional diversity characteristics in wetland communities.

Functional identity and diversity

The functional identity was calculated as the CWM of each trait value, which was generated by calculating the abundance (plant cover)-weighted mean of the species trait values as follows:

$$CWM = \sum_{i=1}^n p_i \times \text{trait}_i \quad (1)$$

where p_i is the relative contribution of species i to the cover of the whole community, n is the number of species, and trait_i is the trait value of species i , as described by de Vries et al.⁹⁵. We performed PCA with the CWMs of the five traits to obtain a composite functional identity via the 'psych' package in R⁹⁶. We used the first axis (CWM_{PC1} , which explained 39% of the variation) and the second axis (CWM_{PC2} , 32% of the variation) of the PCA as variables of functional identity. CWM_{PC1} is associated with resource acquisitive versus conservative strategies and is strongly related to high CWM_{SLA} and CWM_{LNC} values and low CWM_{LDMC} values. CWM_{PC2} was positively related to CWM_{LA} and CWM_{Height} .

Four functional diversity indices, namely, functional richness (FR_{ic}), functional dispersion (FD_{is}), functional divergence (FD_{iv}), and functional evenness (FE_{ve}), were calculated via the 'fundiversity' package⁹⁷. We calculated the four functional diversity indices for all five traits combined (SLA, LNC, LDMC, leaf area, and plant height), as well as separately for resource economics traits (SLA, LNC, and LDMC) and plant size traits (leaf area and plant height). FD_{is} consistently exhibited greater explanatory power than the other three indices for productivity and stability (Supplementary Fig. 15). Therefore, we used FD_{is} , which is the mean distance of each species to the basal-area-weighted centroid of all species in functional trait space⁹⁸, to indicate functional diversity in the analysis.

Wetland productivity and stability

We used the annual maximum NDVI as a proxy for vegetation productivity at the wetland sites. This value corresponds to the yearly maximum photosynthetic activity of vegetation and is considered an indicator of ecosystem productivity⁴⁶. To account for temporal variability and support robust assessments of productivity, we retrieved the NDVI time series covering the period of 2006–2021, which included five years before and after the NWCA sampling period (2011 and 2016). Owing to variations in satellite data coverage and quality, the NDVI data from 2006 to 2011 were obtained from Landsat 5, the data from 2012 to 2013 were sourced from Landsat 7, and the data from 2014 to 2021 were derived from Landsat 8. The NDVI values were calculated via surface reflectance data from the Landsat 5, 7 and 8 Collection 2 Tier 1 datasets (30-m spatial resolution), courtesy of the U.S. Geological Survey, via the Google Earth Engine⁹⁹. Owing to the significant interference of cloud pixels on the NDVI (Supplementary Fig. 16), cloud masking was implemented before computing the NDVI by utilizing the QA_PIXEL band, and pixels flagged as clouds, cloud shadows, snow, and other distortions were filtered and removed from calculations. The NDVI was then calculated as follows:

$$NDVI = \frac{NIR - RED}{NIR + RED} \quad (2)$$

where the NIR and RED bands represent the near-infrared and red bands of the Landsat image, respectively. Following previous studies^{76,100}, the NDVI at each site was calculated as the mean NDVI across nine Landsat pixels within a 3×3 pixel window (90×90 m) approximating the 40-m radius of NWCA field assessment areas (Supplementary Fig. 1). This pixel window includes the pixel corresponding to the NWCA site center and its eight surrounding pixels (Supplementary Fig. 1). Although the nine Landsat pixels cover a slightly larger area than the NWCA site assessment areas and may include minor positional offsets (within 15 m horizontally and vertically), this method provides a more accurate reflection of the site's productivity than other approaches, such as satellite data with 250 m resolution. Owing to the differences in band wavelengths from the ETM (Landsat 5/7) and OLI (Landsat 8) sensors, we transformed the NDVIs of the Landsat 8 OLI to match those of the Landsat 5/7 ETM via a linear correction method¹⁰¹. We then averaged the site-level annual maximum NDVI across 16 years (2006–2021) as an indicator of site productivity and calculated the long-term (2006–2021) mean-to-SD ratio of the annual maximum NDVI to represent the temporal stability of productivity. We further conducted a correlation analysis to test the potential impact of cloud frequency on productivity and stability and observed minimal responses (Supplementary Fig. 17), indicating a low sensitivity to cloud coverage frequency.

Statistical analysis

To assess the effects of functional diversity and identity on productivity and stability, multiple linear regression models were constructed. To meet the assumption of normality, right-skewed stability data were log-transformed, and left-skewed primary productivity data were reflected and subsequently log-transformed prior to statistical analyses. Full models incorporating four functional indices (FD_{is} of resource economics traits, FD_{is} of plant size traits, CWM_{PC1} , and CWM_{PC2}) were fitted. We further performed multiple linear regression models that included interaction terms to evaluate the effects of functional indices on productivity and stability for different wetland types and different anthropogenic disturbance levels. The initial full model included the effects of all four functional indices and their interactions with vegetation types (herbaceous and woody), hydrological types (inland and tidal), or disturbance levels (least, intermediate, and most disturbed). A model selection procedure based on the Akaike information criterion (AIC) was then

implemented to identify the most parsimonious model using the ‘dredge’ function in the *MuMIn* package¹⁰². ANOVA (Type II sums-of-squares) was used to test the effect of each variable in multiple linear regression models. Partial regression plots were plotted using the ‘ggpredict’ function from the *ggeffects* package¹⁰³ to show independent relationships between functional indices and response variables (that is, productivity and stability) based on the results of multiple linear regression models. We used the ‘emtrends’ function in the *emmeans* package to estimate the standardized coefficients (slope) of the functional indices for each wetland group in the multiple linear regression models¹⁰⁴.

Piecewise SEM was used to distinguish the direct and indirect effects of environmental factors, functional identity and functional diversity on primary productivity and stability. The SEMs were constructed on the basis of the a priori model (Supplementary Fig. 3). We assumed that climate variables (MAT and CMI), soil pH, WTD and disturbance intensity could affect primary productivity and stability by regulating functional identity and functional diversity^{60,105}. Moreover, primary productivity and stability can also be directly affected by climate variables, soil factors, and disturbance intensity^{7,8}. To qualify the effect of anthropogenic disturbances in SEM, the disturbance intensity was converted from the original three-level scale (least, intermediate, and most disturbed) to a binary variable (0, least disturbed; 1, intermediate or most disturbed). We first fitted the full SEMs that included all plausible pathways based on the a priori model. Then, we applied stepwise selection via the ‘stepAIC’ function to sequentially eliminate variables that did not substantially contribute to the model paths. Next, a final piecewise SEM was built to integrate the identified significant paths, and model fit was evaluated via Shipley’s test of d-separation: Fisher’s C statistic ($P > 0.05$ for a satisfactory fit) was calculated using the *piecewiseSEM* package¹⁰⁶. Bootstrap resampling (500 iterations) was applied to generate parameter estimates for each path coefficient via the ‘bootEff’ function in the *semEff* package¹⁰⁷. The total effects and 95% confidence intervals of each variable with respect to productivity and stability were calculated via the ‘semEff’ function in the *semEff* package¹⁰⁷. SEM was conducted across all wetland sites, as well as separately for different wetland types and varying levels of anthropogenic disturbance. The effects of binary anthropogenic disturbances were not included in the models for wetland sites under different anthropogenic disturbance levels. For all the models, the assumption of normality was checked by visually inspecting histograms of the residuals. A variance inflation factor (VIF) threshold of less than 3 was applied to prevent multicollinearity among variables. All the statistical tests were two-sided, and all the statistical analyses were performed in R 4.4.2¹⁰⁸.

Reporting summary

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

Data availability

The wetland vegetation and soil factor data were downloaded from the NWCA database (<https://www.epa.gov/national-aquatic-resource-surveys/nwca>). Species mean values of leaf traits and plant height were downloaded from the TRY database (<https://www.try-db.org>) and the BIEN 4 database (<https://bien.nceas.ucsb.edu/bien/>). The Landsat surface reflectance data are available in the Google Earth Engine Data Catalog (<https://developers.google.com/earth-engine/datasets/catalog/landsat>). The climate data were collected from the CHELSA database (<https://chelsa-climate.org>). The data that support the findings of this study are available in figshare (<https://doi.org/10.6084/m9.figshare.26509651>)¹⁰⁹. Source data are provided in this paper.

Code availability

All codes are archived in figshare (<https://doi.org/10.6084/m9.figshare.26509651>)¹⁰⁹.

References

- Zedler, J. B. & Kercher, S. Wetland Resources: Status, trends, ecosystem services, and restorability. *Annu. Rev. Environ. Resour.* **30**, 39–74 (2005).
- Leifeld, J. & Menichetti, L. The underappreciated potential of peatlands in global climate change mitigation strategies. *Nat. Commun.* **9**, 1071 (2018).
- Loreau, M. et al. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808 (2001).
- Xi, Y., Peng, S., Ciais, P. & Chen, Y. Future impacts of climate change on inland Ramsar wetlands. *Nat. Clim. Chang.* **11**, 45–51 (2021).
- Isbell, F. et al. Expert perspectives on global biodiversity loss and its drivers and impacts on people. *Front. Ecol. Environ.* **21**, 94–103 (2022).
- Diaz, S. & Cabido, M. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Eco. Evol.* **16**, 646–655 (2001).
- van der Plas, F. Biodiversity and ecosystem functioning in naturally assembled communities. *Biol. Rev.* **94**, 1220–1245 (2019).
- He, N. et al. Predicting ecosystem productivity based on plant community traits. *Trends Plant Sci.* **28**, 43–53 (2023).
- Moor, H. et al. Towards a trait-based ecology of wetland vegetation. *J. Ecol.* **105**, 1623–1635 (2017).
- Mokany, K., Ash, J. & Roxburgh, S. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *J. Ecol.* **96**, 884–893 (2008).
- Petchey, O. L. & Gaston, K. J. Functional diversity (FD), species richness and community composition. *Ecol. Lett.* **5**, 402–411 (2002).
- Barry, K. E. et al. The future of complementarity: Disentangling causes from consequences. *Trends Eco. Evol.* **34**, 167–180 (2019).
- Grime, J. P. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902–910 (1998).
- Rahman, M. M. et al. Functional composition outweighs taxonomic and functional diversity in maintaining ecosystem properties and processes of mangrove forests. *Glob. Chang. Biol.* **30**, e17152 (2024).
- Engel, T. et al. Traits of dominant plant species drive normalized difference vegetation index in grasslands globally. *Glob. Ecol. Biogeogr.* **32**, 695–706 (2023).
- Lepš, J., de Bello, F., Šmilauer, P. & Doležal, J. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* **34**, 856–863 (2011).
- Májeková, M., de Bello, F., Doležal, J. & Lepš, J. Plant functional traits as determinants of population stability. *Ecology* **95**, 2369–2374 (2014).
- Isbell, F. I., Polley, H. W. & Wilsey, B. J. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecol. Lett.* **12**, 443–451 (2009).
- Craven, D. et al. Multiple facets of biodiversity drive the diversity–stability relationship. *Nat. Eco. Evol.* **2**, 1579–1587 (2018).
- Chen, C., Xiao, W. & Chen, H. Y. H. Meta-analysis reveals global variations in plant diversity effects on productivity. *Nature* **638**, 435–440 (2025).
- Reich, P. B. et al. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336**, 589–592 (2012).
- Wagg, C. et al. Biodiversity–stability relationships strengthen over time in a long-term grassland experiment. *Nat. Commun.* **13**, 7752 (2022).
- Zhang, Y., Wang, R., Kaplan, D. & Liu, J. Which components of plant diversity are most correlated with ecosystem properties? A case study in a restored wetland in northern China. *Ecol. Indic.* **49**, 228–236 (2015).

24. Zhang, Y., He, N., Loreau, M., Pan, Q. & Han, X. Scale dependence of the diversity-stability relationship in a temperate grassland. *J. Ecol.* **106**, 1227–1285 (2018).
25. Ratcliffe, S. et al. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecol. Lett.* **20**, 1414–1426 (2017).
26. Garcia-Palacios, P., Gross, N., Gaitan, J. & Maestre, F. T. Climate mediates the biodiversity-ecosystem stability relationship globally. *Proc. Natl. Acad. Sci. USA* **115**, 8400–8405 (2018).
27. Gopal, B. *The Wetlands Handbook* (Blackwell Publishing, Oxford, UK, 2009).
28. Schenk, H. J. & Jackson, R. B. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *J. Ecol.* **90**, 480–494 (2002).
29. Lang, N., Jetz, W., Schindler, K. & Wegner, J. D. A high-resolution canopy height model of the Earth. *Nat. Eco. Evol.* **7**, 1778–1789 (2023).
30. Dimitrakopoulos, P. G. & Schmid, B. Biodiversity effects increase linearly with biotope space. *Ecol. Lett.* **7**, 574–583 (2004).
31. Niklaus, P. A., Baruffol, M., He, J. S., Ma, K. & Schmid, B. Can niche plasticity promote biodiversity-productivity relationships through increased complementarity? *Ecology* **98**, 1104–1116 (2017).
32. Ammer, C. Diversity and forest productivity in a changing climate. *N. Phytol.* **221**, 50–66 (2019).
33. Maestre, F. T., Callaway, R. M., Valladares, F. & Lortie, C. J. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* **97**, 199–205 (2009).
34. Moi, D. A. et al. Human pressure drives biodiversity–multifunctionality relationships in large Neotropical wetlands. *Nat. Eco. Evol.* **6**, 1279–1289 (2022).
35. Wilsey, B., Martin, L., Xu, X., Isbell, F. & Polley, H. W. Biodiversity: Net primary productivity relationships are eliminated by invasive species dominance. *Ecol. Lett.* **27**, e14342 (2024).
36. Chacon-Labela, J. et al. How to improve scaling from traits to ecosystem processes. *Trends Eco. Evol.* **38**, 228–237 (2023).
37. Wright, I. J. et al. The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004).
38. Violle, C. et al. Let the concept of trait be functional!. *Oikos* **116**, 882–892 (2007).
39. Diaz, S. et al. The global spectrum of plant form and function. *Nature* **529**, 167–171 (2016).
40. Freschet, G. T., Cornelissen, J. H. C., Van Logtestijn, R. S. P. & Aerts, R. Evidence of the ‘plant economics spectrum’ in a subarctic flora. *J. Ecol.* **98**, 362–373 (2010).
41. Reich, P. B. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* **102**, 275–301 (2014).
42. Lavorel, S. & Grigulis, K. How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *J. Ecol.* **100**, 128–140 (2012).
43. Li, Y. et al. Leaf size of woody dicots predicts ecosystem primary productivity. *Ecol. Lett.* **23**, 1003–1013 (2020).
44. Fajardo, A., Siefert, A. & Laughlin, D. C. Wood density and leaf size jointly predict woody plant growth rates across (but not within) species along a steep precipitation gradient. *J. Ecol.* **112**, 374–388 (2023).
45. Liu, X. et al. Enhancing ecosystem productivity and stability with increasing canopy structural complexity in global forests. *Sci. Adv.* **10**, ead11947 (2024).
46. Pettorelli, N. et al. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Eco. Evol.* **20**, 503–510 (2005).
47. Dronova, I., Taddeo, S. & Harris, K. Plant diversity reduces satellite-observed phenological variability in wetlands at a national scale. *Sci. Adv.* **8**, eabl8214 (2022).
48. U.S. Environmental Protection Agency. National Wetland Condition Assessment: 2011 Technical Report, Technical Report EPA-843-R-15-006 (U.S. Environmental Protection Agency, Washington, DC, 2016).
49. U.S. Environmental Protection Agency. National Wetland Condition Assessment: 2016 Technical Support Document, Technical Report EPA-841-B-23-001 (U.S. Environmental Protection Agency, Washington, DC, 2023).
50. Wang, S. et al. How complementarity and selection affect the relationship between ecosystem functioning and stability. *Ecology* **102**, e03347 (2021).
51. Zhang, Y., Chen, H. Y. H. & Coomes, D. Individual size inequality links forest diversity and above-ground biomass. *J. Ecol.* **103**, 1245–1252 (2015).
52. Wilcox, K. R. et al. Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecol. Lett.* **20**, 1534–1545 (2017).
53. Wright, A. J. et al. Plants are less negatively affected by flooding when growing in species-rich plant communities. *N. Phytol.* **213**, 645–656 (2017).
54. Bennett, A. C., McDowell, N. G., Allen, C. D. & Anderson-Teixeira, K. J. Larger trees suffer most during drought in forests worldwide. *Nat. Plants* **1**, 15139 (2015).
55. Williams, L. J. et al. Enhanced light interception and light use efficiency explain overyielding in young tree communities. *Ecol. Lett.* **24**, 996–1006 (2021).
56. Finegan, B. et al. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *J. Ecol.* **103**, 191–201 (2015).
57. Poorter, L. et al. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* **89**, 1908–1920 (2008).
58. Eskelinen, A., Harpole, W. S., Jessen, M. T., Virtanen, R. & Hautier, Y. Light competition drives herbivore and nutrient effects on plant diversity. *Nature* **611**, 301–305 (2022).
59. Chandregowda, M. H. et al. Root trait shifts towards an avoidance strategy promote productivity and recovery in C3 and C4 pasture grasses under drought. *Funct. Ecol.* **36**, 1754–1771 (2022).
60. Polley, H. W., Isbell, F. I. & Wilsey, B. J. Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity. *Oikos* **122**, 1275–1282 (2013).
61. Siefert, A. et al. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.* **18**, 1406–1419 (2015).
62. Trebitz, A. S., Nestlerode, J. A. & Herlihy, A. T. USA-scale patterns in wetland water quality as determined from the 2011 National Wetland Condition Assessment. *Environ. Monit. Assess.* **191**, 266 (2019).
63. Chen, X., Reich, P. B., Taylor, A. R., An, Z. & Chang, S. X. Resource availability enhances positive tree functional diversity effects on carbon and nitrogen accrual in natural forests. *Nat. Commun.* **15**, 8615 (2024).
64. Fischer, F. M. et al. Plant species richness and functional traits affect community stability after a flood event. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150276 (2016).
65. Minden, V., Andratschke, S., Spalke, J., Timmermann, H. & Kleyer, M. Plant trait–environment relationships in salt marshes: Deviations from predictions by ecological concepts. *Perspect. Plant Ecol. Evol. Syst.* **14**, 183–192 (2012).
66. Minden, V. & Kleyer, M. Ecosystem multifunctionality of coastal marshes is determined by key plant traits. *J. Veg. Sci.* **26**, 651–662 (2015).
67. Bourgeois, C. F. et al. Four decades of data indicate that planted mangroves stored up to 75% of the carbon stocks found in intact mature stands. *Sci. Adv.* **10**, eadk5430 (2024).

68. Schulte Ostermann, T. et al. Unraveling plant strategies in tidal marshes by investigating plant traits and environmental conditions. *J. Veg. Sci.* **32**, e13038 (2021).
69. Perri, S., Detto, M., Porporato, A. & Molini, A. Salinity-induced limits to mangrove canopy height. *Glob. Ecol. Biogeogr.* **32**, 1561–1574 (2023).
70. MacDougall, A. S., McCann, K. S., Gellner, G. & Turkington, R. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* **494**, 86–89 (2013).
71. Carreño-Rocabado, G. et al. Effects of disturbance intensity on species and functional diversity in a tropical forest. *J. Ecol.* **100**, 1453–1463 (2012).
72. Branoff, B. L. Quantifying the influence of urban land use on mangrove biology and ecology: A meta-analysis. *Glob. Ecol. Biogeogr.* **26**, 1339–1356 (2017).
73. Rout, M. E. & Callaway, R. M. An invasive plant paradox. *Science* **324**, 734–735 (2009).
74. Leishman, M. R., Cooke, J., Richardson, D. M. & Newman, J. Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. *J. Ecol.* **102**, 1451–1461 (2014).
75. Pollock, M. M., Naiman, R. J. & Hanley, T. A. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology* **79**, 94–105 (1998).
76. Taddeo, S., Dronova, I. & Depsky, N. Spectral vegetation indices of wetland greenness: Responses to vegetation structure, composition, and spatial distribution. *Remote Sens. Environ.* **234**, 111467 (2019).
77. Byrd, K. B., O’Connell, J. L., Di Tommaso, S. & Kelly, M. Evaluation of sensor types and environmental controls on mapping biomass of coastal marsh emergent vegetation. *Remote Sens. Environ.* **149**, 166–180 (2014).
78. Dronova, I. & Taddeo, S. Canopy leaf area index in non-forested marshes of the California Delta. *Wetlands* **36**, 705–716 (2016).
79. van Leeuwen, W. J. D., Orr, B. J., Marsh, S. E. & Herrmann, S. M. Multi-sensor NDVI data continuity: Uncertainties and implications for vegetation monitoring applications. *Remote Sens. Environ.* **100**, 67–81 (2006).
80. Sun, C., Fagherazzi, S. & Liu, Y. Classification mapping of salt marsh vegetation by flexible monthly NDVI time-series using Landsat imagery. *Estuar. Coast. Shelf Sci.* **213**, 61–80 (2018).
81. Ashok, A., Rani, H. P. & Jayakumar, K. V. Monitoring of dynamic wetland changes using NDVI and NDWI based landsat imagery. *Remote Sens. Appl. Soc. Environ.* **23**, 100547 (2021).
82. Lenoir, J. et al. Unveil the unseen: Using LiDAR to capture time-lag dynamics in the herbaceous layer of European temperate forests. *J. Ecol.* **110**, 282–300 (2022).
83. Bai, Y., Han, X., Wu, J., Chen, Z. & Li, L. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* **431**, 181–184 (2004).
84. Herlihy, A. T. et al. Striving for consistency in the National Wetland Condition Assessment: developing a reference condition approach for assessing wetlands at a continental scale. *Environ. Monit. Assess.* **191**, 327 (2019).
85. Burton, P. J., Jentsch, A. & Walker, L. R. The ecology of disturbance interactions. *Bioscience* **70**, 854–870 (2020).
86. Karger, D. N. et al. Climatologies at high resolution for the earth’s land surface areas. *Sci. Data* **4**, 170122 (2017).
87. Kattge, J. et al. TRY plant trait database - enhanced coverage and open access. *Glob. Chang. Biol.* **26**, 119–188 (2020).
88. Maitner, B. S. et al. The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol. Evol.* **9**, 373–379 (2017).
89. Stekhoven, D. J. & Bühlmann, P. MissForest—non-parametric missing value imputation for mixed-type data. *Bioinformatics* **28**, 112–118 (2011).
90. Carmona, C. P. et al. Fine-root traits in the global spectrum of plant form and function. *Nature* **597**, 683–687 (2021).
91. Barajas Barbosa, M. P. et al. Assembly of functional diversity in an oceanic island flora. *Nature* **619**, 545–550 (2023).
92. Penone, C. et al. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods Ecol. Evol.* **5**, 961–970 (2014).
93. Jin, Y. & Qian, H. V. PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* **42**, 1353–1359 (2019).
94. Smith, S. A. & Brown, J. W. Constructing a broadly inclusive seed plant phylogeny. *Am. J. Bot.* **105**, 302–314 (2018).
95. de Vries, F. T. et al. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecol. Lett.* **15**, 1230–1239 (2012).
96. Revelle, W. *psych: Procedures for Psychological, Psychometric, and Personality Research.* (2024).
97. Grenié, M. & Gruson, H. fundiversity: a modular R package to compute functional diversity indices. *Ecography* **2023**, e06585 (2023).
98. Laliberte, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305 (2010).
99. Gorelick, N. et al. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* **202**, 18–27 (2017).
100. Taddeo, S., Dronova, I. & Harris, K. The potential of satellite greenness to predict plant diversity among wetland types, ecoregions, and disturbance levels. *Ecol. Appl.* **29**, e01961 (2019).
101. Roy, D. P. et al. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. *Remote Sens. Environ.* **185**, 57–70 (2016).
102. Barton, K. *MuMIn: Multi-Model Inference.* (2024).
103. Lüdtke, D. ggeffects: Tidy data frames of marginal effects from regression models. *J. Open Source Softw.* **3**, 772 (2018).
104. Lenth, R. V. et al. *emmeans: Estimated Marginal Means, aka Least-Squares Means.* (2025).
105. Diaz, S. et al. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. USA* **104**, 20684–20689 (2007).
106. Lefcheck, J. S. & Freckleton, R. piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).
107. Murphy, M. V. *semEff: Automatic Calculation of Effects for Piecewise Structural Equation Models.* (2024).
108. Core, R. Team. *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing. (2020).
109. Liu, H. et al. Plant functional identity contributes more to productivity and stability than functional diversity in wetlands. *figshare* <https://doi.org/10.6084/m9.figshare.26509651> (2025).

Acknowledgements

The National Wetland Condition Assessment 2011 and 2016 data were a result of the collective efforts of dedicated field crews, laboratory staff, data management and quality control staff, analysts and many others from EPA, states, tribes, federal agencies, universities, and other organizations. We acknowledge the TRY initiative and the BIEN database, along with their contributors and administrators. We thank Xinxin Wang and Xi Zhang for their assistance with remote sensing analysis. This work was supported by the National Key Research and Development Program of China (2023YFF1304504, M.N.), the National Natural Science Foundation of China (32430065, M.N.), the Shanghai Science and Technology Innovation Action Plan (23015810100, B.L.), the Shanghai Pilot Program for Basic Research—Fudan University 21TQ1400100 (21TQ004, M.N.), and the Science and Technology Plan Project of Shanghai (23DZ1202700, M.N.).

Author contributions

M.N. conceived the ideas. H.L. collected data and performed statistical analyses with help from J.X., X.Q., and X.X. H.L. wrote the first draft, and M.N., J.W., and B.L. revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41467-025-65822-9>.

Correspondence and requests for materials should be addressed to Ming Nie.

Peer review information *Nature Communications* thanks Yingji Pan, and the other anonymous reviewer(s) for their contribution to the peer review of this work. A peer review file is available.

Reprints and permissions information is available at <http://www.nature.com/reprints>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2025