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What are the impacts of *Spartina alterniflora* invasion on intertidal macrobenthic communities? A global meta-analysis

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What are the impacts of *Spartina alterniflora* invasion on intertidal macrobenthic communities? A global meta-analysis

Wei Hu[‡], Dawei Wu[‡], Zhenqi Wang[‡], Shuqing An[§], Changhu Lu[‡]

‡College of Life Sciences, Nanjing Forestry University, Longpan Street, Nanjing, Jiangsu Province, China

§ Nanjing University School of Life Sciences, Xianlin Street, Nanjing, Jiangsu Province, China

Corresponding author: Changhu Lu (luchanghu@njfu.com.cn)

Abstract

There is currently no consistent conclusion about the impacts of global *Spartina alterniflora* invasion on intertidal macrobenthic communities, and the impact mechanisms are also not clear enough due to the limitations in study sites and duration. Here, after collecting and extracting 2110 data from 96 studies around the world, we utilized hierarchical meta-analysis to quantify the impacts of *Spartina alterniflora* invasion on intertidal macrobenthic communities, and systematically analyzed and summarized the factors influencing invasion results for the first time. The results showed that the invasion of *Spartina alterniflora* generally has a negative impact on macrobenthic communities, but has a positive impact on species number and richness index of macrobenthic communities. The pattern of influence strongly depends on the native habitat, invasion duration, average annual temperature, sediment type and tide level, which indicates that *Spartina alterniflora* affects macrobenthic communities by altering the external environment of the invaded area, and the habitat heterogeneity in different intertidal zones also leads to diverse impacts of *Spartina alterniflora* invasion on macrobenthic communities. Our study provides important insights for a comprehensive understanding of biological invasions and offers new perspectives for future ecological restoration in intertidal zones.

Keywords

Biodiversity, biological invasion, coastal wetlands, macrobenthos, smooth cordgrass

Introduction

Plant invasions in the intertidal zone are complex and challenging issues on a global scale (Powell et al. 2011). As ecological engineers, exotic plants can alter the biological community structure and diversity level of the intertidal zone by modifying external environmental factors (Crooks 2002). While they have a negative impact on the ecosystem, they are sometimes often accompanied by some positive effects (Rodriguez 2006). Most plants of the genus *Spartina* originate from the Gulf of Mexico and the Atlantic coasts of North America. Many species in this genus are recognized as highly invasive (Thiebaut 2007), especially *Spartina alterniflora*.

Many researchers have conducted extensive research on the impact of the invasion of *Spartina alterniflora* on macrobenthos globally, especially in coastal areas of China. Some of them believe that the invasion of *Spartina alterniflora* can cause serious negative impacts on macrobenthic communities (Zhou et al. 2009; Su et al. 2020; Chen et al. 2023), while others hold the opposite view (Quan et al. 2016; Han et al. 2022; Lu et al. 2022). However, there is still no unified conclusion so far.

The response of macrobenthic communities to *Spartina alterniflora* invasion may be regulated by multiple environmental factors. Many studies have shown that various factors such as invasion duration, sampling season, invaded habitat, and tide level can affect the results (Chen et al. 2019; Ge et al. 2019; Qiu et al. 2019; Li et al. 2023). Additionally, our long-term field surveys suggest that different latitudes, temperatures, coastal types and sediment types in intertidal zones invaded by *Spartina alterniflora* will also have varying impacts on macrobenthic communities, but most studies may have overlooked these issues due to their focus on a small study area.

Ning et al. analyzed the effects of *Spartina* invasion and removal on intertidal native animal communities (Ning et al. 2021). However, it has paid less attention to the effects of *Spartina alterniflora* invasion on macrobenthos, and lacked analysis of environmental factors associated with *Spartina alterniflora* invasion that may affect macrobenthic communities.

Therefore, we conducted a global meta-analysis to quantify the extent and direction of the impact of *Spartina alterniflora* invasion on macrobenthic community structure and biodiversity, and summarized the key factors that controlled the research results, providing a theoretical basis for the global ecological restoration of the intertidal zone to be carried out efficiently, economically and purposefully in the future.

Materials and methods

Literature sources and screening

We conducted a systematic literature search for publications in China National Knowledge Infrastructure (https://www.cnki.net/), Web of Science (http://www.webofknowledge.com/), Google Scholar (https://scholar.google.com/) and some other resources. The search was performed form December 2023 to January 2024 by using the following search terms: (Smooth Cordgrass or *Spartina alterniflora*) and (Macrobenthos or Macrobenthic community or Benthic macrofauna or Benthic macrofaunal community). After removing publications without full-text access, we collected a total of 322 publications published between December 1984 and January 2024.

We selected relevant studies according to title and full text, finally we selected studies that met the following criteria: (1) Evaluating the impact of *Spartina alterniflora* invasion on one or more indices of macrobenthic species number, density, biomass and diversity index (including the Shannon-Wiener diversity index, Pielou evenness index, Margalef species richness index and Simpson dominance index); (2) Including replicated studies with treatment groups (invaded habitat) and control groups (uninvaded habitat), where mean values and sample sizes were presented. (3) The study sites must be located outside the native range of *Spartina alterniflora* (i.e. outside the Atlantic coast of North America). (4) Studies about the impacts of other *Spartina* species or hybrid *Spartina* species on macrobenthos communities would be excluded. (5) Exclude studies on the effects of removing *Spartina alterniflora* on macrobenthic communities. To avoid omissions or duplication, the collection and screening of publications were completed independently by three researchers and then handed over to one researcher for proofreading and summary. In addition, since most reports on the Simpson index in publications refer to the Simpson dominance index, to ensure the accuracy of the analysis results, the Simpson diversity index reported in few publications were converted into the Simpson dominance index. Finally, based on mentioned priori criteria, 96 publications, including 67 research articles, 1 preprint article and 28 dissertations, were retained in our meta-analysis. Appendix S1 and Appendix S1 provide the PRISMA flow diagram and a list of these above publications.

Data extraction and proceeding

First, we extracted the sample sizes, mean values and standard deviation of treatment and control groups from these publications. The mean values include the species number, density, biomass, shannon-wiener diversity index, pielou evenness index, margalef abundance index and simpson dominance index in each study site (Appendix S1). Since quadrats and traps are primarily used to collect macrobenthos in the intertidal zone, the number of quadrats or traps was used as the sample size during the sampling process.

Second, We extracted environmental factors from publications that could potentially influence the analysis results as explanatory variables, including: (1) Latitude; (2) Average Annual Temperature (AAT: °C); (3) Sediment type (ST: Mud, Mix, Sand); (4) Costal landform (CL: Accumulation, Erosion); (5) Tide level (TL: Low, Middle, High); (6) Invasion duration (ID: 0 to5 year, 5 to 10 year, 10 to 15 year, Over 15 year); (7)

Sampling season (SS: Spring, Summer, Autumn, Winter); (8) Native habitat (CH: Bare flat, *Suaeda salsa*, *Scirpus mariquete*, *Phragmites australis*, *Tamarix chinensis*, Mangrove); (9) Invasive habitat (IH: *Spartina alterniflora*, *Spartina alterniflora* & *Scirpus mariquete*, *Spartina alterniflora* & *Phragmites australis*, *Spartina alterniflora* & Mangrove). Because the seasonal changes in the Northern and Southern Hemispheres are opposite, we adjusted the sampling seasons in the Southern Hemisphere during the data entry process, while the division and entry of other influencing factors were based on the publications. Additionally, we extracted supplementary data, including study site location, longitude, author's name and publication year to distinguish different research cases.

Third, we extracted data from these 96 publications following these criteria: (1) If a study includes cases from different study areas or sampling seasons, each case is entered into the database as an independent sample. (2) If there are multiple treatment groups using the same control group in a study, each treatment group will be entered into the database as an independent case. (3) Habitat types in treatment groups must correspond to the native habitat in the controls. For example, the control of *Spartina alterniflora* & mangrove habitat in the treatment group is the mangrove habitat. (4) If some publications don't have information about latitudes and longitudes, they were identified on Google Earth (https://earth.google.com/). (5) Sample sizes, means, and standard deviation of treatment and control groups were extracted either from tables or measured from figures using the GetData Graph Digitizer 2.26 (http://getdata-graph-digitizer.com/). In order to reduce errors caused by researchers during the data extraction process, it was completed independently by three people, and then handed over to one person for proofreading and entry into the database.

Finally, we extracted 2110 data from 96 publications, and the research locations were distributed along the Pacific coast of Asia, the Pacific coast of North America, and the Atlantic coast of South America (Figure 1).

Effect size and variance calculation

We used log response ratio (LRR) to measure the effect size, and calculated the variance (υ) of each effect size (Hedges et al. 1999).

$$LRR = ln(Xt/Xc)\,,$$

$$v = \frac{SDt^2}{Nt \times Xt^2} + \frac{SDc^2}{Nc \times Xc^2}\,,$$

Where Nt and Nc are the sample sizes of the treatment and control groups, Xt and Xc are the mean values of the treatment and control groups, SDt and SDc are the standard deviations of the treatment and control groups, respectively. If several cases are missing standard deviations, the square root of the mean value is used to calculate them for species data that conforming to the Poisson distribution, and the standard deviation for other data is calculated using the standard error multiplied by the square root of the sample size. If standard errors are also missing, the “Bracken1992” method is used to estimate the missing standard errors.

Meta-analysis

Our meta-analysis mainly includes three parts: cumulative effect size calculation, explanatory variable analysis and assessment of publication bias.

During the calculation of the cumulative effect size, variations exist not only within cases, but also among different cases due to differences in time, personnel, methods, and study sites, and the nested structure of some data in the database can also lead to the non-independence of the effect size (Solgaard 2020). Therefore, to ensure the accuracy of the results, in meta-analysis, we need to consider not only the variance within the case but also the variance between the cases. So after constructing a variance-covariance matrix, we used hierarchical random-effects meta-analysis to evaluate the impact of *Spartina alterniflora* invasion on various indicators of macrobenthic communities (Lajeunesse 2011; Veroniki et al. 2016; Wallace et al. 2017).When the heterogeneity of the cumulative effect size is significant ($P < 0.05$), and its 95% confidence interval (95%CI) didn't overlap with 0, it indicates a significant positive or negative effect, and there are explanatory variables that can create heterogeneity in the cumulative effect size.

For each explanatory variables, we used multilevel meta-analysis models with random effects to account for differences between studies (Veroniki et al. 2016; Wallace et al. 2017). The heterogeneity of effect sizes (Qt) can be divided into the variance explained by explanatory variables (Qm) and the residual error variance (Qe).When the heterogeneity of Qm value is significant ($P<0.05$), it means that the explanatory variable has an impact on the effect size, and the direction of this impact (positive or negative) can be determined by the estimated value and its 95% confidence interval (Borenstein et al. 2021).To avoid strong correlations between explanatory variables that could decrease model confidence and interpretability, we evaluated the correlation and collinearity between explanatory variables using Spearman's rank correlation coefficient and variance inflation factor (VIF) (Moreira et al. 2018). Subsequently, we analyzed whether the explanatory variables that significantly impact the cumulative effect size exhibit significant differences at different levels through multiple comparisons, and conducted multi-model selection using Akaike's information criterion (AIC) to determine the relative importance of each explanatory variable on the cumulative effect value.

To test the potential publication bias in each cumulative effect size, we first graphed the funnel plots for each cumulative effect size, and then examined funnel plot asymmetry using Egger's regression test (Sterne and Egger 2005; Nakagawa et al. 2017). If the effect size is symmetrically distributed in the funnel plot ($P>0.05$), it indicates that the results are not affected by publication bias; If the effect size is asymmetric in the funnel plot ($P<0.05$), trim and fill is also used to adjust for funnel plot asymmetry from publication bias (Duval and Tweedie 2000). Additionally, Rosenberg's fail-safe number was also used to examine the robustness of cumulative effect size (Rosenberg 2005). A fail-safe number can estimate the number of unpublished or missing studies that are needed to be added to reduce cumulative effect size of heterogeneity to a non-significant level ($P > 0.05$). The result is often considered robust if the fail-safe number of the cumulative effect size is greater than 5K +10, where K is the number of studies included in meta-analysis

Data processing, statistical analysis and graph production were completed by using "metafor", "metagear", "ggplot2", "glmulti, "orchard" in R 4.3.3 and Excel 2021 (Viechtbauer 2010; Wolfgang 2010; Nakagawa et al. 2021).

Results

Responses of macrobenthic communities to *Spartina alterniflora* invasions

Overall, *Spartina alterniflora* invasion had a significant negative impact on macrobenthos communities ($P < 0.05$), and this impact varied across different indicators ($P < 0.001$). Specifically, *Spartina alterniflora* invasion significantly reduced biomass ($P < 0.001$) while significantly increasing species number and the Margalef richness index ($P < 0.05$). Although not statistically significant, there was a decreasing trend observed in the abundance, Shannon-Wiener diversity index, Pielou evenness index due to *Spartina alterniflora* invasion, while the Simpson dominance index showed an increasing trend (Figure 2).

Test results of heterogeneity and significance

The results of the heterogeneity test revealed that the cumulative effect size heterogeneity (Qt) for all indicators was significant ($P < 0.0001$), and the ratio of the variance between cases to the total variance (I^2) exceeded 98%, indicating high heterogeneity among them (Higgins et al., 2003). Therefore, it was necessary to introduce explanatory variables for interpretation (I^2 and Qt values of each cumulative effect value are shown in Table S1).The results of the collinearity test showed that there was significant collinearity between the average annual temperature and latitude. After excluding the explanatory variable "latitude", the correlation between the remaining explanatory variables (|r| < 0.7) and the VIF value (all less than 5) are all low (Table S2). Subsequently, we analyzed the effects of different explanatory variables on the cumulative effect value of each indicator. The results indicated that, except for the invaded habitat (IH), which had no significant effect on the cumulative effect value of each indicator, the remaining explanatory variables had significant effects on the cumulative effect value of each indicator in different degrees (Figure 3 and Figure 4, specific values of each variable are shown in Table S3).

The impact of explanatory variables on mean effect size

In general, the annual average temperature has a significant positive correlation with the cumulative effect value. For each classification index, the species number, density and biomass of macrobenthic communities in the invaded area increased with the rising annual average temperature, while the Simpson dominance index decreased with the increase of temperature. However, the influence of annual average temperature on the Shannon-Wiener diversity index, Pielou evenness index, and Margalef richness index was not significant.

For sediment types, the impact of *Spartina alterniflora* invasion on macrobenthic communities was significantly positive in sandy and mixed tidal zones, and significantly negative in muddy tidal zones. The effect size of species number, density, Shannon-Wiener diversity index and Margalef species richness index showed the same trend as the general population, but the effect size of biomass, Pielou evenness index and Simpson dominance index were not significantly affected by the sediment type.

For coastal landform, although it has no significant effects on the macrobenthic communities in *Spartina alterniflora* invasion area, the invasion of *Spartina alterniflora* can significantly increase the number of macrobenthos species and reduce macrobenthos biomass in accumulation coast, while showing the opposite trend in erosion coast.

The species number, density, and biomass of macrobenthos typically increased during the early stage of *Spartina alterniflora* invasion (0 to 5 years). However, this effect became less significant with increasing invasion time and even exhibited a reverse trend. In contrast, the impact of invasion duration on the diversity indexes of macrobenthos was not significant.

Except for the significant decrease in the biomass of macrobenthic communities in areas invaded by *Spartina alterniflora* in summer, the impact of the sampling season on various indicators of the macrobenthic communities in *Spartina alterniflora* habitats shows no significant difference.

For native habitat type, *Spartina alterniflora* invasion significantly decreased the density and biomass of macrobenthos on bare flat, and all indexes except Simpson dominance index also showed a decreasing trend with the invasion of *Spartina alterniflora*, although there was no significant difference at the statistical level. While in the intertidal zone covered by native vegetation, the invasion of *Spartina alterniflora* into the habitats of *Suaeda salsa*, *Phragmites australis* and *Tamarix chinensis* tends to increase the number of species in their habitats. Additionally, it increases the Shannon-Wiener diversity index of macrobenthos in the habitat of *Tamarix chinensis*. However, the impact on various indicators of macrobenthos in *Scirpus mariquete* and mangrove habitats is not significant.

Relative importance of explanatory variables

We rank the importance of explanatory variables that have a significant impact on the cumulative effect size by weight, and the results show that: In general, ID, TL, AAT, and CH are identified as key factors influencing the macrobenthic communities in *Spartina alterniflora*-invaded areas. Specifically, TL, AAT, CL, and CH play significant roles in impacting the number of macrobenthos species affected by *Spartina alterniflora* invasion. The density of macrobenthos in *Spartina alterniflora* habitat is mainly influenced by ID, TL, and AAT, while CL and AAT have the greatest impact on macrobenthic biomass in *Spartina alterniflora* habitat. TL primarily affects the Shannon-Wiener diversity index and Pielou evenness index of macrobenthos in *Spartina alterniflora* habitat. The main factors affecting the Margalef richness index and Simpson dominance index of macrobenthos in *Spartina alterniflora* habitat are ST and AAT (Figure 5).

Assessment of publication bias

Egger's regression test showed that the funnel plot of the cumulative effect values of macrobenthos species number, abundance, Shannon-Wiener diversity index, Pielou evenness index, Margalef richness index and Simpson dominance index all exhibited symmetry ($P>0.05$), but there is a slight publication bias in the cumulative effect values of overall and biomass. However, the Rosenberg loss safety factors for both are sufficiently large (both exceeding 5K+10). The research of Doherty et al. (Doherty et al 2021) demonstrates that due to the varying calculation principles among different types of publication bias detection methods, the conclusions generated may be conflicting. Nonetheless, it can be considered that the potential impact of publication bias on the results of meta-analysis is minimal. The funnel plots and loss safety coefficient values of various indicators are shown in Figure S3.

Discussion

Our meta-analysis showed that *Spartina alterniflora* invasion has had an overall negative impact on macrobenthic communities globally. At the species level, *Spartina alterniflora* changes the species composition and distribution of invaded areas and reshapes the biological communities of invaded areas (Zhou et al. 2009), the decrease in density and biomass and the increase in species number and Margalef richness index also reflect such changes, which is consistent with the environmental filtration hypothesis (Kraft et al. 2015). Although there was no statistically significant difference, the Pielou evenness index and Simpson dominance index of macrobenthic communities still showed a trend of decreasing and increasing, respectively, due to the invasion of

Spartina alterniflora. Additionally, the Shannon-Wiener diversity index of the macrobenthos community also showed a decreasing trend. These changes in diversity index indicate that the invasion of *Spartina alterniflora* increased the dominance of some species and decreased the overall biodiversity of the community (Su et al. 2020).

As ecological engineers, invasive plants have a negative impact on native biological communities by changing the natural environment of invaded areas and creating homogenized habitats (Crooks 2022). However, some researchers believe that the facilitation effect of invasive species on native species is also widespread in nature (Rodriguez 2006). The reason for these seemingly contradictory phenomena may be due to the significant differences in natural environment among different regions of the world. The habitat heterogeneity hypothesis holds that high habitat heterogeneity in a local ecosystem can promote the coexistence of more species, thereby increasing the species diversity of the communities (MacArthur 1961). And the moderate disturbance hypothesis holds that when an ecosystem is exposed to moderate levels of disturbance, its biodiversity is highest (Connell 1979).

Some previous studies have suggested that *Spartina alterniflora* invasion leads to the homogenization of the macrobenthic communities in its habitat, rendering the latitudinal differences in macrobenthos communities within the invaded habitat insignificant (Zhang et al. 2019). But our research shows that the impact of *Spartina alterniflora* invasion on macrobenthos is generally negative in areas with low average annual temperature and positive in areas with high average annual temperature. This may be because the intertidal zone is dually regulated by land and ocean, the range of temperature changes is small, and the effect of ocean currents may cause temperature differences on some coasts with similar latitudes (Southward et al. 1995). This is also why latitude is excluded from the collinearity test and the average annual temperature is analyzed.

In sediment types, *Spartina alterniflora* invasion of sandy and mixed intertidal zones has significant positive effects on macrobenthic communities in general, while its invasion of muddy intertidal zones is on the contrary, which may be related to the strong silt-promoting ability of *Spartina alterniflora*. *Spartina alterniflora* can intercept fine particulate matter in seawater (Braga et al. 2024), and its invasion into sandy intertidal zone can gradually transition the sediment bottom to muddy. With the increase in habitat heterogeneity, some species that originally existed only in muddy intertidal zone also appear in sandy beaches. In addition, the vertical distribution of macrobenthos is more uniform in muddy intertidal zones than in sandy intertidal zones. The invasion of *Spartina alterniflora* causes the texture of the underlying sediment to become harder, shortening the vertical distribution space for macrobenthos, which in turn has a negative impact on them (Jiang 2014; Santos et al. 2020).

For different coastal landforms, *Spartina alterniflora* invasion increased the species number and decreased the biomass in accumulation coast, but showed the opposite trend in erosion coast. This may be attributed to the differences in coastal landforms across various intertidal zones, leading to impacts in different directions on the community structure of macrobenthos after the invasion of *Spartina alterniflora*, and this observation is also supported by our long-term field investigation.

The impact of *Spartina alterniflora* invasion on macrobenthos communities varies dynamically with the elevation and invasion duration. This may be due to the moderate intensity of *Spartina alterniflora*'s interference with the intertidal ecosystem in the early stages of invasion, leading to increased habitat heterogeneity. However, with the increase of invasion time and elevation, the degree of disturbance gradually increases, which instead reduces the habitat heterogeneity in the intertidal zone. This result has also been supported by many researchers (Qiu et al. 2019; Ge et al. 2020; Li et al. 2023).

Some studies suggest that the community structure and diversity level of macrobenthos differ significantly between seasons, whether in invasive or native habitats (Liao et al. 2018; Reis et al. 2019). Our study complements this view: Season does lead to differences between invasive habitats and native habitats in terms of biomass, but this effect is not obvious from the overall trend, indicating that season has an impact on the macrobenthos communities in the intertidal zone, but this effect is not highly relevant to *Spartina alterniflora* invasion.

In addition, differences in native vegetation habitats will have a significant impact on the cumulative effect values of multiple indicators. The invasion of *Spartina alterniflora* into bare flat will have a negative impact on macrobenthos communities in the habitat, while invasion of native vegetation habitats generally shows the opposite trend. On one hand, *Spartina alterniflora*'s alterations to hydrological conditions and sediment physical and chemical properties in the invaded area may have a greater impact on bare flat (Quan et al. 2016), making the difference between light flats and native plant habitats greater than the difference between invasive plant habitats and native plant habitats (Chen et al. 2023).On the other hand, *Spartina alterniflora*, as a C4 plant, has higher nutritional value and palatability (Feng et al. 2015), making macrobenthos more inclined to feed on *Spartina alterniflora* and the detritus it produces.

Although the results of the publication bias assessment indicate that our findings are highly robust, there are still some limitations. First, we found that the sediment type and coastal landform in invaded area will have an impact on the macrobenthic communities. However, there is still a lack of relevant research to support this phenomenon. This phenomenon has only been discovered in our long-term field surveys. Second, according to our meta-analysis results, only one explanatory variable among all considered has a significant impact on the cumulative effect values of the Pielou evenness index, Margalef richness index, and Simpson dominance index of the macrobenthic communities. Simultaneously, the heterogeneity of the cumulative effect value residuals (Qe) for each indicator remains highly significant ($P < 0.0001$), suggesting the presence of other unknown explanatory variables influencing the macrobenthic communities in the invaded area. Some previous studies have found that indicators such as *Spartina alterniflora* density (Chen et al. 2023) and vegetation coverage (Li et al. 2023) in invaded areas, as well as heavy metal content (Qu et al. 2023) and salinity (Han et al. 2022) in sediments, will have an impact on macrobenthos communities. Unfortunately, due to the lack of relevant literature and insufficient data, these factors were not included in the meta-analysis of this study. Finally, it is difficult for our study to directly reflect the differences in species composition between invasive habitats and various native habitats in the results.

At the end of 2023, the Chinese government initiated the removal of *Spartina alterniflora* in coastal area, and the ecological restoration work in intertidal zones are also in preparation (National Forestry and Grassland Administration 2022). In the study of the impacts of *Spartina alterniflora* removal on the recovery of intertidal biological communities, many researchers believe that removal measures play a crucial role in community recovery. Measures such as mowing, plowing, spraying herbicides, and planting native vegetation have been found to promote the recovery of native biological communities (Mo et al. 2022; Lyu et al. 2023; Jiang et al. 2024), while removing *Spartina alterniflora* through waterlogging can have serious negative impacts on the intertidal ecosystem (Wang et al. 2021). However, some studies have found that the use of measures other than waterlogging to control *Spartina alterniflora* may lead to its recurrence, and the use of chemical methods may pose a potential threat to the intertidal ecosystem (Paveglio et al. 1996; Xie et al. 2019; Wang et al. 2023). Moreover, it is also difficult for areas cleared of *Spartina alterniflora* to return to their pre-invasion state (Moreno-Mateos et al. 2012; Huang et al. 2022). This undoubtedly makes the removal of *Spartina alterniflora* and the restoration of intertidal zones a long and arduous task. Our research results showed that a though *Spartina alterniflora* invasion has a significant negative impact on the macrobenthos communities in general, the effects vary for each indicator, and many external environmental factors also influence the results. Therefore, the management of *Spartina alterniflora* and restoration efforts in intertidal zones should be tailored to local conditions, while also considering the beneficial role that *Spartina alterniflora* plays in promoting the intertidal ecosystem.

Conclusions

In summary, we conducted a global meta-analysis to investigate the impacts of *Spartina alterniflora* invasion on intertidal macrobenthic communities, and to understand how these impacts occurred. The results show that following the invasion of *Spartina alterniflora* into the intertidal zone, there was a significant increase in both the number and species richness of macrobenthos, along with a significant decrease in their biomass, but no significant effects were observed on density, diversity index, or evenness index. As elevation and invasion duration increased, the impact of *Spartina alterniflora* invasion on macrobenthos communities shifted from positive to negative, while the average annual temperature exhibited the opposite trend. Moreover, variations in sediment properties, coastal types, and vegetation coverage within invaded areas can lead to significantly different impacts on macrobenthos communities. Hence, we speculate that *Spartina alterniflora* may influence macrobenthos communities through intricate interactions with various environmental factors in the intertidal zone, and its underlying mechanism warrants further investigation in future studies. At the end of 2023, the Chinese government initiated the removal of *Spartina alterniflora* in coastal area, and the ecological restoration work in intertidal zones are also in preparation. The intertidal zone along China's coast is a crucial habitat for millions of waterbirds on the East Asian-Australasian Flyway (EAAF) (Hu et al. 2022), with macrobenthos serving as an essential food source for these waterbirds (Zhang et al. 2018). Many scholars believe that removing *Spartina alterniflora* can partially restore native animal communities; however, whether subsequent restoration measures can fully restore wetland ecosystems to their original levels remains to be verified. We believe that intertidal zone management and restoration projects should be tailored to local conditions, taking into full consideration the beneficial role of *Spartina alterniflora* in the intertidal zone ecosystem.

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References

Borenstein M, Hedges LV, Higgins JP, Rothstein HR (2021) Introduction to meta-analysis. John Wiley & Sons (Online): 1-491.

Braga CF, Santos TM, Beasley CR (2024) Variation in macrobenthic community of vegetated and unvegetated habitats in a macrotidal estuary of northern Brazilian Amazon coast. Wetlands Ecology and Management 32: 249-262.

Chen P, Zhang Y, Zhu X, Lu C (2019) Distribution of crabs along a habitat gradient on the Yellow Sea coast after *Spartina alterniflora* invasion. PeerJ. https://doi.org/10.7717/peerj.6775.

Chen Q, Yu Z, Wang M (2023) Effects of *Spartina alterniflora* invasion on macrobenthic faunal community in different habitats of a mangrove wetland in Zhanjiang, South China. Regional Studies in Marine Science. https://doi.org/10.1016/j.rsma.2023.103148.

Connell J H (1979) Response: intermediate-disturbance hypothesis. Science 204: 1345-1345.

Cui B, He Q, An Y (2011) *Spartina alterniflora* invasions and effects on crab communities in a western Pacific estuary. Ecological Engineering 37: 1920-1924.

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97: 153-166.

Doherty TS, Hays GC, Driscoll DA (2021) Human disturbance causes widespread disruption of animal movement. Nature Ecology & Evolution 5: 513-519.

Duval S, Tweedie R (2000) Trim and fill: a simple funnel-plot–based method of testing and adjusting for publication bias in meta-analysis. Biometrics 56: 455-463.

Feng J, Huang Q, Qi F, Guo JM, Lin GH (2015) Utilization of exotic *Spartina alterniflora* by fish community in the mangrove ecosystem of Zhangjiang Estuary: Evidence from stable isotope analyses. Biological Invasions 17: 2113-2121.

Ge B, Jiang S, Liu Q, Zhou C, Tang B (2019) Density, but not distribution pattern of

Assiminea latericea varies on tidal flats with smooth cordgrass *Spartina alterniflora* invasion stage. Regional Studies in Marine Science. https://doi.org/10.1016/j.rsma.2019.100528.

Ge B, Jiang S, Yang L, Zhang H, Tang B (2020) Succession of macrofaunal communities and environmental properties along a gradient of smooth cordgrass *Spartina alterniflora* invasion stages. Marine Environmental Research. https://doi.org/10.1016/j.marenvres.2019.104862.

Han QY, Han QX, Wang Y, Liu D (2022) Comparison of macrobenthic communities between the invasive *Spartina alterniflora* and native *Suaeda glauca* habitats in the Yellow River Delta. Wetlands Ecology and Management 30: 497-511.

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80: 1150-1156.

Higgins JP, Thompson SG, Deeks JJ, Altman DG (2003) Measuring inconsistency in meta-analyses. Bmj 327: 557-560.

Hu W, Chen T, Xu Z, Wu D, Lu C (2022) Occurrence dataset of waterbirds in the tiaozini wetland, a world nature heritage, China. Biodiversity Data Journal. https://doi.org/10.3897/BDJ.10.e90724.

Huang YY, Huang YY, Du XL, Li YM, Tian JT, Chen Q, Huang YH, Lv WW, Yang Y, Liu ZQ, Zhao YL (2022) Assessment of macrobenthic community function and ecological quality after reclamation in the Changjiang (Yangtze) River Estuary wetland. Acta Oceanologica Sinica 41: 96-107.

Jiang J J, Zhao Y J, Guo Y, Gao L, Richards CL, Siemann E, Wu J, Li B, Ju RT (2024) Restoration of native saltmarshes can reverse arthropod assemblages and trophic interactions changed by a plant invasion. Ecological Applications. https://doi.org/10.1002/eap.2740.

Jiang K, Chen X, Bao Y, Li H, Shi W, Wang H, Ren P (2016) Effect of Spartina alterniflora invasion on the vertical structure of microbenthic community. Acta Ecologica Sinica 36: 535-544. (in Chinese)

Kraft NJ, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29: 592-599.

Lajeunesse MJ (2011) On the meta-analysis of response ratios for studies with correlated and multi-group designs. Ecology 92: 2049-2055.

Levine JM, Vilà M, Antonio C. MD, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London. Series B: Biological Sciences 270: 775-781.

Yang L, Shi J, Pan R, Yang R, Li H, Wang S, Ge B (2023) Distribution of mudsnail *Bullacta caurina* along smooth cordgrass *Spartina alterniflora* invasion stages on a coast of the Yellow Sea, China. Marine Environmental Research. https://doi.org/10.1016/j.marenvres.2023.106248.

Liao Y, Shou L, Tang Y, Gao A, Chen Q, Yan X, Chen J (2018) Influence of two non-indigenous plants on intertidal macrobenthic communities in Ximen Island Special Marine Protected Area, China. Ecological Engineering 112: 96-104.

Lu K, Han G, Wu H (2022) Effects of *Spartina alterniflora* invasion on the benthic invertebrate community in intertidal wetlands. Ecosphere. https://doi.org/10.1002/ecs2.3963.

Lyu C, Zhang S, Ren X, Liu M, Leung KS, He T, Chen Q, Choi CY (2023) The effect of *Spartina alterniflora* eradication on waterbirds and benthic organisms. Restoration Ecology. https://doi.org/10.1111/rec.14023.

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42: 594-598.
Mo X, Chen J, Pan Y Zhang M, Zhang Z, Liu J (2022) Impact of applying imazapyr on the control of *Spartina alterniflora* and its eco-environments in the Yellow River Delta, China. Watershed Ecology and the Environment 4: 211-218.

Moreno-Mateos D, Power ME, Comín FA, Yockteng R (2012) Structural and functional loss in restored wetland ecosystems. PLoS Biology. https://doi.org/10.1371/journal.pbio.1001247.

Moreira F, Moreira F, Martins RC., Martins RC, Catry I, Catry I, Catry I, D'Amico M (2018) Drivers of power line use by white storks: A case study of birds nesting on anthropogenic structures. Journal of Applied Ecology 55: 2263–2273.

Nakagawa S, Noble DW, Senior AM, Lagisz M (2017) Meta-evaluation of meta-analysis: ten appraisal questions for biologists. BMC Biology 15: 1-14.

Nakagawa S, Lagisz M, O'Dea RE, Rutkowska J, Yang Y, Noble DW, Senior AM (2021) The orchard plot: cultivating a forest plot for use in ecology, evolution, and beyond. Research Synthesis Methods 12: 4-12.

National Forestry and Grassland Administration: Special Action Plan for the *Spartina alterniflora* (2022-2025). https://www.gov.cn/xinwen/2023-03/16/content_5747029.htm. (in Chinese)

Ning Z, Chen C, Xie T, Zhu Z, Wang Q, Cui B, Bai J (2021) Can the native faunal communities be restored from removal of invasive plants in coastal ecosystems? A global meta-analysis. Global Change Biology 27: 4644-4656.

Paveglio FL, Kilbride KM, Grue CE, Simenstad CA, Fresh KL (1996) Use of rodeo® and X-77® spreader to control smooth cordgrass (*Spartina alterniflora*) in a southwestern washington estuary: 2. Effects on benthic microflora and invertebrates. Environmental Toxicology and Chemistry: An International Journal 15: 969-978.

Powell KI, Chase JM, Knight TM (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. American Journal of Botany 98: 539-548.

Qiu D, Yan J, Ma X, Gao F, Wang F, Wen L, Bai J, Cui B (2019) How vegetation influence the macrobenthos distribution in different saltmarsh zones along coastal topographic gradients. Marine Environmental Research. https://doi.org/10.1016/j.marenvres.2019.104767.

Quan W, Zhang H, Wu Z, Jin S, Tang F, Dong J (2016) Does invasion of *Spartina alterniflora* alter microhabitats and benthic communities of salt marshes in Yangtze River estuary? Ecological Engineering 88: 153-164.

Qu F, Wang S, Wang W, Liu S, Li S, Liu H, Zhang Z (2023) Macrobenthic community structure of Rudong coastal wetland, China: the impact of invasive *Spartina alterniflora* and its implication for migratory bird conservation. Wetlands Ecology and Management 31: 159-168.

Reis A, Krull M, Carvalho LR, Barros F (2019) Effects of tropical saltmarsh patches on the structure of benthic macrofaunal assemblages. Wetlands 39: 945-954.

Rosenberg MS (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. Evolution 59: 464-468.

Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions 8: 927-939.

Santos TM, Rabelo DM, Beasley CR, Braga CF (2020) Vertical distribution of macrobenthic community of tropical saltmarshes on the Amazon coast. Regional Studies in Marine Science. https://doi.org/10.1016/j.rsma.2020.101536.

Thomsen MS (2020) Indiscriminate data aggregation in ecological meta-analysis underestimates impacts of invasive species. Nature Ecology & Evolution, 4: 312-314.

Southward AJ, Hawkins SJ, Burrows MT (1995) Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology 20: 127-155.

Su Z, Qiu G, Fan H, Li M, Fang C (2020) Changes in carbon storage and macrobenthic communities in a mangrove-seagrass ecosystem after the invasion of smooth cordgrass in southern China. Marine Pollution Bulletin 152: 110887.

Sterne J A, Egger M (2005) Regression methods to detect publication and other bias in meta-analysis. Publication bias in meta-analysis: Prevention, assessment and adjustments (Online): 99-110.

Thiebaut G (2007) Invasion success of non-indigenous aquatic and semi-aquatic plants in their native and introduced ranges. A comparison between their invasiveness in North America and in France. Biological Invasions 9: 1-12.

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36: 1-48.

Veroniki AA, Jackson D, Viechtbauer W, Bender R, Bowden J, Knapp G, Kuss O, Higgins J, Lagan D, Salanti G (2016) Methods to estimate the between-study variance and its uncertainty in meta-analysis. Research Synthesis Methods 7: 55-79.

Wallace BC, Lajeunesse MJ, Dietz G, Dahabreh IJ, Trikalinos TA, Schmid CH, Gurevitch J (2017) Open MEE: Intuitive, open-source software for meta-analysis in ecology and evolutionary biology. Methods in Ecology and Evolution 8: 941-947.

Wang S, Sheng Q, Zhao F, Zhang T, Zhuang P (2021) Variable effects on benthic community from diking to eradicate invasive plants in the Yangtze Estuary salt marsh. Frontiers in Marine Science. https://doi.org/10.3389/fmars.2021.706353.

Wang Y, He Y, Qiao P, Mei B, Wang X, Han G, Xie B (2023) Control effects of different herbicides on *Spartina alterniflora*. Ecological Indicators 154: 110824.
Wolfgang, V (2010) Conducting Meta-Analyses in R with the metafor Package. Journal of Statistical Software 36: 1-48.

Xie B, Han G, Qiao P, Mei B, Wang Q, Zhou Y, Zhang A, Song w, Guan B (2019) Effects of mechanical and chemical control on invasive *Spartina alterniflora* in the Yellow River Delta, China. PeerJ. https://doi.org/10.7717/peerj.7655.

Zhang SD, Ma ZJ, Choi CY, Peng HB, Bai QQ, Liu WL, Tan K, Melville DS, He P, Chan YC, Vangils JA, Piersma T (2018) Persistent use of a shorebird staging site in the Yellow Sea despite severe declines in food resources implies a lack of alternatives. Bird Conservation International 28: 534-548.

Zhang Y, Pennings S C, Li B, Wu J (2019) Biotic homogenization of wetland nematode communities by exotic *Spartina alterniflora* in China. Ecology. https://doi.org/10.1002/ecy.2596.

Zhou H X, Liu J, Qin P (2009) Impacts of an alien species (*Spartina alterniflora*) on the macrobenthos community of Jiangsu coastal inter-tidal ecosystem. Ecological Engineering 35: 521-528.

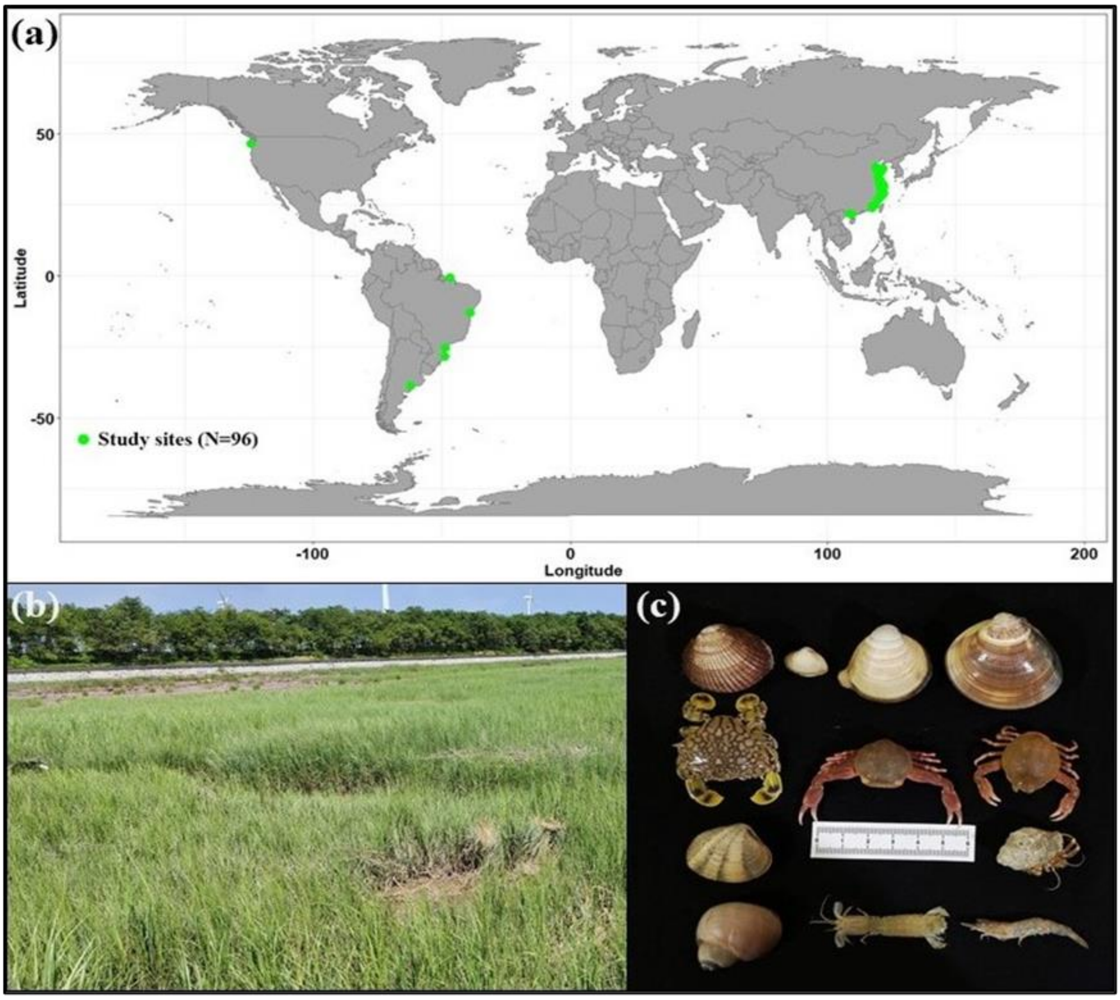

Fig 1.
(a) Global distribution of *Spartina alterniflora* invasion studies. (b) *Spartina alterniflora* habitat, (c) Some species of macrobenthos in intertidal zone.

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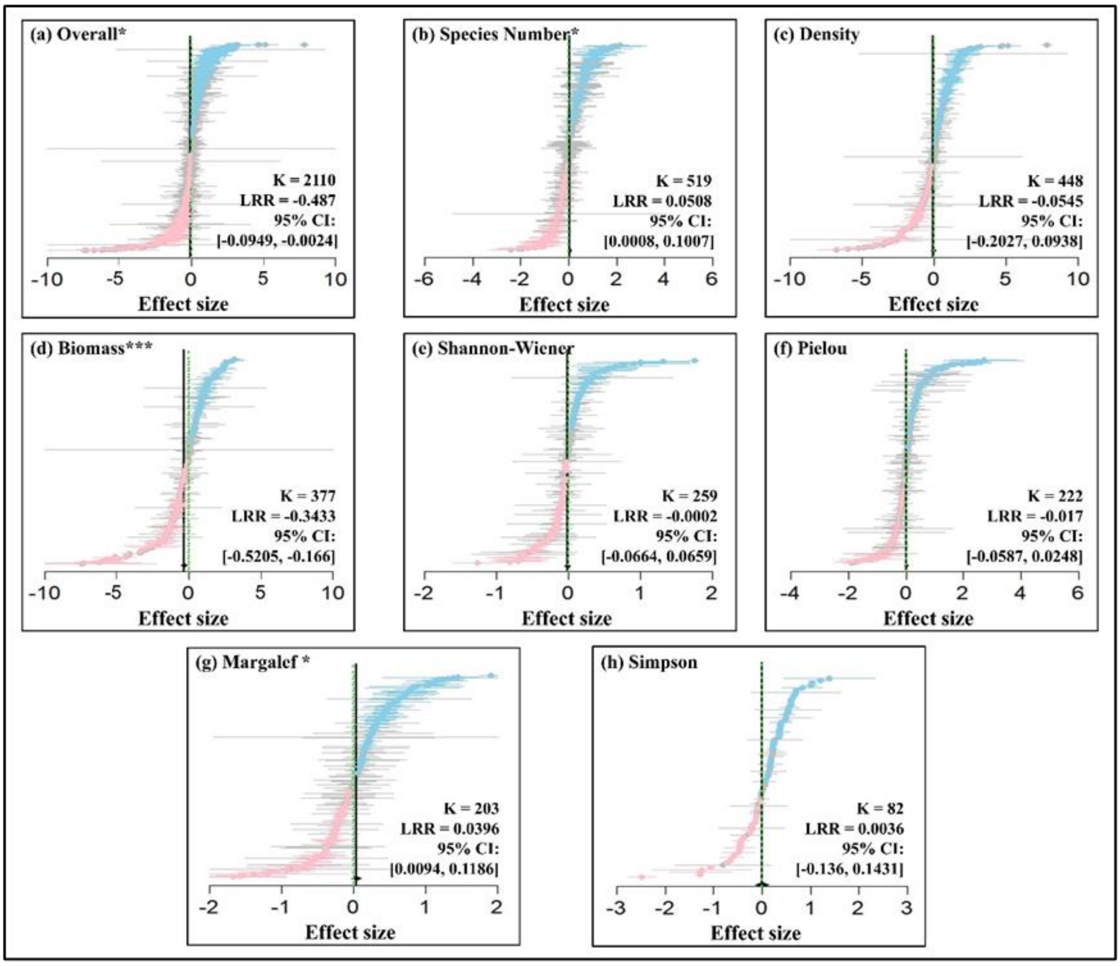

Fig 2.

Subfigures (a) to (h) show the effect of *Spartina alterniflora* invasion on each macrobenthic community indicator. In the figures, pink represents cases with significant negative effects, sky blue represents cases with significant positive effects, and gray represents cases with insignificant effects, K is the number of cases, LRR is the mean effect size, and 95% CI is the 95% confidence interval. Effect sizes are considered significantly different from zero when the 95% CI does not overlap 0 (***p < 0.001; **p < 0.01; and *p < 0.05).

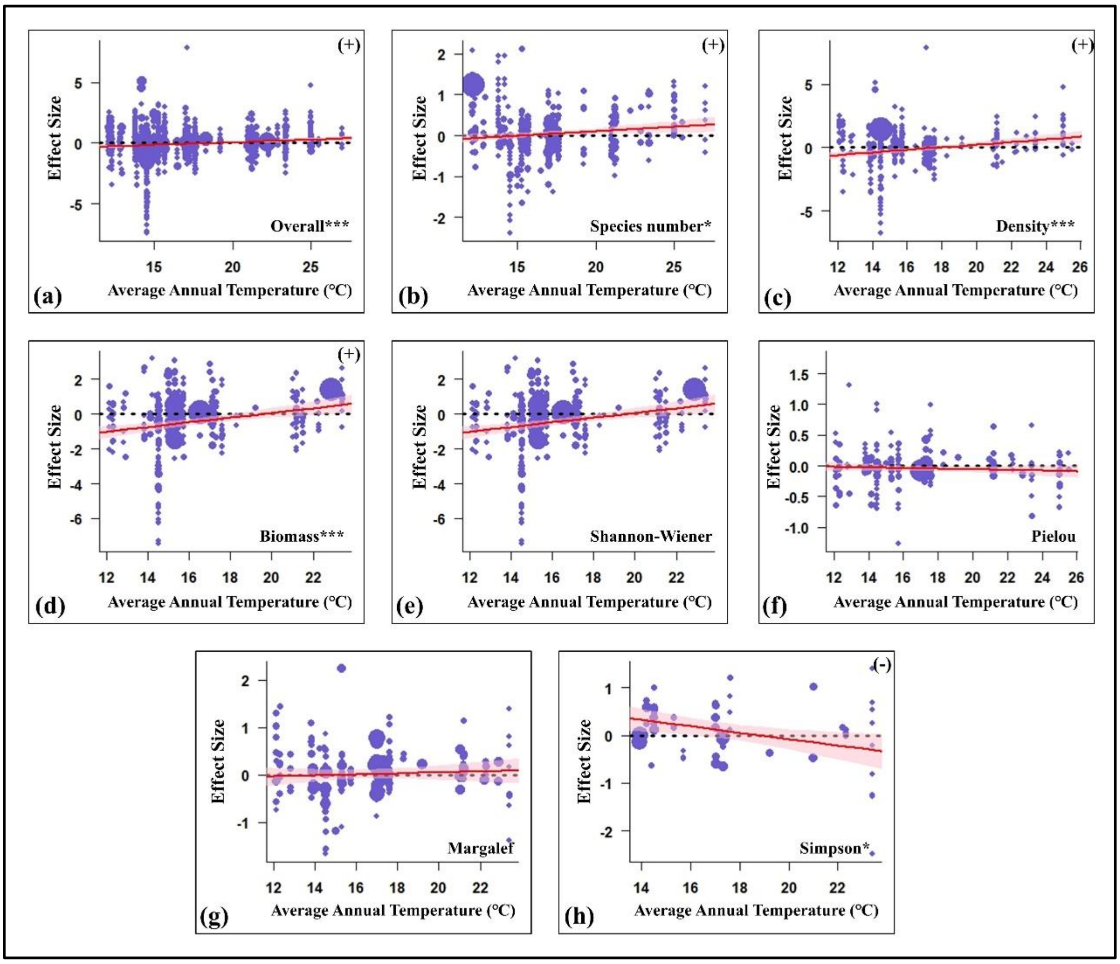

Fig 3.

Subfigures (a) to (h) show the impact of annual average temperature on the effect size for each indicator. The red line is the fitted regression curve, the pink area represents the 95% confidence interval of the regression curve, and the dotted line represents the zero mark. Each purple point represents a case, and the size of the point indicates the weight of the case. (+)/ (-) indicates the positive/negative effect of annual average temperature on the effect size, ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

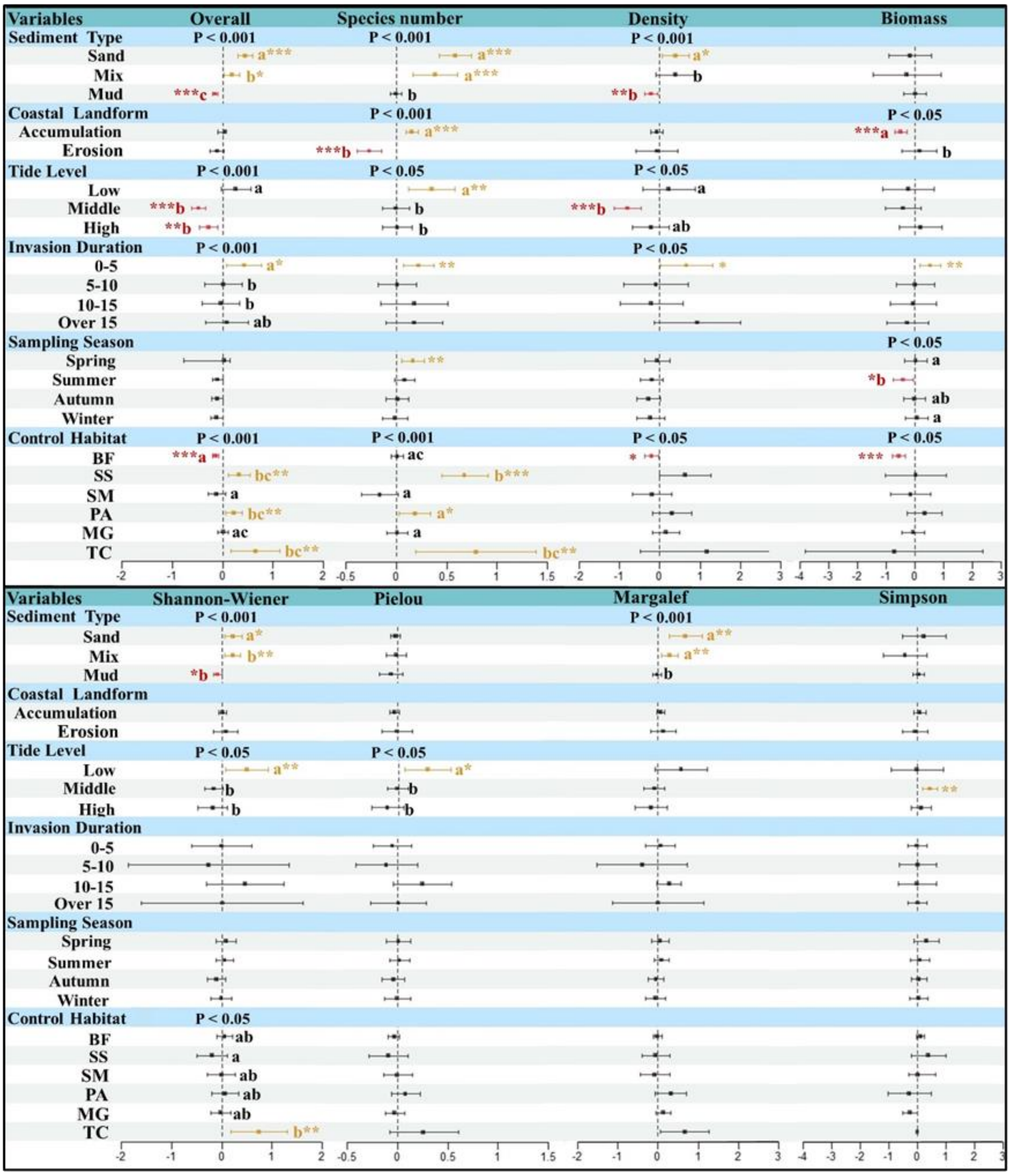

Fig 4.

The impact of various classification variables in the *Spartina alterniflora* invasion area on the effect values of various indicators on the macrobenthic communities. Display the Q test results and multiple comparison results for categorical variables with significant heterogeneity. Effect sizes are considered significantly different from zero when the 95% CI does not overlap 0 (***p < 0.001; **p < 0.01; and *p < 0.05), gold/red represent significant positive/negative effects respectively.

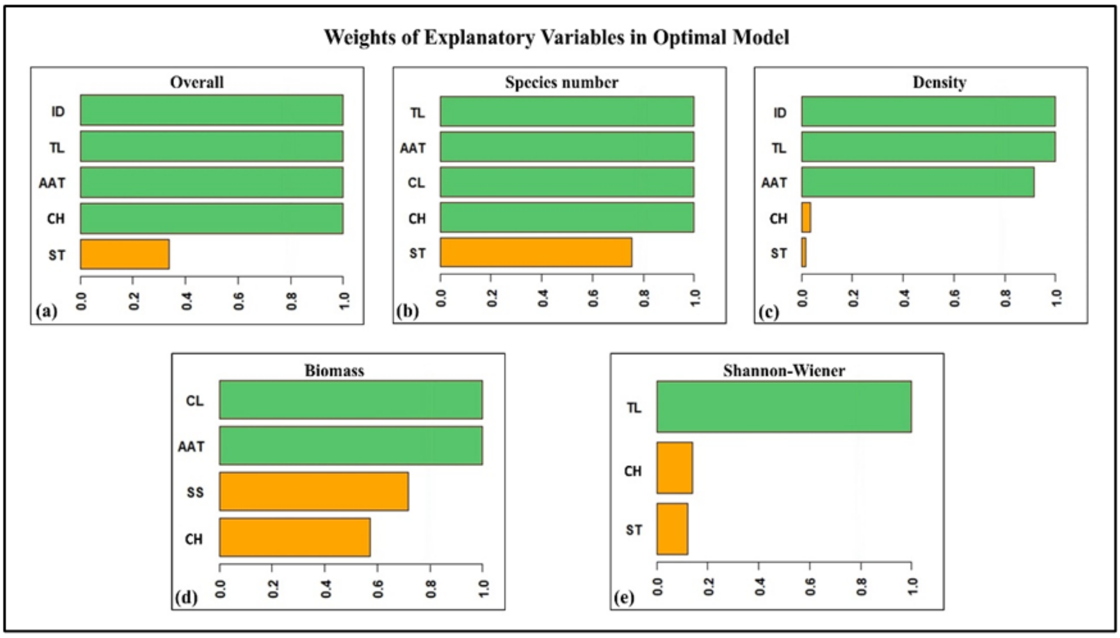

Fig 5.

Akaike weights of explanatory variables that have a significant impact on the effect size based on model selection. In the figures, green represents explanatory variables with higher weights in the optimal model, while orange represents explanatory variables with lower weights in the optimal model, AAT is average annual temperature, ST is sediment type, CL is coastal landform, TL is tide level, ID is invasion duration, SS is sampling season, CH is control habitat. Because only one explanatory variable in the Pielou evenness index, Marglef species richness index, and Simpson dominance index had a significant impact on the effect size, model selection was not performed on them.