

## Article

# Contrasted Impacts of Yellow Flag Iris (*Iris pseudacorus*) on Plant Diversity in Tidal Wetlands within Its Native and Invaded Distribution Ranges

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**Abstract:** We conducted an intercontinental biogeographic survey to analyze the effects of an invasive plant species in its native and invaded ranges. Our study system included tidal wetlands colonized by *Iris pseudacorus* L. (yellow flag iris, Iridaceae) along salinity gradients in two estuaries in its native European (Guadalquivir Estuary) and invaded North American (San Francisco Bay-Delta Estuary) ranges. We hypothesized *I. pseudacorus* would impart more negative community-level impacts on plant species diversity in the invaded range compared to the native range. Our results show that the colonization of *Iris pseudacorus* has very different effects on the diversity of tidal plant communities in its native and invaded ranges. In the native range, *I. pseudacorus* promoted plant diversity by increasing evenness and species richness. On the contrary, *I. pseudacorus* greatly reduced plant diversity in the invaded range, being this reduction higher in those communities with higher species richness and diversity levels. In view of these results, urgent management practices are needed to control and eradicate *I. pseudacorus* from the inland Sacramento-San Joaquin Delta Estuary since this invasive macrophyte is reducing plant diversity at local and landscape scales.

**Keywords:** biodiversity; estuary; evenness; Guadalquivir River; *Iris pseudacorus*; invasive species; intertidal marshes; Sacramento-San Joaquin Delta Estuary; species richness



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## 1. Introduction

The human-mediated movement of species has increased significantly with economic globalization and, as a result, biological invasions have become a main component of global change with increasing negative effects on ecosystems. In fact, the accumulation of multiple exotic invasive species within ecosystems around the globe is one of the most important causes of biodiversity loss [1]. However, such invader impacts on biological diversity can be highly variable at landscape scales and are influenced by processes in the native ecosystem [2]. At the same time, in a dialectic relationship, biological invasions are frequently associated with habitat disturbance and changing environmental conditions [3]. In this sense, exotic invasive species directly impact on native species through competitive displacement over common resources and through invasion-driven ecosystem modifications [4].

In this general scenario, conflicting evidence as to whether plant invasions pose a great threat to native plant diversity is still debated [5]. Some studies argue that invasive

species can cause biotic differentiation, but in many cases biological invasions actually decrease biodiversity locally through biotic homogenization [6]. Moreover, competitive impacts of invasive species may vary across invaded ranges and local to regional scales [7]. Frequently, native species-rich communities are more successful at resisting invasion by exotic species than are species-poor communities at the local scale, according to the biotic resistance hypothesis [8], owing to competition for limiting resources [9]. Instead, following the biotic acceptance hypothesis, species-rich communities are often more vulnerable to invasions by exotic species than species-poor communities at larger spatial scales [10,11]. In fact, native species can facilitate invader abundance by changing environmental conditions, with positive interactions as important drivers of invasion success [12]. Thus, the impacts of plant invasions on plant species richness are not universal [13], and the relative role of species richness in predicting invasion success is not fully understood [14]. Furthermore, the characteristics of recipient communities seem to be one of the most important determinants of invasion impacts [5], but little is known about the full range of direct and indirect interactions among native and exotic species [15]. Ecological interactions rarely enable communities to resist invasion but instead constrain the abundance of invasive species once they have successfully established themselves [16]. Additionally, according to the invasional meltdown hypothesis (IMH), exotic species facilitate one another's invasion and can benefit newly arriving invasive species by increasing their likelihood of survival. Moreover, they may synergistically increase habitat invasibility, promote further spread, and impart negative impacts in the native community [17,18]. Understanding the processes that influence invasion by exotic species remains a challenge in ecology.

Comparisons of the role of exotic species in relation to native plant communities in their native and invaded ranges represent a crucial step when studying invaders. In general, invasive plants are assumed to behave more aggressively in their invaded ranges than in their native one [19–21]. Some invasive plant species form dense mono-dominant stands in invaded areas while having sparse distribution in their native ranges, which has been linked to their impacts on biodiversity [22,23]. Higher abundance of invaders in the introduced range are often explained by a reduction in negative species interactions, although results are equivocal [12]. In addition, invasive species often evolve rapidly in response to the novel environmental conditions in their introduced range [24].

We conducted an intercontinental biogeographic survey to analyze the effects of an invasive plant species, *Iris pseudacorus* L. (yellow flag iris, Iridaceae), on plant community diversity in its native and invaded ranges. Climate drives plant diversity over large spatial scales more than any other factor [25]. The global distribution of *I. pseudacorus* encompasses a wide range of climate zones and bioregions, including populations in arctic, subarctic, temperate and subtropical climates [26–28]. Given the increasing high costs of controlling invasive plant species, it is important to understand the degree to which an invasive species drives significant negative impacts such as a decline in biological diversity and the magnitude of its influence at spatial scales where impacts potentially occur [29]. Therefore, to examine the role of invader impacts on diversity, we focused our investigation on tidal wetlands colonized by *I. pseudacorus* along broad tidewater salinity gradients in two estuaries with similar latitude (~37 °N) and warm Mediterranean climates in its native European and invaded North American ranges. This aquatic macrophyte has been introduced as an ornamental aquatic plant worldwide and has escaped cultivation and naturalized, becoming invasive in freshwater wetlands of South and North America, South Africa, New Zealand, Australia, India and Japan, where it is displacing native plant species [26,28,30,31]. Intertidal marsh habitat has not often been considered vulnerable to invasion by *I. pseudacorus*, yet unexpected colonization and spread of invasive plants into estuarine environments (e.g., [32]) underscores the need for improved understanding of invasion dynamics and impacts across expanding environmental gradients.

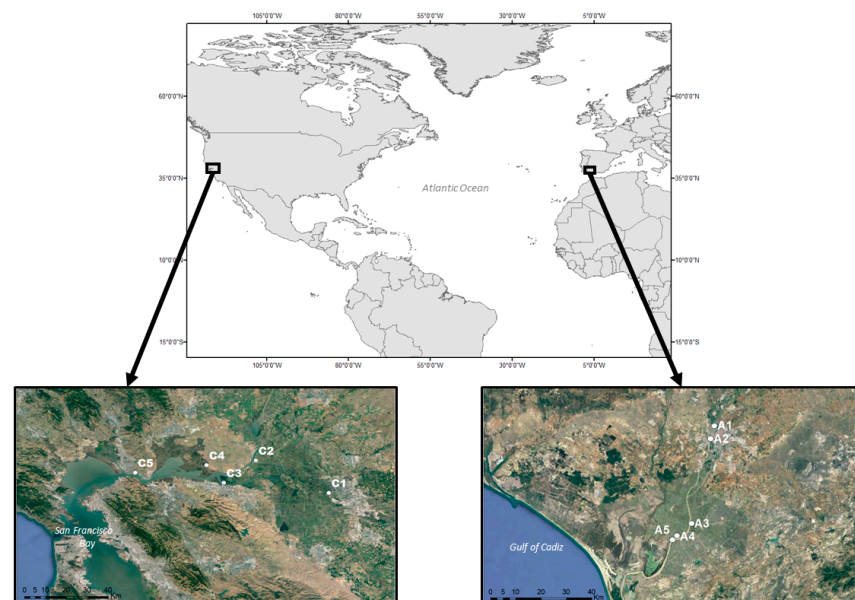
Exotic invasive species of aquatic macrophytes have been identified as a major cause of biodiversity loss [33]. Following the biotic acceptance hypothesis, we hypothesized *I. pseudacorus* would impart more negative community-level impacts on plant species

diversity in the invaded range, where plant diversity was apparently higher compared to the native range. We also postulated impacts on plant community diversity would vary along a salinity gradient that corresponds to more diverse freshwater tidal areas or to less diverse brackish wetlands. Comparative studies of invasive plants in their native and naturalized ranges are crucial for understanding factors that limit species distributions and impacts, yet most studies focus on areas of introduction [34,35]. Results of this inquiry are useful for understanding the dynamics and impacts of *I. pseudacorus* on plant communities to inform management planning and contribute new knowledge to the on-going debate about the role of invasive species in native plant communities.

## 2. Materials and Methods

### 2.1. Study Sites

We studied the effects of *Iris pseudacorus* presence on plant diversity in its invaded and native ranges. We studied populations of *I. pseudacorus* naturalized in the San Francisco Bay-Delta Estuary (Pacific Coast of North America, CA, USA) (Figures 1 and S1). This area has mixed semi-diurnal tides and a Mediterranean climate with cool and wet winters and hot and dry summers and some summer fog for locations closer to the Pacific Ocean. According to the climatic series (1981–2010), mean annual temperature is +15.2 °C; minimum mean daily temperature is +9.2 °C in January, and maximum mean daily temperature is +20.3 °C in July [36]. In the United States (USA), *I. pseudacorus* first established in the late 19th century in northeastern Atlantic coastal states, while first records in California were from rivers and inland lakes in the 1950s [37] and have long been limited to inland freshwater habitats. By 1969, an invasive population had established in freshwater tidal wetlands of the inland Sacramento-San Joaquin Delta [38]. Downstream spread into brackish tidal wetlands in the greater San Francisco Bay-Delta Estuary has recently occurred, raising concerns about persistent impacts and spread with sea level rise [39].



**Figure 1.** Location map of study locations of *Iris pseudacorus* in the native range (Guadalquivir River Estuary, Andalusia, Spain, A1–A5) and the invaded range (Sacramento-San Joaquin Delta, California, USA, C1–C5). Source: Google Earth 2020 (accessed on 1 July 2021).

We established comparative study sites in the native European range of *I. pseudacorus* in the Guadalquivir River Estuary (Southwest Iberian Peninsula, Andalusia, Spain) (Figures 1 and S1). This mesotidal estuary experiences semidiurnal tides (tidal range 3.5 m in spring tides) from the mouth of Guadalquivir River to the Alcalá del Río Dam located 110 km upstream [40]. Similar to the California sites, the climate is Mediterranean with Atlantic

Ocean influence with a mean annual temperature of +18.7 °C, and mean daily minimum and maximum temperatures are +10.8 °C in January and +27.1 °C in July, respectively, for the climatic series 1981–2010 [41]. *I. pseudacorus* was found in fringing emergent intertidal wetlands adjacent to transitional riparian ecotones that included some tree species at both geographical ranges (*Acer negundo* L., *Alnus rhombifolia* Nutt., *Juglans regia* L. and *Salix laevigata* Bebb in the invaded range and *Populus alba* L., *Salix alba* L. and *Ulmus minor* Mill. in the native range). Observations of herbivory within populations were recorded. We observed signs of herbivory on *I. pseudacorus* by livestock (cows and sheep) at populations A2 and A5.

## 2.2. Data Collection

### 2.2.1. Establishment of Monitoring Plots

In July 2017, monitoring plots were established at five locations within population patches of *I. pseudacorus* representing invasions along an estuarine gradient from near the port of Stockton in fringing freshwater tidal wetlands to downstream brackish reach at Carquinez Strait in the San Francisco Bay-Delta Estuary ( $n = 7$ –8 patches per locations). In 2018, comparative monitoring plots with native *I. pseudacorus* were established in fringing shoreline wetlands along an estuarine gradient in the Guadalquivir River Estuary, from a freshwater tidal reach at Seville city to brackish tidal wetlands near the Gulf of Cadiz (Table S1). We established pairs of fixed square monitoring plots (1 m<sup>2</sup>), coincident with the central areas of discrete patches of *I. pseudacorus* and adjacent areas not colonized by *I. pseudacorus*. Methods for evaluation of vegetation and environmental variables were developed during the initial study in California, standardized for implementation across all study sites in both estuaries, and principal investigators directly collaborated on research in both estuaries.

### 2.2.2. Sediment Electrical Conductivity

Electrical conductivity (EC) of sediment interstitial water is a standard indirect measure of salinity in wetland sediment. Sediment EC was recorded in our study because the sampled tidal marshes were distributed along estuaries where salinity is the most important changing environmental stress factor [42], and because *I. pseudacorus* shows marked functional responses to salinity [43]. Sediment EC was recorded concurrently with plant community composition. Soil cores (4.5 cm diameter  $\times$  10 cm depth) were collected from each monitoring plot inside *Iris* clumps (1–3 cores per plot), stored in coolers with blue ice and transported to the laboratory. Sediment EC (mS cm<sup>−1</sup>) (invaded range: Oakton CON2700, Oakton Instruments, Vernon Hills, IL, USA; native range: Crison EC-meter Basic 30, Crison Instruments, Barcelona, Spain) was recorded using the standard method for saturation paste extraction with distilled water.

### 2.2.3. Plant Community Composition

The observed vegetation distribution pattern was complex in structure. Therefore, following [44], we established two linear transects up to 1.0 m long that originated at the centre of each fixed/paired monitoring plot (with *I. pseudacorus*; without *I. pseudacorus*) and were at 90° to one another. We recorded the presence of each plant taxon every 10 cm along both transects. These data were used to calculate the absolute cover of each plant taxa. A cover of 2.5% was adjudicated to those plant taxa observed to be present in a plot that were not recorded along the transects. In addition, to study the distribution of plant taxa in relation to the structure of *Iris* patches, both perpendicular transects were extended to the edge of *Iris* occupied patches for assessment of vegetation within the total area of each patch. Plant taxa were taxonomically evaluated and identified following [45,46] for California flora and [47,48] for the Guadalquivir Estuary. Vegetation assessment was limited to emergent species rooted in the plots and did not include minor areas with over-hanging canopies from nearby riparian tree species.

### 2.3. Data Analyses

Relative cover (%) for each species was calculated as the number of points in which it was present in relation to the total number of sampling points and multiplied by 100. To examine the impact of *I. pseudacorus* on the invaded plant communities, we calculated mean plant species richness ( $S$ ; number of discrete plant taxa), evenness ( $J'$ ), and Shannon–Wiener  $\alpha$ -diversity ( $H'$ ) for plant species in invaded and uninvaded plots [49] from plant abundance (relative cover from 1 m long transects) matrices using the ‘vegan: ecological diversity’ package of the R-software [50]. To evaluate the effect of *I. pseudacorus* on changes in plant community composition at landscape scale (comparing floristic differences among plots where *I. pseudacorus* was present or absent), we calculated the Morisita–Horn pairwise dissimilarity index from cover matrices using the ‘vegdist’ function of R-software to obtain a pairwise dissimilarity matrix, and the Sørensen dissimilarity index using the ‘betadist (sor method)’ function in the ‘vegan: ecological diversity’ package of R-software [51]. In addition, we used the function ‘indicators’ of the package ‘indicspecies’ of R-software that explores the indicator value of the simultaneous occurrence of sets of species. The method is described in [52] and is a generalization of the Indicator Value method of [53]. The statistical significance of the relationships was tested with a permutation test.

Deviations were calculated as standard errors of the mean (SE). A significance level ( $\alpha$ ) of 0.05 was applied for every analysis. Prior to conduct the analyses, data series were tested for normality using the Kolmogorov–Smirnov test and for homoscedasticity applying Levene’s test. When necessary, data series were transformed using  $1/x$ ,  $\sqrt{x}$  and  $\ln(x)$  functions trying to address the assumptions needed for parametric tests. Since homogeneity of variance was not accomplished after data transformations, sediment EC was compared between distribution ranges (native and invaded) and between locations (ordered in each range sequentially according to their distance to the ocean) using the Gamma Generalized Linear Model (GLM) (Poisson distribution) with chi-square ( $\chi^2$ ) de Wald [54]. *I. pseudacorus* cover from 1 m long transects was next compared between distribution ranges and between locations using a General Linear Model (LM) with sediment EC as covariant. Multivariate analysis of variance (MANOVA) and Pillai’s Trace were conducted for diversity indices ( $S$  was square root transformed) using distribution range, *I. pseudacorus* presence (with or without *Iris*) and location (ordered in each range sequentially according to their distance to the ocean) as grouping factors, with sediment EC as covariant. The analyses of multivariate variance protect subsequent analyses from type I error [55]. Once multivariate significance was confirmed via MANOVA, the main univariate differences were evaluated for each diversity and dissimilarity index with LMs. Particular differences between distribution ranges and between plots with and without *I. pseudacorus* were tested using Student *t*-test. When normality or homogeneity of variance was not achieved after data transformation, univariate differences were analyzed using GLM with chi-square ( $\chi^2$ ) de Wald [54] and particular differences using Man–Whitney U-test. These analyses were repeated excluding exotic species, and the most interesting results are reported in comparison with analyses including native and exotic species. Relationships between sediment electrical conductivity, *I. pseudacorus* cover and diversity indices were analyzed using correlation analysis, Pearson ( $r$ ) or Spearman ( $\rho$ ) correlation coefficient, and lineal regression analysis. Data from the whole patch diameter were analyzed using regression analysis between mean distance from the center of the *Iris* patch and species richness. All these analyses were conducted using IBM SPSS V. 20 (IBM Corp., Armonk, NY, USA).

## 3. Results

### 3.1. Sediment Electrical Conductivity

Sediment EC changed significantly between the distribution ranges, as did the interaction between ranges (invaded, native) and population patch location (Table 1). Mean sediment EC was 18% higher in the native range ( $2400 \pm 184 \mu\text{S cm}^{-1}$ ) than in the invaded range ( $1960 \pm 344 \mu\text{S cm}^{-1}$ ). However, sediment EC increased 92% seaward among population sites in the invaded range varying from  $412 \pm 75$  to  $5327 \pm 1114 \mu\text{S cm}^{-1}$ . In contrast,

sediment EC increased only 70% along the estuarine gradient in the native range, varying from  $1127 \pm 105$  to  $3768 \pm 104 \mu\text{S cm}^{-1}$ .

**Table 1.** Generalized Linear Model for sediment electrical conductivity comparing between distribution ranges (native and invaded) and locations (ordered according to their distance to the ocean).

|                         | Chi-Square of Wald | Degrees of Freedom | <i>p</i> |
|-------------------------|--------------------|--------------------|----------|
| Intersection            | 166,897.467        | 1                  | <0.0001  |
| Range                   | 1030.079           | 1                  | <0.0001  |
| Location                | 51,983.170         | 4                  | <0.0001  |
| Range $\times$ Location | 6,778.427          | 4                  | <0.0001  |

### 3.2. *Iris pseudacorus* Abundance

The relative cover of *I. pseudacorus* changed significantly between the distribution ranges, as did the interaction between ranges and population patch location (Table 2). *I. pseudacorus* cover was 17% lower in the native range ( $62 \pm 4\%$ ) than cover of the species in the invaded range ( $75 \pm 2\%$ ). The cover of *I. pseudacorus* varied just 15% between populations in its invaded range (changing between  $69 \pm 4\%$  and  $81 \pm 4\%$ ), whereas it varied 48% in its native range (between  $38 \pm 9\%$  and  $74 \pm 11\%$ ).

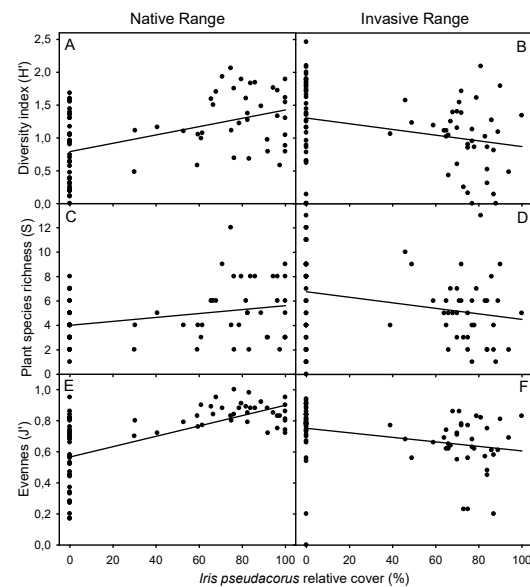
**Table 2.** General Linear Model for the relative cover of *Iris pseudacorus* comparing between distribution ranges (native and invaded) and population locations (ordered in each range sequentially according to their distance to the ocean), with sediment electrical conductivity (EC) as covariate. Significant differences are marked in bold.

|                         | Sum of Squares Type III | Degrees of Freedom | Mean Square       | F              | <i>p</i>          |
|-------------------------|-------------------------|--------------------|-------------------|----------------|-------------------|
| Corrected model         | <b>10,920.305</b>       | <b>10</b>          | <b>1092.030</b>   | <b>3.391</b>   | <b>0.001</b>      |
| Intersection            | <b>56,945.542</b>       | <b>1</b>           | <b>56,945.542</b> | <b>176.821</b> | <b>&lt;0.0001</b> |
| EC                      | 41.287                  | 1                  | 41.287            | 0.128          | 0.721             |
| Range                   | <b>2960.432</b>         | <b>1</b>           | <b>2960.432</b>   | <b>9.192</b>   | <b>0.003</b>      |
| Location                | 2160.140                | 4                  | 540.035           | 1.677          | 0.166             |
| Range $\times$ Location | <b>4082.218</b>         | <b>4</b>           | <b>1020.554</b>   | <b>3.169</b>   | <b>0.019</b>      |
| Error                   | 21,255.410              | 66                 | 322.052           |                |                   |
| Total                   | 395,743.000             | 77                 |                   |                |                   |
| Corrected total         | 32,175.714              | 76                 |                   |                |                   |

### 3.3. *Iris pseudacorus* Impacts on Plant Community Diversity

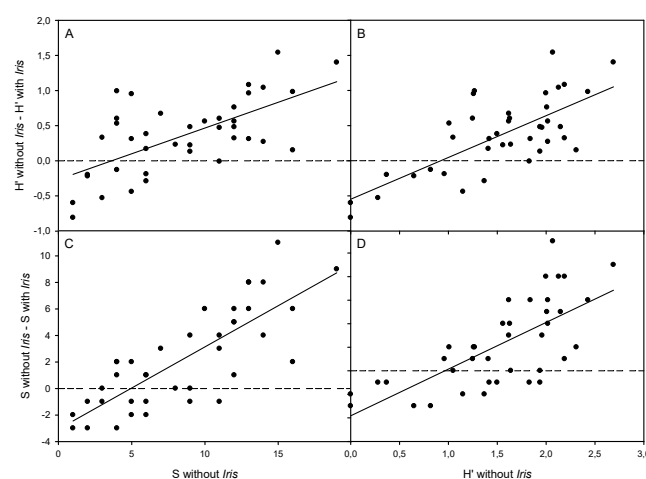
A total of 30 native plant species and only 2 exotic species were recorded in the native range of *I. pseudacorus*, whereas 55 native and 19 exotic species were recorded in the invaded range (Tables S2 and S3).

All calculated diversity indices of vegetation from plots with and without *I. pseudacorus* were independent of sediment EC in both distribution ranges when native and exotic species were included in the analyses (Pearson or Spearman correlation coefficient,  $p > 0.05$ ). In contrast, when exotic species were excluded from the analysis,  $\alpha$ -diversity and the number of plant species decreased at higher sediment EC in the invaded range ( $H'$ :  $r = -0.261$ ,  $p = 0.022$ ,  $n = 78$ ;  $S$ :  $r = -0.260$ ,  $p = -0.260$ ,  $n = 78$ ). Moreover, the differences in diversity indices between areas with and without *I. pseudacorus* were independent of EC along estuarine gradients studied in the native and invaded ranges, both including exotic and native plant species and only native species (Pearson or Spearman correlation coefficient,  $p < 0.05$ ). In addition, all diversity indices decreased with increasing *I. pseudacorus* cover in the invaded range, showing the opposite response in the native range (Pearson or Spearman correlation coefficient,  $p < 0.05$ ) (Figure 2).



**Figure 2.** Relationship between the  $\alpha$ -diversity ( $H'$ ), plant species richness ( $S$ ) and evenness ( $J'$ ) with *Iris pseudacorus* relative cover in native (Guadalquivir Estuary) and invaded (San Francisco Bay-Delta Estuary) distribution ranges. Regression equations: (A)  $y = 0.7921 + 6.335 \times$  ( $R = 0.429$ ,  $p < 0.0001$ ,  $n = 76$ ); (B)  $y = 1.304 - 4.333 \times$  ( $R = 0.274$ ,  $p < 0.05$ ,  $n = 78$ ); (C)  $y = 4.012 + 0.016 \times$  ( $R = 0.302$ ,  $p < 0.01$ ,  $n = 76$ ); (D)  $y = 6.764 - 0.023 \times$  ( $R = 0.252$ ,  $p < 0.05$ ,  $n = 78$ ); (E)  $y = 0.567 + 3.333 \times$  ( $R = 0.624$ ,  $p < 0.0001$ ,  $n = 75$ ); (F)  $y = 0.752 - 1.453 \times$  ( $R = 0.302$ ,  $p < 0.01$ ,  $n = 73$ ).

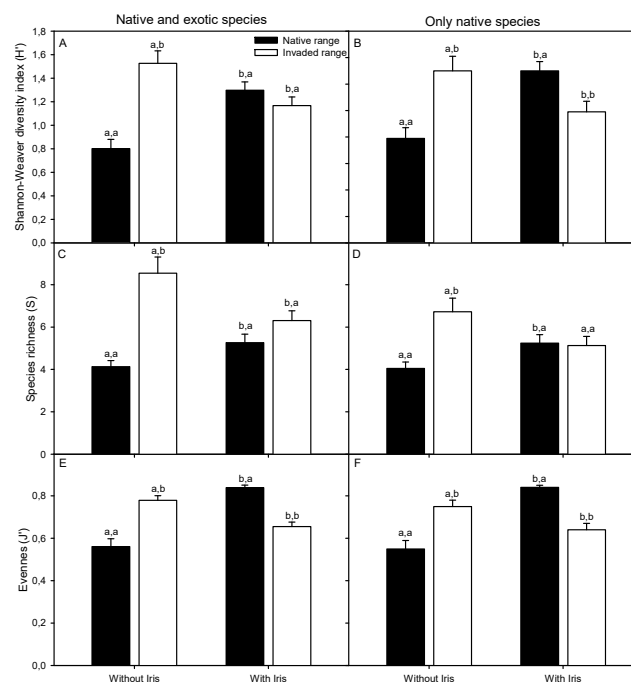
Shannon–Wiener  $\alpha$ -diversity and number of plant species within *I. pseudacorus* patches increased together with their values recorded outside of occupied patches in both distribution ranges (Figure S2). In contrast, species evenness within *I. pseudacorus* patches only increased together with evenness outside of *Iris* patches in the native range (Figure S2). In addition, the differences in plant species diversity and richness between areas without and with *I. pseudacorus* increased together with values of diversity and richness without *Iris*, respectively, only in the invaded range; these relationships were non-significant for species evenness (Figure 3).



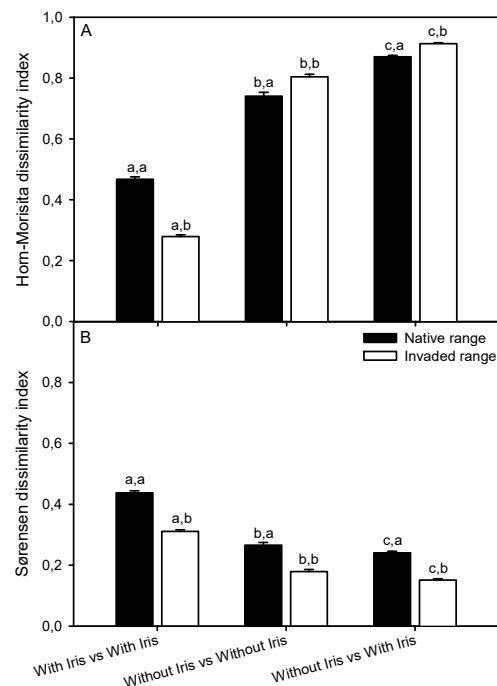
**Figure 3.** Relationship between the differences in  $\alpha$ -diversity ( $H'$ ) and plant species richness ( $S$ ) without and with *Iris pseudacorus* and  $H'$  values at study populations in the invaded San Francisco Bay-Delta Estuary. Regression equations: (A)  $y = -0.266 + 0.073 \times$  ( $R = 0.645$ ,  $p < 0.0001$ ,  $n = 39$ ); (B)  $y = -0.548 + 0.595 \times$  ( $R = 0.723$ ,  $p < 0.0001$ ,  $n = 39$ ); (C)  $y = -3.074 + 0.621 \times$  ( $R = 0.795$ ,  $p < 0.0001$ ,  $n = 39$ ); (D)  $y = -3.822 + 3.963 \times$  ( $R = 0.702$ ,  $p < 0.0001$ ,  $n = 39$ ).

Distribution range, location along the estuarine gradient and the interactions between range and *I. pseudacorus* presence, range and location, and the three-way interaction among range, *I. pseudacorus* presence and location all had a significant effects on diversity indices (MANOVA,  $p < 0.05$ ) (Table S4). According to the lineal models,  $\alpha$ -diversity and species richness changed significantly between distribution ranges and locations. Species evenness varied significantly between *I. pseudacorus* presence and locations. In addition, there were also a number of interactive effects of distribution range, location and invader presence that influenced diversity indices (Table S5).

$H'$   $\alpha$ -diversity was 48% lower in the native than in the invaded range of *I. pseudacorus* in areas of the plant community where the invader was absent. These areas were characterized by lower species richness and evenness. In contrast, diversity and species richness within *Iris*-occupied plots were similar in both distribution ranges, whereas evenness was 22% higher within *Iris*-occupied plots in the native range than was documented in the invasive range (Figure 4; Table S6). When discarding exotic species from the analysis,  $\alpha$ -diversity within *Iris*-occupied plots was 24% higher in the native than in the invaded range (Figure 4; Table S7). The reported differences in diversity indices between distribution ranges were reflected in lower values of the Morisita–Horn dissimilarity index in the native vs. the invaded range when comparing un-invaded plots with themselves and with invaded plots. In contrast, higher Morisita–Horn dissimilarity indices were found for plots with *I. pseudacorus* in the native compared to the invaded range (Figure 5A, Table S8). The Sørensen dissimilarity index was always higher in the native than in the invaded range for every plot combination with and without *I. pseudacorus* (Figure 5B, Table S9).



**Figure 4.** Shannon–Wiener  $\alpha$ -diversity ( $H'$ ) (A,B), species richness ( $S$ ) (C,D) and  $J'$  evenness (E,F) with and without *Iris pseudacorus* in its native (Guadalquivir Estuary) and invaded (San Francisco Bay-Delta Estuary) distribution ranges, analyzing both native and exotic species (A,C,E) and only native species (B,D,F). Different letters indicate significant differences between paired plots with *I. pseudacorus* presence or absence within each range (first letter) and between ranges (second letter) ( $t$ -test or U-test,  $p < 0.05$ ). Values are mean  $\pm$  SE ( $n = 38$ –39).

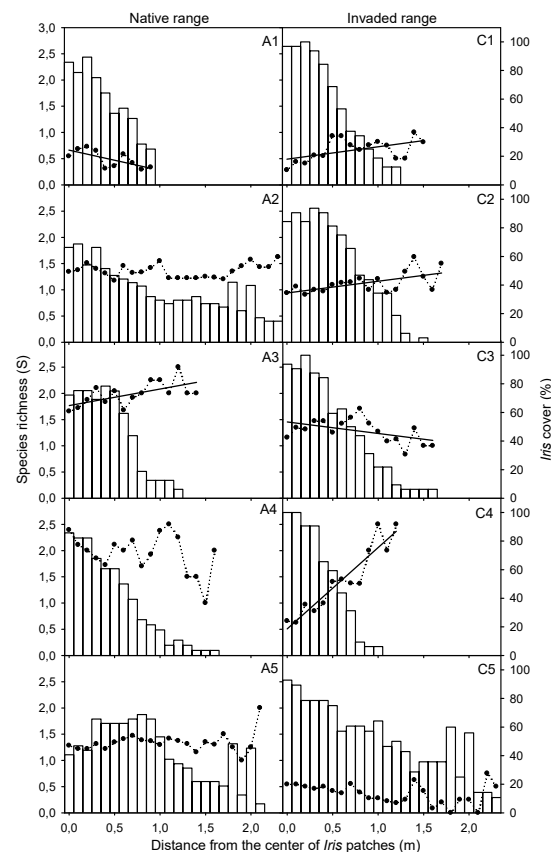


**Figure 5.** Horn–Morisita (A) and Sørensen (B) dissimilarity indices between plant communities with and without *Iris pseudacorus* in its native (Guadalquivir Estuary) and invaded (San Francisco Bay-Delta Estuary) distribution ranges. Different letters indicate significant differences between plant communities within each range (first letter) (Kruskal–Wallis test and Man–Whitney U-test,  $p < 0.05$ ) and between ranges for the same plant community (second letter) (Man–Whitney U-test,  $p < 0.05$ ). Values are mean  $\pm$  SE ( $n = 703$ – $1521$ ).

In the native range,  $\alpha$ -diversity was lower by 38% in plots where *I. pseudacorus* was not present due to lower number of plant taxa and species evenness values than where the *Iris* was a community member (Figure 4; Table S6), but eight rare plant taxa (with a frequency of occurrence lower than 6–14%) were recorded growing out of *I. pseudacorus* patches and were absent from within those patches (Table S2). In contrast, results documented the opposite impact of *I. pseudacorus* on the plant community in the invaded California range where  $\alpha$ -diversity, species richness, evenness were significantly reduced in plots with *I. pseudacorus* (Figure 4; Table S6). Species richness did not change significantly between areas with and without *I. pseudacorus* when exotic species were excluded from the analysis (Figure 4; Table S7). In this invaded range,  $\alpha$ -diversity was 24% higher in plots where the *I. pseudacorus* was absent compared to species poor plant community composition associated with the focal species. At these study sites, 11 native and only 2 exotic plant taxa (12 taxa with frequencies  $<9\%$ ) were recorded growing beyond of *Iris* patches, but they were not present in adjacent *Iris*-invaded habitat with otherwise comparable environmental conditions. In contrast, only 5 native species (with frequency  $<9\%$ ) grew within *Iris*-occupied plots, and these same species were absent from areas free of *Iris* in the invaded range (Table S3). *Iris pseudacorus* was mainly associated with six native species (*Polygonum salicifolium* Brouss., *Cynodon dactylon* (L.) Pers., *Oenanthe lachenalii* C.C. Gmel., *Phragmites australis* (Cav.) Trin. ex Steud., *Bolboschoenus maritimus* (L.) Palla and *Atriplex chenopodioides* Batt.) in its native range and with four native species (*Juncus balticus* Willd. (syn. *J. arcticus* var. *balticus* (Willd) Trautvetter), *Calystegia sepium* (L.) R.Br., *Schoenoplectus acutus* (Muhl. ex J.M. Bigelow) A. Löve & D. Löve and *Schoenoplectus californicus* (C.A. Mey.) Steud.) in its invaded range (Table S10). In general, the plant taxa with higher relative cover values beyond plots with *I. pseudacorus* also occurred at greater abundance (higher relative cover) within the *Iris*-occupied plots. Furthermore, most of the species that were in the greater community but did not occur within plots with *I. pseudacorus* had relative cover lower than 20% where without the *Iris* (Figure S3).

Species richness decreased towards the center of *I. pseudacorus* patches in three of the five study locations in the invaded range, while this pattern was only observed at one location in the native range. In contrast, the number of plant species increased towards the center of *I. pseudacorus* patches in only one study location in each distribution range. Moreover, the pattern of species richness was characterized by waves along the radius of *I. pseudacorus* patches, and at every location, the peaks of species richness were at nearly the same distance intervals from the patch centers (0.0–0.3 m, 0.5–0.8 m, 1.0–1.2 m and 1.4–1.7 m). The pattern of these peaks of species richness within *I. pseudacorus* patches was c. 20–30 cm long and c. 20–30 cm away from each other (Figure 6).

In both distribution ranges, the Horn–Morisita dissimilarity index was higher when comparing areas with and without *I. pseudacorus* than when comparing areas with *I. pseudacorus* among them (Figure 5A, Table S8). On the contrary, the Sørensen dissimilarity index showed the highest absolute values when comparing areas with *I. pseudacorus* among themselves (Figure 5B, Table S9).



**Figure 6.** Relationship between species richness (S) and distance (m) to the center of *Iris pseudacorus* population patches in Andalusia (A1–A5), Guadalquivir Estuary (native range), compared to this relationship in California (C1–C5), San Francisco Bay-Delta Estuary (invaded range). Columns indicate relative cover (%) of *I. pseudacorus*. Regression equations: (A1)  $y = 0.663 - 0.385 \times$  ( $R = -0.699$ ,  $p = 0.05$ ,  $n = 10$ ); (C1)  $y = 0.490 + 0.235 \times$  ( $R = 0.532$ ,  $p = 0.034$ ,  $n = 16$ ); (C2)  $y = 0.939 + 0.224 \times$  ( $R = 0.600$ ,  $p = 0.008$ ,  $n = 18$ ); (A3)  $y = 1.768 + 0.315 \times$  ( $R = 0.613$ ,  $p = 0.015$ ,  $n = 15$ ); (C3)  $y = 1.455 - 0.221 \times$  ( $R = -0.497$ ,  $p = 0.042$ ,  $n = 17$ ); (C4)  $y = 0.506 + 1.552 \times$  ( $R = 0.942$ ,  $p < 0.0001$ ,  $n = 13$ ).

#### 4. Discussion

Our study reveals that the colonization of *Iris pseudacorus* has very different effects on the diversity of tidal plant communities in its native and invaded range. In the native range, *I. pseudacorus* was associated with plant diversity by increasing evenness and species richness. On the contrary, greatly reduced plant diversity was associated with *I. pseudacorus*

in the invaded range. In addition, the effects of *I. pseudacorus* on every diversity index were independent of sediment EC along the estuarine gradients in both study ranges.

Plant  $\alpha$ -diversity levels in plots without *I. pseudacorus* were 48% lower in the native than in the invaded range, due to lower species richness and evenness. This geographical difference could be the product of many factors. For example, our field observations suggest high herbivory levels by livestock as a main factor that could explain reduced plant diversity in most of the native study populations. In contrast, there was no grazing or other significant herbivory observed at our study sites in the invaded range. Heavy grazing is reported to eliminate sensitive species and increase the density of graminoids in high marsh habitats [56] as we recorded in the most grazed locations in the native range, where *Cynodon dactylon* dominated plant communities.

Plant  $\alpha$ -diversity was similar within *I. pseudacorus* patches in both distribution ranges, even though higher  $\alpha$ -diversity was recorded without *I. pseudacorus* in the invaded range. This can be explained by the contrasted effects of *I. pseudacorus* on plant diversity between geographical ranges:  $\alpha$ -diversity increased 38% within *I. pseudacorus* patches in the native range and decreased 24% in the invaded range, in relation to areas not colonized by *I. pseudacorus*. These contrasted differences in  $\alpha$ -diversity within *I. pseudacorus* invaded areas were related to differences in both evenness and species richness. Thus, we found native range microenvironments associated with *I. pseudacorus* harbored more species than were recorded outside of *I. pseudacorus* patches. In contrast, *I. pseudacorus* presence corresponded to decreasing local plant species richness in the invaded range. *Iris pseudacorus* cover was 17% lower in the native range than in the invaded range, which enabled some low-abundant plant taxa to colonize and coexist within *I. pseudacorus* patches in the native range where the presence of *I. pseudacorus* limits the abundance of dominant species. Nevertheless, *I. pseudacorus* presence limited the colonization of eight low-frequently occurring plant taxa that were recorded only outside of *I. pseudacorus*-occupied patches in the native range. This phenomenon of displacing low-abundant taxa was also recorded in the invaded range, where *I. pseudacorus* negatively impacted  $\alpha$ -diversity levels. Nevertheless, diversity levels were independent of *I. pseudacorus* foliar cover in both distribution ranges, pointing to a complexity of factors at play that can control biodiversity. In this context, sediment EC changed between 70–92‰ along the estuarine gradients in the native and invaded study areas, but diversity indices for the plant communities and the effects of *I. pseudacorus* on them were surprisingly independent of this environmental factor. In the invaded range, we recorded more exotic species in intertidal marshes with lower sediment salinity than at locations with higher salinities, but this pattern did not relate to the effects of *I. pseudacorus* on diversity indices. These results indicate *I. pseudacorus* reaches a level of abundance as a successful invader that disrupts the composition, structure and biodiversity function of native plant communities along broad brackish estuarine gradients. Nevertheless, *I. pseudacorus* shows negative responses at 17 ppt salinity (EC c. 27.5 mS cm<sup>-1</sup>) [43], whereas the maximum sediment EC recorded in our study was  $3.7 \pm 0.1$  mS cm<sup>-1</sup>. The competitive ability of *I. pseudacorus* could also differ between distribution ranges due to a range of other factors such as resource availability or genetic differences that are expressed as contrasting phenotypes. In this sense, invasive plant species are likely to be more competitive with native flora as a result of greater size (ex. height) and density [5,57,58]. For example, the invasive aquatic macrophyte *Typha* sp. is capable of rapidly colonizing habitats and forming monodominant vegetation stands due to traits such as robust size, rapid growth rate, and rhizomatic expansion [59], which are plant traits shared also by *I. pseudacorus* in the invaded range [43]. Moreover, invasion success of exotic species may be based on selective introduction of specific preadapted and plastic genotypes or on adaptive evolution to contrasted environmental conditions in the introduced range [19,24,60]. In addition, plant species interacting with *I. pseudacorus* may show different responses to *I. pseudacorus* colonization between distribution ranges. Thus, high competitive ability, biomass and diversity of recipient communities, long-term coexistence (coevolutionary history) and

species filtering have been reported as responsible for lower impacts of invasive species in their native range [14,20,23].

In accordance with our hypothesis, *I. pseudacorus* had greater negative impacts on diversity where species richness and  $\alpha$ -diversity were higher in plots without the *Iris* in the invaded range. In this sense, [5] suggested that invasion impacts may be a continuum across an entire invaded range. This changing impact of *I. pseudacorus* invasion on recipient plant communities depending on their diversity was due to dominant perennial rhizomatous native species, including *Juncus balticus* (Baltic rush), *Schoenoplectus acutus* (hardstem bulrush) and *Schoenoplectus californicus* (California bulrush). These four native emergent macrophytes persisted despite introduction and spread of *I. pseudacorus* in their community, suggesting they are more resistant to invasion by *I. pseudacorus* than rare and low-abundance species that succumb to competitive displacement. There was a spatial context to the invasion impact on diversity in our invaded study populations. *Iris pseudacorus* displaced the more rare, low-abundant species (cover < 20%) from more interior areas within its patches, where *I. pseudacorus* was present at higher cover levels and during longer periods than at the periphery of the invading patches. The interspecific displacement of native species by *I. pseudacorus* showed a spatial pattern organized in 20–30 cm wide concentric rings of high and low species richness alternating along the *I. pseudacorus* patch radius. This spatial pattern would respond to the clonal growth of *I. pseudacorus* in successive waves of aerial sprouts coming from 20–30 cm long rhizomes. This clonal growth pattern has been described before for other clonal plant species [61–63].

Our results agree with other inter-continental studies on exotic plant species comparing their effects on plant communities in their native versus invaded ranges. In this sense, *Centaurea melitensis* L. (Asteraceae) was more dominant in invaded sites than in native ones, which may be related to different climatic and soil nutrient conditions [19]. Reference [20] reported that the richness of native species responded more negatively to three dominant species cover in its invaded rather than native range, suggesting this was the result of long-term coexistence and species filtering. Reference [23] also suggested that coevolutionary history between native-range neighbors may lead to different outcomes of the interactions between *Chromolaena odorata* (L.) R.M. King & H. Rob. (Asteraceae) and neighbor plants in its native and invaded ranges. Moreover, [21] recorded negative impacts between macrophyte richness and cover and *Eichhornia crassipes* Kunth (Pontederiaceae) biomass only in its invaded range and mainly on rare species. This was likely due to the role of invasive *E. crassipes* as an ecosystem engineer that decreases habitat heterogeneity.

To support ecological restoration, it is important to understand how the invasiveness (abundance) and community-level impacts of an invasive plant species vary in response to changing environmental conditions [64]. The simplification of plant communities within invasive *I. pseudacorus* patches (relatively low  $\alpha$ -diversity) was also accompanied by a homogenization at the landscape scale ( $\beta$ -diversity) along the estuarine gradient that was reflected on dissimilarity indexes. Thus, we recorded lower Morisita–Horn index values and higher Sørensen index values when comparing areas colonized by *I. pseudacorus* among themselves than with areas free of *I. pseudacorus*, showing that *I. pseudacorus* invasion promoted similarity in the relative abundance of species and dissimilarity in species presence [51]. Results of recent studies of *I. pseudacorus* support updated risk assessments highlighting the continued high invasion potential of *I. pseudacorus* under sea level rise and other changing environmental conditions. For example, high production of viable seeds that withstand fresh to high aqueous salinity ranges [39] and rapid hydrochorous dispersal of buoyant *I. pseudacorus* seeds can be expected to continue to contribute to invasion spread [65]. In view of our results, urgent management practices are needed to control and eradicate *I. pseudacorus* from the inland Sacramento-San Joaquin Delta Estuary since this invasive macrophyte is reducing plant diversity at local and landscape scales along an extensive estuarine gradient. In this context, eradication and control efforts should initially prioritize impacted freshwater tidal areas in the upper inland Delta, where more low-abundant native species are being displaced by invasive *I. pseudacorus*. Timing of

management actions prior to seed production is also crucial, to prevent dispersal and further spread of the exotic species downstream in the estuary.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14050326/s1>. Figure S1: Field pictures of sampled locations colonized by *Iris pseudacorus* in its native (Guadalquivir River Estuary, Andalusia, Spain, A1–A5) and the invaded range (Sacramento-San Joaquin Delta Estuary, CA, USA, C1–C5).; Figure S2: Relationship between the  $\alpha$ -diversity ( $H'$ ), plant species richness ( $S$ ) and evenness ( $J'$ ) with and without *Iris pseudacorus* in native (Guadalquivir Estuary) and invaded (San Francisco Bay-Delta Estuary) distribution ranges. Dashed lines indicate means values. Regression equations: A,  $y = 0.871 + 0.533 \times$  ( $R = 0.598$ ,  $p < 0.0001$ ,  $n = 38$ ); B,  $y = 0.548 + 0.405 \times$  ( $R = 0.581$ ,  $p < 0.0001$ ,  $n = 39$ ); C,  $y = 1.581 + 0.891 \times$  ( $R = 0.445$ ,  $p < 0.005$ ,  $n = 38$ ); D,  $y = 3.074 + 0.379 \times$  ( $R = 0.624$ ,  $p < 0.0001$ ,  $n = 39$ ); E,  $y = 0.764 + 0.132 \times$  ( $R = 0.397$ ,  $p = 0.015$ ,  $n = 37$ ).; Figure S3: Relationship between cover (%) of plant taxa in paired plots with and without invasive *Iris pseudacorus* in *Iris*-invaded study locations in tidal wetlands along an estuarine gradient in the San Francisco Bay-Delta Estuary (CA, USA). Regression equation:  $y = 4.076 + 0.467 \times$  ( $R = 0.408$ ,  $p < 0.0001$ ,  $n = 75$ ). Table S1: Geographical coordinates and number of study patches for locations colonized by native and invasive *Iris pseudacorus* populations. Locations are numbered from the most inland location to the closest to the sea; Table S2: Native and exotic plant taxa growing without and with *Iris pseudacorus* along the Guadalquivir River Estuary; Table S3: Native and exotic plant taxa growing without and with *Iris pseudacorus* along the Sacramento-San Joaquin Delta Estuary; Table S4: F-statistics and Pillai's trace from MANOVAs for diversity indices for the factors distribution range (native and invaded), *Iris pseudacorus* presence (with and without *Iris*), locations (grouped in each range sequentially according to their distance to the ocean) and their interactions, with sediment electrical conductivity as covariate, including main effect and model degrees of freedom (d.f.); Table S5: General Linear Model or Generalized Linear Model for the Shannon–Wiener index ( $H'$ ), species richness ( $S$ ) and evenness ( $J'$ ) comparing between distribution ranges (native and invaded), presence of *Iris pseudacorus* (with and without *Iris*) and locations (ordered in each range sequentially according to their distance to the ocean) and their corresponding interactions, with sediment electrical conductivity (EC) as covariate. Significant differences are marked in bold; Table S6: Student t-test or Man-Whitney U-test comparing Shannon–Wiener index ( $H'$ ) (A), number of plant species ( $S$ ) (B), and evenness ( $J'$ ) (C) without and with *Iris pseudacorus* in its native (Guadalquivir Estuary) and invaded (Sacramento-San Joaquin Delta Estuary) distribution range, including all recorded species in the analyses. Significant differences are marked in bold. d.f., degrees of freedom; Table S7: Student t-test or Man-Whitney U-test comparing Shannon–Wiener index ( $H'$ ) (A), number of plant species ( $S$ ) (B), and evenness ( $J'$ ) (C) without and with *Iris pseudacorus* in intertidal marshes within its native (Guadalquivir Estuary) and invaded (Sacramento-San Joaquin Delta Estuary) distribution range, including only native species in the analyses. Significant differences are marked in bold. d.f., degrees of freedom; Table S8: Generalized Linear Model for Morisita–Horn dissimilarity index comparing plant communities with and without *Iris pseudacorus* and between its distribution ranges (native and invaded); Table S9: Generalized Linear Model for Sørensen dissimilarity index comparing plant communities with and without *Iris pseudacorus* and between its distribution ranges (native and invaded); Table S10: Indicator values for the simultaneous occurrence of plant species with *Iris pseudacorus* (Itps) in intertidal marshes within its native and invaded ranges. A, Positive predictive power of species combinations; B, Sensitivity of species combinations; sqrtIV, Square root of indicator value of species combinations; P, P-value of the permutation test of statistical significance. We show results with sqrtIV > 0.05.

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