

Phenotypic trait differences between *Iris pseudacorus* in native and introduced ranges support greater capacity of invasive populations to withstand sea level rise

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Abstract

Aim: Tidal wetlands are greatly impacted by climate change, and by the invasion of alien plant species that are being exposed to salinity changes and longer inundation periods resulting from sea level rise. To explore the capacity for the invasion of *Iris pseudacorus* to persist with sea level rise, we initiated an intercontinental study along estuarine gradients in the invaded North American range and the native European range.

Location: San Francisco Bay-Delta Estuary; California, USA and Guadalquivir River Estuary; Andalusia, Spain.

Methods: We compared 15 morphological, biochemical, and reproductive plant traits within populations in both ranges to determine if specific functional traits can predict invasion success and if environmental factors explain observed phenotypic differences.

Results: Alien *I. pseudacorus* plants in the introduced range had more robust growth than plants in the native range. The vigour of the alien plants was reflected by expression of higher leaf water content, fewer senescent leaves per leaf fan, and more carbohydrate storage reserves in rhizomes than plants in the native range. Moreover, alien plants tended to show higher specific leaf area and seed production than native plants. *I. pseudacorus* plants in the introduced range were less affected by increasing salinity and were exposed to deeper inundation water along the estuarine gradient than those in the native range.

Main Conclusions: Functional trait differences suggest mature populations of *I. pseudacorus* in the introduced range have greater adapted capacity to adjust to environmental stresses induced by rising sea level than those in the native range. Knowledge of these trait responses can be applied to improve risk assessments in invaded estuaries and to achieve climate-adapted conservation goals for conservation of the species in its native range.

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KEYWORDS

biogeography, functional plant traits, Guadalquivir estuary, phenotypic traits, plant invasions, San Francisco Bay-Delta estuary, sea level rise, tidal wetlands

1 | INTRODUCTION

Alien plant invasions are global environmental changes that result from anthropogenic movement of species beyond their natural dispersal barriers to new geography and distribution ranges (Vitousek et al., 1997). Global climate change is also dynamically changing habitat conditions in introduced and native ranges of species (IPPC, 2022). Invasion risk is expected to continue to change with climate change because invaders may be better able to succeed in novel and altered environments and benefit from increases in resource availability (e.g. nitrogen and CO₂). This highlights a crucial need to improve understanding of invasion risk under global change to support management programmes relevant for the 21st century (Bradley et al., 2010).

The ability to predict what biological attributes drive the invasiveness of plant species can provide foundational support for preventing introductions of alien species with traits that deem them a risk for invasion. Reviews (Pyšek & Richardson, 2008) and meta-analyses (Davidson et al., 2011; Palacio-López & Gianoli, 2011; van Kleunen et al., 2010) suggest functional plant traits related to growth, biomass allocation, physiology, fecundity, and phenotypic plasticity support invasiveness of alien plant species. Environmental variation within intercontinental distributions of invasive alien plant species can influence plant traits that support their fitness, establishment, and spread (Hierro et al., 2005; Pearson et al., 2022). Therefore, investigations conducted through a biogeographical framework coupled with a functional trait approach (Drenovsky et al., 2012) can provide unique insights on how an invasive plant species responds to environmental factors affected by climate change. Incorporating biological traits into conservation biogeography across species ranges can also be crucial for development of risk assessment predictions addressing responses of vulnerable ecosystems to environmental change (Dong et al., 2022; Miatta et al., 2021).

Alien populations that become invasive in introduced ranges are often assumed to be more abundant and grow larger than their conspecific populations in the native range, though most research has been limited to the introduced range (Guo, 2006; Hierro et al., 2005). The few studies focused on plants in their native range that are invasive elsewhere suggest some species are pre-adapted to invasion (Schlaepfer et al., 2010; van Kleunen et al., 2011; Jelbert et al., 2015). Some alien species may acclimate to environmental change and maintain fitness through phenotypic plasticity without evolutionary adaptation (Barrett, 2000; Pearman et al., 2008). Adaptive phenotypic plasticity can alter functional traits to maintain fitness and alter the ecological niche breadth (Colautti et al., 2017). In addition, release from environmental stress and natural enemies (e.g., herbivores) in introduced habitats may favour establishment and spread of alien species and may alleviate the negative effects on

fitness of depletion of genetic variation derived from demographic bottlenecks (Colautti et al., 2017; Schrieber & Lachmuth, 2017). Purging genetic loads from founder effects are also now thought to enable alien plants to adapt more quickly via rapid evolution (Marchini et al., 2016). As a result of the continuing evolution of alien plant species, some functional plant traits specifically underlie their success (Bajwa et al., 2016; van Kleunen et al., 2010).

Understanding which plant traits might lead to invasion success is particularly important in sensitive wetland habitats. Wetlands account for less than 6% of Earth's landmass yet have been highly vulnerable to biological invasions due to their landscape sink position, with 24% of plant species identified as the world's worst invaders being wetland plants (Zedler & Kercher, 2004). Of these wetlands, tidal marsh ecosystems have been highly impacted by the invasion of alien species (Adam, 2002). With global climate change, plant species colonizing tidal marshes are being exposed to sea level rise (SLR) and concomitant changes in tidewater salinity and inundation (Morris et al., 2002; Thorne et al., 2018). The modification of salinity and inundation regimes is crucial since these key environmental stressors drive wetland vegetation change in response to SLR (Baldwin & Mendelssohn, 1998). The distribution patterns across freshwater to brackish estuarine gradients are rapidly shifting in response to SLR (Mathiventhan et al., 2022), and rapidly assembled plant communities at these moving fronts will favour alien plant species with superior colonization ability (Grewell et al., 2013). Those plant species with a greater tolerance to modifications in environmental factors and broader ecological niches will influence the future configuration of ecosystems (Thuiller et al., 2005). A key need for conservation of estuarine ecosystem functions is to increase our knowledge of the responses of alien invasive species to changing environmental conditions.

Iris pseudacorus L. (yellow flag iris; Iridaceae) is a perennial macrophyte native to the British Isles, Scandinavia, Europe, the Mediterranean Region, and western Asia (Encyclopedia of Life, 2022). *Iris pseudacorus* has highly attractive yellow flowers which enticed 18th century botanical collectors to import it to North America (e.g., Hayden Reichard & White, 2001). In North America, *I. pseudacorus* was introduced in Virginia before 1771, and by 1800 it was growing along the tidal Potomac River (Wells & Brown, 2000). Accidental introductions of plants through ballast water discharges are also significant invasion pathways (Lehan et al., 2013). *Iris pseudacorus* was documented as a significant plant in ballast water discharge to coastal Atlantic USA harbours (Torrey Botanical Club, 1888), and therefore likely to other estuaries. By 1948, the introduced range included the Pacific Northwest and California (Consortia of California and Pacific Northwest Herbaria; California Academy of Sciences). Despite regulatory restrictions on its transport and sale, horticulture continues to play a role in *I. pseudacorus*

introductions (Beaury et al., 2021; Molina-Montenegro et al., 2018). The global distribution of *I. pseudacorus* includes 16 Köppen-Geiger climate zones (Minuti et al., 2022). The species has invaded and displaced native wetland vegetation in nearly every global ecozone (Gervazoni et al., 2020; Hayasaka et al., 2018; Mopper et al., 2016). In California tidal marshes, *I. pseudacorus* reduces species richness and diversity of invaded native plant communities, in contrast to its ecological role as a native species in the Iberian Peninsula, where it co-exists within diverse wetland plant communities (Gallego-Tévar et al., 2022). Recent downstream spread into brackish reaches of the greater San Francisco Bay-Delta Estuary was unexpected, as it had long been assumed this species would be limited to freshwater wetlands. The risk for further spread with increasing salinity and tidal ranges is not clear (Cloern et al., 2011). Given the prevalence of *I. pseudacorus* in the world's estuarine vegetation, it is important to understand the potential fate or persistence of the species in the native and introduced ranges as SLR continues.

To begin to understand the capacity for the invasion of *I. pseudacorus* to be sustained with SLR, we carried out a field study at a focused patch scale within populations. *I. pseudacorus* plants produce many rhizomes, resulting in a dense clonal tussock or clumping growth form. Therefore, hereafter, "patch scale" refers to the fine-scale assessment level within the study population, and each "patch" is our monitoring plot that spatially encompasses this discrete tussock growth form within a population. Within each assessment patch, we evaluated variation in functional plant traits and environmental variables at peak summer growth along estuarine salinity and inundation gradients in both the introduced and native ranges. Our objective was to determine whether functional traits of *I. pseudacorus* can explain its invasive success in the introduced range and if current environmental factors can explain phenotypic differences between ranges. We hypothesized that alien *I. pseudacorus* plants would express enhanced functional traits supporting greater plant vigour, with lower sensitivity to increasing salinity and inundation along estuarine gradients in comparison to native plants.

2 | METHODS

2.1 | Study sites

We established our study at *I. pseudacorus* population sites distributed along estuarine gradients from the freshwater tidal to brackish tidal marshes in the native range within the Guadalquivir River Estuary (GRE; Southwest Iberian Peninsula), and in the introduced range within the San Francisco Bay-Delta Estuary (SFE; Pacific Coast of North America; Figure 1). The estuaries each occur near continental plate margins, and both are classified as tectonically shaped drowned river estuaries with geomorphic complexity (Atwater, 1979; Rodríguez-Ramírez et al., 2019). Tidal marshes in both estuaries experience mixed semi-diurnal tidal regime with meso-tidal ranges and are influenced by local watershed inflow, freshwater diversions for beneficial uses such as irrigation and

municipal water supply, and dam-regulated outflow from upstream reservoir releases. Mediterranean climate prevails at both estuaries, with cool, wet winters and hot, dry summers moderated by Atlantic (GRE) or Pacific (SFE) influence (AEMET, 2020; Kimmerer, 2004).

The native Palearctic biogeographic range of *I. pseudacorus* is believed to include central and southern Scandinavia, the British Isles, Europe, northern Africa, and western Asia (Gervazoni et al., 2020; Sutherland & Walton, 1990). However, early occurrence records (17th–19th century) are scant and are mainly limited to records from Great Britain and France (GBIF). The Royal Botanic Garden of Madrid founded in 1755 greatly increased 1804 and later collections of *I. pseudacorus* specimens from the Iberian Peninsula, including an 1849 specimen from Chiclana tidal marshes near our Guadalquivir River Estuary study sites (CSIC-Real Jardín Botánico, 2022).

While alien *I. pseudacorus* had established in the upper freshwater tidal reach of Atlantic North American coastal Virginia's Potomac River by 1800 (Wells & Brown, 2000), invasions in the Pacific Northwest and California are more recent. Records of naturalized *Iris pseudacorus* date to 1948 in coastal southern California, and populations were well-established in the Merced River tributary to the Sacramento-San Joaquin River Delta by 1959 (CCHI Portal Biodiversity Data, Consortium of California Herbaria, 2023). Alien populations were established in freshwater tidal wetlands of the inland Sacramento-San Joaquin Delta by 1969 (Light et al., 2005). Downstream spread into brackish tidal wetlands in the greater San Francisco Bay-Delta Estuary has recently occurred (Gallego-Tévar et al., 2022; Gillard et al., 2021).

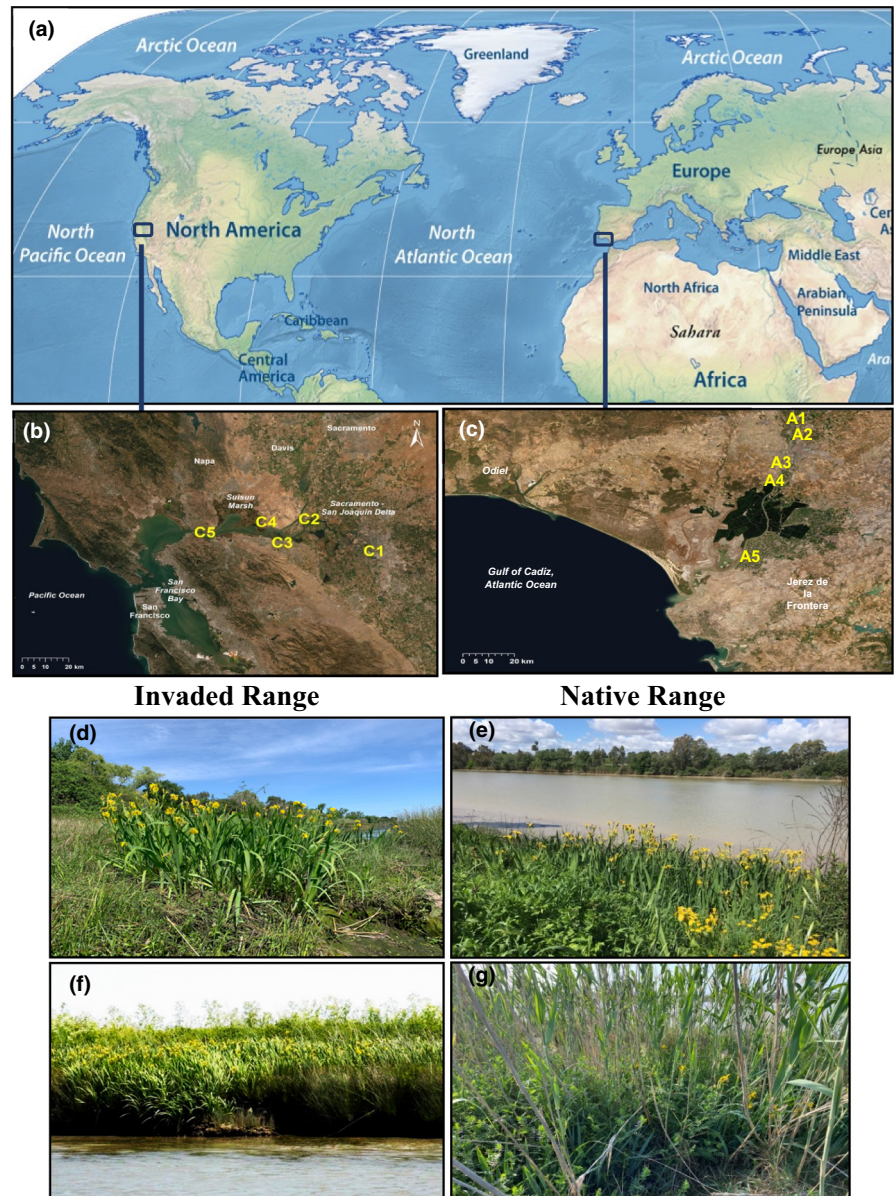
Study plots were established in native populations of *I. pseudacorus* distributed from the freshwater tidal reach to the most downstream population in brackish marshes in the GRE just above the Gulf of Cadiz. At SFE, population study sites were distributed from freshwater tidal reaches to brackish wetlands in the Carquinez Strait where the estuary penetrates California's Coast Range (Figure 1). Using standardized methods at all study sites, we evaluated variation in 15 functional plant traits and 11 environmental variables within fixed patch-scale monitoring plots corresponding to discrete plant tussocks ($n = 7-8$ per population) at five study populations of *I. pseudacorus* extant along estuarine gradients in both the introduced and native ranges.

2.2 | Data collection and laboratory analyses

2.2.1 | Plant traits

Using a line intercept method, the presence of *I. pseudacorus* was recorded at 10-cm intervals along two perpendicular transects across the maximum length and width of each patch-scale monitoring plot of *I. pseudacorus*. The absolute cover (%) of *I. pseudacorus* was calculated as the number of points the species was present in relation to the total number of points of both transects and multiplied by 100. Maximum length and width of study patches (individual *I. pseudacorus* clonal plants covering circular to elliptical areas) within

FIGURE 1 (a) Geographical locations of the study in the introduced North American and native European ranges. Locations of *Iris pseudacorus* population sites in (b) San Francisco Bay-Delta Estuary, California, USA and (c) Guadalquivir River Estuary, Andalusia, Spain. Photographs of *I. pseudacorus* study populations at (d) Brannon Island (C2; alien), (e) Guadalquivir River at Seville (A2; native), (f) Montezuma Slough, Suisun Marsh (C4; alien) and (g) Guadalquivir River near Acequia de Reina Victoria (A4; native).



each population were measured along perpendicular transects using a reel tape. In situ measurements of leaf morphology (maximum length and width) were recorded in the field for five randomly selected, fully expanded adult leaves in each plot at each population during peak summer growth. The number of live and senescent leaves per leaf fan used for leaf morphology measurements was also recorded in each plot ($n = 5$ leaf fans per plot). *I. pseudacorus* retains senescent leaves attached to stems as new leaves emerge through the growing season. Therefore, it is meaningful to count senescent leaves together with live leaves as a record of total leaf production by the plant.

Each measured live leaf was harvested and transported to the laboratories in coolers with blue ice for analysis of leaf water content (LWC), specific leaf area (SLA), and total carbon (C) and nitrogen (N) concentrations. Leaf area was measured using image analysis software (introduced range: WinFOLIA 2009a, Regent Instruments, Saint-Foy, Quebec, Canada; native range: Medición de Hojas v1.0,

ADN software). SLA was calculated by dividing the leaf area by dry mass from five randomly chosen adult leaves per plant following Garnier et al. (2001). Total C and N concentration of alien leaf tissue were analysed using a Perkin Elmer 2400 CHNS/O analyser (Perkin Elmer, Waltham, MA, USA), and a LECO TruSpec Micro CHN/CHNS/O analyser (LECO Corporation).

At all population sites in both estuaries, the team determined apical leaf elongation rates (LER) in the field by marking the base of ten leaves per plot with waterproof sealant and measuring the distance from the mark to the leaf base after 48 h (Castillo et al., 2014). Reproductive traits were also recorded. The number of capsules (0 to X) produced on each flowering stem within each discrete patch was counted. At two sites in the introduced range (C1, C3) where it was not possible to distinguish a discrete individual patch given extensive contiguous linear bands of plants, we counted capsules within a 2×2 m subplot which was representative of the average area sampled for discrete patches. Mature capsules were collected

randomly based on capsules present ($n = 1$ to a maximum of 40 capsules per plot) and evaluated for seed count per capsule, then air-dried, and weighed to obtain mean seed mass ($n = 4$ –10 capsules per plot; 10 seeds per capsule). In the native range, seed traits were determined for a subset of population patches given early dispersal or herbivory. Rhizome samples were randomly hand-excavated from shallow soil. Sample sizes were stratified based on scale of the occupied area of the study patch, with one sample from small patches ($<1.5\text{ m}^2$), two samples from medium plots (1.5 – 4.0 m^2), and three from large plots ($>4.0\text{ m}^2$). Rhizomes were stored in coolers with blue ice and transported to the laboratory. Rhizome samples (2–3 cm diameter \times 5 cm length) were dried, ground to pass through 40-mesh sieve in preparation for analysis of total nonstructural carbohydrate concentrations (TNC). TNC concentration in rhizome samples was analysed with a colorimetric assay of reducing sugars following ethanol extraction (Chow & Landh usser, 2004) and enzymatic digestion of the starch residue (Quentin et al., 2015).

2.2.2 | Environmental variables

In situ environmental conditions including soil physico-chemical characteristics and plant species cover, were sampled and assessed in each study patch of *I. pseudacorus* simultaneous with plant trait measurements. The presence associated plant species within *I. pseudacorus* patches was recorded as previously explained for *I. pseudacorus* using the same transects.

Soil cores (4.5 cm diameter \times 10 cm depth) were collected from each monitoring plot using the same patch size-stratified sampling scheme previously described for rhizome sampling. Cores were placed in coolers with blue ice and transported to the laboratory. Samples were oven-dried at 60°C for 48 h and then ground to pass through a 40-mesh sieve. Soil bulk density (BD) was calculated from soil dry mass and volume of the core. Soil organic matter (OM) content was determined standard loss on ignition (Nelson & Sommers, 1996). Total soil C and N concentrations were measured using the same methodology reported above for leaves. A set of soil cores (4.5 cm diameter \times 5.0 cm depth) were also collected at each plot for determination of soil pH and electrical conductivity (EC) of interstitial soil water. These samples were air-dried, ground, and passed through a 20-mesh sieve. Saturated paste extracts were obtained through vacuum filtration, and the extract was measured for soil pH (introduced range: Accumet AB15 Plus, Thermo Fisher Scientific; native range: Crison pH-meter Basic 20, Crison Instruments) and EC (mS cm^{-1}) (introduced range: Oakton CON2700, Oakton Instruments) fitted with a Accumet AB15 Plus pH probe (Thermo Fisher Scientific; native range: Crison EC-meter Basic 30, Crison Instruments).

At SFE study sites, GPS measurements of geographical coordinates and elevations were acquired at middle within-patch elevations for all iris patches using a Leica GS14 Real-Time Kinematic (RTK) rover ($\pm 1\text{ cm}$ horizontal, $\pm 2\text{ cm}$ vertical accuracy; Leica Geosystems Inc., Norcross Georgia). Geographic coordinates and elevations in the native range were obtained using a GNSS RTK Geomax Zenith

25 Pro ($\pm 1\text{ cm}$ horizontal, $\pm 2\text{ cm}$ vertical accuracy; Conyca-GeoMax; Table S1). Hydrologic distance (HyDx) was recorded as the distance by tidal channels from the mouth of the estuary to each study population. Geographic coordinates and elevation data were used to reference occupied area of the *I. pseudacorus* population patches to model and determine hydrologic parameters in occupied patches relative to local monitoring station data. For the analysis in the SFE, we used sea-level monitoring data (2017–2018) from a long-term NOAA gauge (Port Chicago, station: 9415144) as well as data collected with pressure-transducing dataloggers (Solinst Edge; Ontario, Canada) deployed in marsh channels at Brown's Island, Rush Ranch NERR, and Miners Slough. The logger data were corrected for barometric pressure using data from nearby airports or a separate barometric pressure datalogger; the dataloggers were surveyed with RTK GPS relative to NAVD88. For the analysis in the GRE, we obtained sea level data from UNESCO Intergovernmental Oceanographic Commission for the Bonanza station for 2019–2020 (UNESCO, 2022). To allow for data comparisons between ranges, sea level data were converted to the Instituto Geografico Nacional (IGN) vertical datum by subtracting the published offset of 1.419 m from the Bonanza data. Percent time inundated (IP) for each study patch was determined by summing the water level records that were greater than patch elevation and dividing by the number of water level observations. Additionally, we calculated maximum water inundation depth (MID) for each *I. pseudacorus* study patch by subtracting patch elevation from the maximum water level.

2.3 | Data analyses

Standard error (SE) was calculated for each arithmetic mean. Prior to conducting the analyses, data series were tested for normality with the Shapiro–Wilk test, for homoscedasticity with the Levene's test, and for redundancy with correlation analysis using the software SigmaPlot v. 12 (Systat Software). The variable elevation was transformed using the function $1/x$ and two variables (leaf N and soil organic matter) using the function $\log(x)$ to address the assumptions needed for parametric tests. Multivariate analysis of variance (MANOVA) using the Pillai's Trace test statistic were conducted for plant traits and environmental conditions recorded in the field, separately, using population as grouping factor. The analyses of multivariate variance protect subsequent analyses from type I error (Scheiner, 2001). Once multivariate significance was established, General Linear Models (GLM) with Bonferroni–Dunn's test as post hoc analysis were used to assess the main univariate differences of each variable recorded in the field using range (native or introduced) and population as grouping factors. When homogeneity of variance was not accomplished after data transformation, univariate differences were analysed using the Gamma Generalized Linear Model (GGLM) with Chi-square (χ^2) de Wald (Ng & Cribbie, 2017). In addition, we also used plant traits and environmental conditions as response variables in linear mixed models, using restricted maximum likelihood, to test the effect of range as a fixed effect and population as a random effect. To test specifically whether recorded

environmental factors affected our global estimates of the difference between native and introduced ranges (fixed effect), following Colautti et al., 2009, we ran two linear mixed models, using restricted maximum likelihood: (i) the first model excluding environmental factors and (ii) the second model including environmental factors as covariables and the interactions of geographical range with each environmental factor. Linear correlation (Pearson correlation coefficient, r) and regression analyses were used to characterize the relationships between plant traits and environmental variables. All these analyses were conducted using IBM SPSS V. 20 (IBM Corp).

Principal Components Analysis (PCA) was carried out for plant trait values from both geographic ranges to identify plant traits with the most significant changes within and between the native and introduced ranges. Independent PC factors with eigenvalues >1 were extracted, assessing convergence of the correlation matrix with maximum 25 iterations without rotation. Canonical Correspondence Analyses (CCA) were conducted using a full model to test the significance of the relationship between the environmental variables measured and the plant trait matrix together in both native and introduced ranges. Monte-Carlo permutation tests (999 permutations) were performed for assessing significance of the canonical correlation coefficients using R software (R Core Team, 2022). Number of seeds per capsule and seed mass data were not included in the PCA and CCA because of missing data for several native populations due to herbivory.

3 | RESULTS

3.1 | Plant traits

Iris pseudacorus presented approximately 80% absolute cover in the native and introduced ranges, though lower abundance (60% cover) was recorded in native population A5 (Figure S1). In addition, *I. pseudacorus* had approximately five live leaves per fan that were typically about 100 cm long and had consistent c. 400 mg g⁻¹ carbon concentrations in both geographic ranges. In addition, LER decreased three times seaward and showed no difference between ranges (Figure 2; Tables 1 and S2). Although these few plant traits were comparable in both geographic ranges, overall plant traits of *I. pseudacorus* in populations along estuarine gradients in the native ($n = 38$ plots) and introduced ($n = 39$ plots) ranges were quite different (MANOVA, Pillai's Trace = 4.096; $F_{12,117} = 4.047$; $p < .0001$). Alien *I. pseudacorus* plants had 40% more capsules per stem than native plants, yet native population A2 had seeds with c. 40% greater mass than most alien populations (Figure 2; Tables 1 and S2). Leaf width, the number of senescent leaves per leaf fan, SLA, LWC, leaf N concentration, and the number of capsules per stem showed significant differences between geographical ranges when environmental factors were excluded in the model. However, when the environmental matrix is included, the differences were not significant. In contrast, patch area and the cover of iris only showed significant differences between ranges when environmental factors were included as covariables (Table S3).

Principal Components Analysis grouped plant traits into four factors that together explained 64.3% of the total variance in functional plant trait values that separated relative to intercontinental ranges. The first factor (PC1) explaining 24.7% of the variance was positively related to the number of capsules per stem, LWC and leaf length, and was negatively related to the number of senescent leaves per fan (Table S4). PC1 separated seaward populations of native iris with negative values from upstream native populations and most alien populations that showed positive values (Figure 3). In the native range, the most upstream populations (A1–2) had approximately 60% longer leaves than the most seaward study population (A5). LWC was c. 6% lower in the native than in the introduced range, decreasing seaward at both estuaries (Figure 2; Tables 1 and S2). The populations from the native range had increased numbers of senescent leaves per leaf fan seaward, with double the values of senescent leaves recorded in the introduced range.

PC2 explaining 15.5% of the variance was negatively related to leaf N concentration and SLA (Table S4), separating the native populations along the estuarine gradient more than alien populations (Figure 3). Live leaves in the native range presented c. 20% higher leaf N concentration than in the introduced range (Tables 1 and S2). Leaf N concentration was the highest for the most inland population in the native range (A1). Mean SLA was consistent among populations in the introduced range and 50% higher than SLA in the native range where SLA decreased by five times moving downstream in the estuarine gradient. PC3 and PC4 explained 14.0% and 10.0%, respectively (Table S4). PC3 was positively correlated with the cover of iris and negatively correlated with rhizome TNC concentration which was c. 50% higher in introduced compared to native populations (Tables 1 and S2). Finally, PC4 was positively correlated with the number of live leaves per fan, which doubled upstream in the introduced range and, on the contrary, increased seaward in populations in the native range (Figure 2).

3.2 | Environmental conditions

Environmental conditions varied between *I. pseudacorus*-occupied plots in the native and introduced ranges (MANOVA, Pillai's Trace = 4.635; $F_{8,99} = 6.275$; $p < .0001$). The cover of plant species co-occurring in the vegetation with *I. pseudacorus* was approximately 50% higher in native populations than in the invaded plant communities (Figure 2; Tables 1 and S2).

Soil EC decreased upstream in both the native (from 3.77 ± 0.13 to 1.13 ± 0.10 mS cm⁻¹) and the introduced (from 5.47 ± 1.26 to 1.22 ± 0.35 mS cm⁻¹) range (Figure 2; Tables 1 and S2). The amount of soil OM and total N in the soil was higher in the introduced range (OM: $15 \pm 2\%$, N: 3.36 ± 0.35 mg g⁻¹) than in the native range (OM: $6 \pm 0\%$, N: 1.60 ± 0.11 mg g⁻¹) (Figure 2; Tables 1 and S2). BD of soil was higher in the native (1.01 ± 0.02 g cm⁻³) than in the introduced range (0.74 ± 0.05 g cm⁻³). Soil pH was similar between ranges (native, 7.6 ± 0.0 ; introduced, 6.7 ± 0.2), but more variable in the introduced range where it increased seaward along the estuarine gradient (Figure S2; Tables 1 and S2).

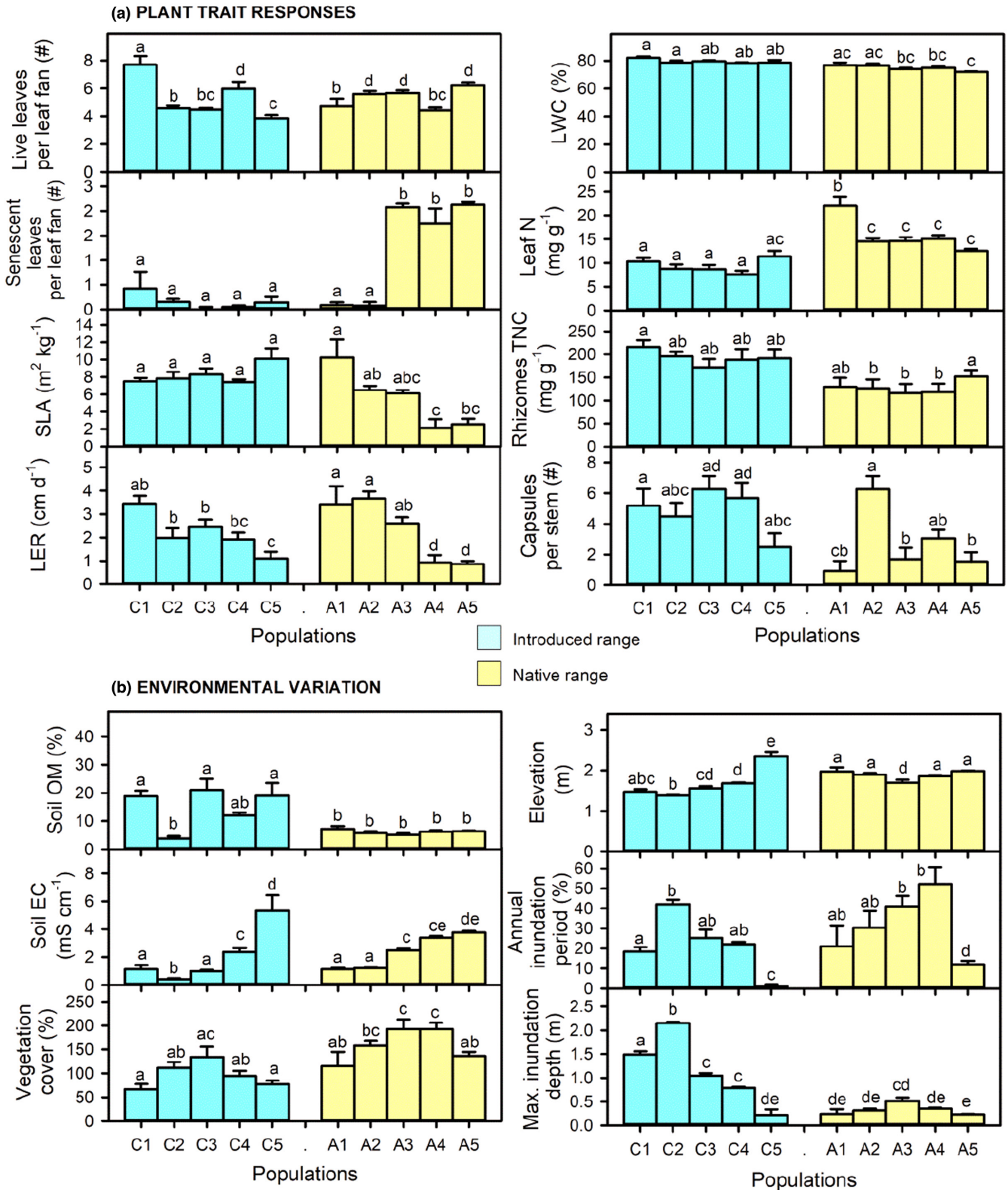


FIGURE 2 (a) Plant trait responses and (b) environmental variation in *Iris pseudacorus* populations in the introduced (California, C; cyan bars) and native (Andalusia, A; yellow bars) ranges along estuarine gradients (1, upstream; 5, seaward). Data are mean \pm SE ($n = 7-8$). Different letters indicate significant differences between populations (GLM or GGLM, $p < .05$). Abbreviations: EC, soil electrical conductivity; LER, leaf expansion rate; LWC, leaf water content; OM, soil organic matter content; SLA, specific leaf area; TNC, total non-structural carbohydrates.

In the introduced range, mean elevation was 1.67 ± 0.06 m, increasing to a maximum of 2.65 m seawards. Mean elevation in the native range was 1.88 ± 0.03 m, with a range of 0.62 m between the highest and the lowest values. Maximum HyDx was 141 km in the introduced range and 95 km in the native range. Maximum inundation depth was 75% greater in the introduced range than in the native range (Figure 2; Tables 1 and S2).

3.3 | Relationships between plant traits and environmental conditions

Plant traits and associated environmental conditions clearly distinguished *I. pseudacorus* populations in the introduced range from those in the native range (CCA ordination, Figure 4). The first two

axes of the CCA explained 82.5% of the total variance in the relationships between recorded iris plant traits and the range of environmental variables associated with the monitoring plots. Axis 1 explained 60.3% of the variance and was negatively correlated with MID, soil OM, the number of capsules per stem and rhizome TNC, and positively with soil pH, BD, and leaf N concentration. Almost all the monitoring plots in the introduced range were negatively related and most plots in the native range were positively related to Axis 1 (Figure 4; Table S5). Axis 2 explained 22.2% of the variance and was negatively correlated with HyDx and LER and positively with soil EC. More upstream monitoring plots tended to show more negative values along Axis 2 than those plots located closer to the sea. Axes 3, 4, 5, and 6 represented just 16.4% of total variance (Figure 4; Table S5).

Simple regression analyses illustrate the relationships between soil EC and plant traits, highlighting marked differences between

TABLE 1 Mean and standard error, *F*-statistic and *p*-values of GLMs and GGLMS for plant traits and environmental conditions recorded in the field comparing between geographic ranges (introduced range, California, USA; native range, Andalusia, Spain) and between populations in both geographic ranges (*N* = 77) as fixed factors.

Variables	Introduced range	Native range	Geographic range	Population
Plant traits				
Patch area (m ²)	4.1 ± 0.8	4.2 ± 0.1	$\chi^2 = 0.018, p = .893$	$\chi^2 = 28.597, p = .001$
Iris cover (%)	74.4 ± 2.0	78.5 ± 3.1	$F_{1,75} = 1.225, p = .272$	$F_{9,67} = 2.425, p = .019$
Leaf length (cm)	114.7 ± 5.0	116.5 ± 6.5	$F_{1,75} = 0.052, p = .819$	$F_{9,67} = 7.320, p < .0001$
Leaf width (cm)	2.9 ± 0.1	2.5 ± 0.1	$F_{1,75} = 10.428, p < .005$	$F_{9,67} = 3.137, p = .003$
Live leaves per fan (#)	5.4 ± 0.3	5.4 ± 0.2	$\chi^2 = 0.001, p = .976$	$\chi^2 = 109.429, p < .0001$
Senescent leaves per fan (#)	0.2 ± 0.1	1.2 ± 0.2	$F_{1,75} = 35.771, p < .001$	$F_{9,67} = 34.540, p < .0001$
SLA (m ² kg ⁻¹)	8.2 ± 0.3	5.5 ± 0.6	$F_{1,75} = 13.983, p < .0001$	$F_{9,67} = 9.135, p < .0001$
Leaf elongation rate (cm d ⁻¹)	2.3 ± 0.2	2.3 ± 0.3	$\chi^2 = 0.014, p = .906$	$\chi^2 = 78.203, p < .0001$
Leaf water content (%)	79.5 ± 0.6	74.8 ± 0.6	$F_{1,75} = 33.205, p < .0001$	$F_{9,67} = 6.000, p < .0001$
Leaf C concentration (mg g ⁻¹)	408 ± 1	412 ± 2	$F_{1,75} = 2.561, p = .114$	$F_{9,66} = 1.443, p = .188$
Leaf N concentration (mg g ⁻¹)	9 ± 0	16 ± 1	$F_{1,75} = 62.473, p < .0001$	$F_{9,67} = 19.089, p < .0001$
Rhizome TNC (mg g ⁻¹)	193 ± 8	129 ± 8	$F_{1,75} = 32.587, p < .0001$	$F_{9,67} = 4.166, p < .0001$
Capsules per stem (#)	4.9 ± 0.5	2.7 ± 0.4	$F_{1,75} = 17.866, p < .0001$	$F_{9,67} = 7.064, p < .0001$
Seeds per capsule (#)	58.0 ± 2.9	57.9 ± 4.3	$F_{1,41} = 0.001, p < .978$	$F_{8,34} = 0.680, p < .706$
Seed mass (mg)	61.1 ± 2.1	74.3 ± 6.3	$F_{1,36} = 5.612, p < .023$	$F_{8,29} = 7.494, p < .0001$
Environmental variables				
Soil bulk density (g cm ⁻³)	0.7 ± 0.1	1.0 ± 0.0	$F_{1,75} = 21.201, p < .0001$	$F_{9,67} = 5.935, p < .0001$
Soil organic matter (%)	14.8 ± 1.6	6.1 ± 0.3	$F_{1,75} = 29.110, p < .0001$	$F_{9,67} = 10.512, p < .0001$
Total soil C concentration (mg g ⁻¹)	47.2 ± 6.4	56.5 ± 1.0	$\chi^2 = 1.618, p = .203$	$\chi^2 = 161.893, p < .001$
Total soil N concentration (mg g ⁻¹)	3.4 ± 0.4	1.6 ± 0.1	$F_{1,75} = 22.297, p < .0001$	$F_{9,67} = 8.384, p < .0001$
Soil pH	6.7 ± 0.2	7.6 ± 0.0	$\chi^2 = 26.621, p < .0001$	$\chi^2 = 87.649, p < .0001$
Soil electrical conductivity (mS cm ⁻¹)	2.0 ± 0.3	2.4 ± 0.2	$\chi^2 = 1.341, p = .247$	$\chi^2 = 205.225, p < .0001$
Cover of plant species associates	97.3 ± 7.0	161.5 ± 9.2	$\chi^2 = 29.606, p < .0001$	$F_{9,67} = 7.569, p < .0001$
Intertidal elevation (m)	1.7 ± 0.1	1.9 ± 0.0	$\chi^2 = 10.030, p < .005$	$\chi^2 = 220.607, p < .0001$
Hydrologic distance (km)	96.9 ± 4.4	63.4 ± 3.8	$F_{1,75} = 32.969, p < .0001$	$F_{9,67} = 369749.838, p < .0001$
Inundation period (%)	22 ± 2	31 ± 4	$\chi^2 = 14.809, p < .0001$	$\chi^2 = 79.393, p < .0001$
Maximum inundation depth (m)	1.16 ± 0.11	0.33 ± 0.03	$\chi^2 = 57.485, p < .0001$	$\chi^2 = 113.989, p < .0001$

Note: Significant differences are marked in bold.

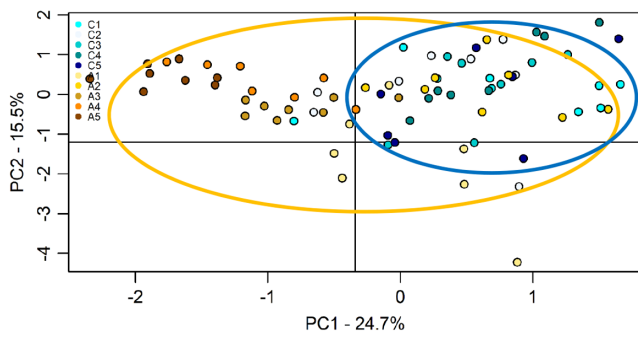


FIGURE 3 Principal Components Analysis (PCA) plot for *Iris pseudacorus* plant traits recorded in the field in the alien populations (C1–C6, California, USA) and native populations (A1–A5, Andalusia, Spain). The yellow ellipse groups most of the native plants from those with high number of senescent leaves (negative values) to those with high leaf water content (positive values) along PC2, and the blue ellipse groups most of the alien plants.

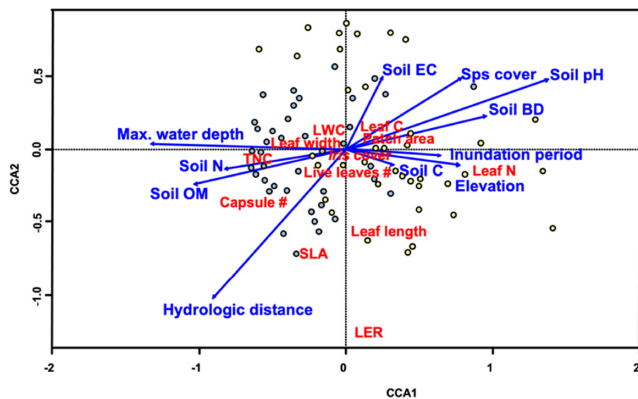


FIGURE 4 Ordination diagram of a Canonical Correspondence Analysis (CCA) with plant traits (red circles), monitoring plots in the invaded range (purple circles) and native range (green circles), and environmental variables (blue arrows). Plant traits: C, carbon concentration; LER, leaf elongation rate; LWC, leaf water content; N, nitrogen concentration; SLA, specific leaf area; TNC, rhizome total non-structural carbohydrates. Environmental variables: BD, bulk density; C, carbon content; EC, electrical conductivity; N, nitrogen content; OM, organic matter.

geographic ranges (Figure 5). In the native range, *I. pseudacorus* was more sensitive to increasing interstitial soil EC than plants in the introduced range as expressed by several key traits. Soil EC was negatively related to LWC and LER for both alien and native plants; however, the decreases at higher salinities were doubled for native than alien plants. In contrast, soil EC was positively related with senescent leaf number per fan and negatively with leaf length and width, leaf N concentration, and SLA only for native plants (Figure 5). The number of live leaves per fan increased with increasing IP and MID in the introduced range but not in the native range (Figure 5). In fact, all plant traits recorded in the native range were independent of IP and MID (Pearson correlation, $p > .05$), except the number of senescent leaves per fan that increased together with MID ($r = .344$, $p = .034$, $n = 38$).

4 | DISCUSSION

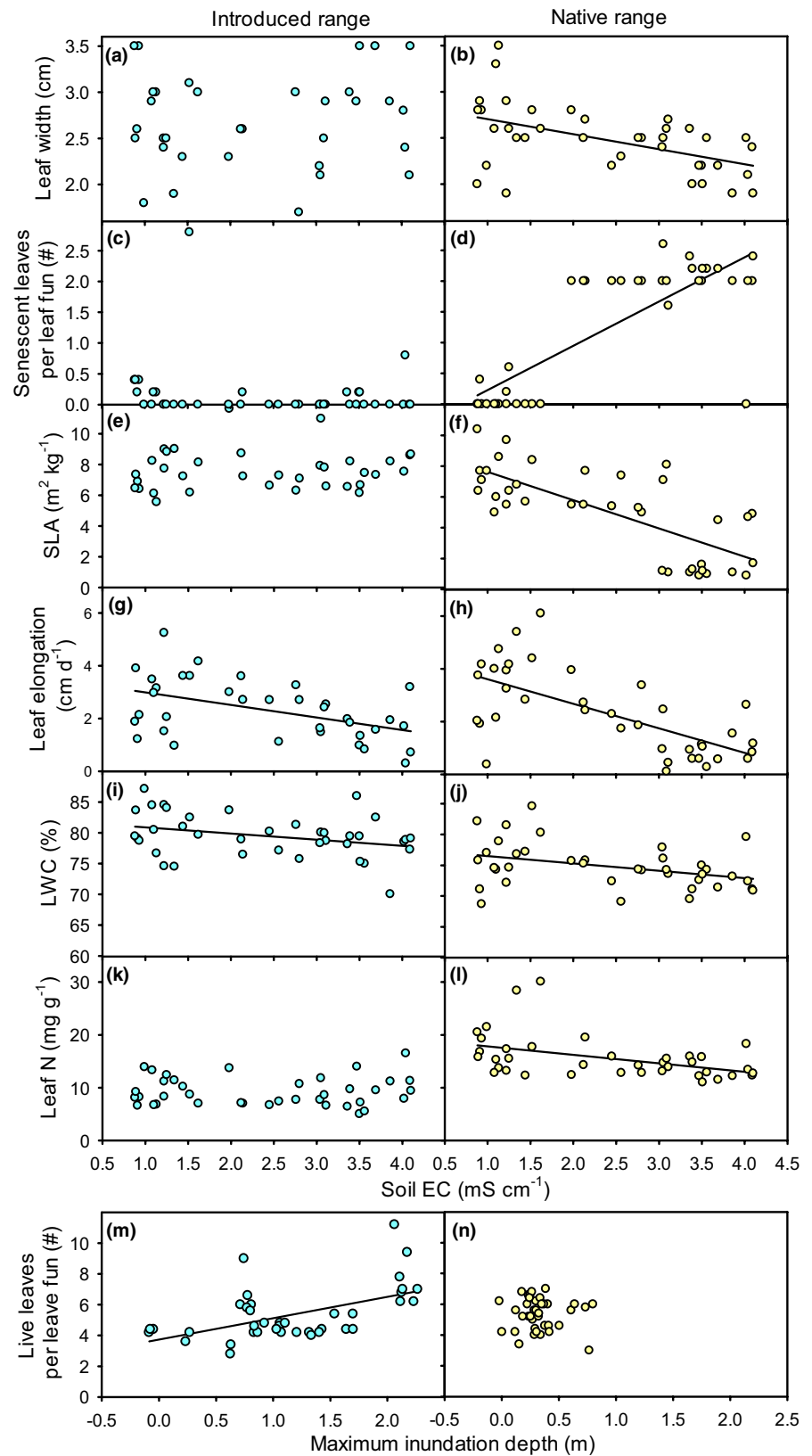
We measured and compared expressed functional traits of *I. pseudacorus* that are key to the relationship with environmental variation between the native and introduced ranges. In accordance with our hypotheses, *I. pseudacorus* plants invading the SFE had greater functional trait support to counter environmental stress and maintain fitness than those native plants in the GRE. The intercontinental differences in performance-related plant trait responses illustrate the capacity of *I. pseudacorus* to counter changing environmental conditions such as SLR. *Iris pseudacorus* plants in the introduced range were less affected by increasing salinity and maintained growth and fitness in deeper water along the estuarine gradient than those in the native range.

Iris pseudacorus has been described as a salt-sensitive species in a greenhouse study (Grewell et al., 2021), coinciding with its LWC and LER decreasing seaward where soils were more saline (higher EC) in both intercontinental ranges. In fact, most of plant trait values sampled at soil salinities c. 2 ppt in the field were in the range of those recorded at salinity as high as 15 ppt in a greenhouse experiment (Grewell et al., 2021). This result suggests *I. pseudacorus* plants were growing in suboptimal conditions with elevated soil salinity at both study locations. In this context, native plants were more sensitive to increasing salinity along the estuarine gradient than alien plants. This result is informative regarding the response of *I. pseudacorus* to global warming and SLR in Mediterranean climate zones where soil salinity in tidal marshes is increasing (Vicente & Boscaiu, 2020).

Physiological traits that underlie water loss and carbon uptake and allocation by plants are highly plastic in response to environmental heterogeneity and are key determinants of growth and fitness (Ackerly et al., 2000; Sage, 1994). Thus, native *I. pseudacorus* plants tended to show lower SLA, but higher leaf N concentrations than alien plants in the introduced range, and higher numbers of senescent leaves per sprout with increasing salinity. Previous studies have recorded an increase in salt tolerance related to ion accumulation in senescent leaf tissue (Reddy et al., 2017) and increased SLA (Grewell et al., 2021; Zong et al., 2021). In contrast, alien plants, exposed to similar soil salinities as the native plants, also had decreased LWC and LER with increasing salinity gradient, but responded with about half the decrease in these leaf traits than observed for native plants.

Plant traits considered to represent variation in life history relevant to predicting invasiveness include high SLA (Hamilton et al., 2005). In this regard, the greater performance of alien *I. pseudacorus* plants exposed to increasing salinity was supported by leaves with 50% higher SLA and greater hydration (LWC) and growth (LER) than those in the native range. Greater SLA has been associated with higher relative growth rates and greater competitive ability in productive environments, while a lower SLA indicative of a lower relative growth rate, can provide a selective advantage in unfavourable habitats (Lambers & Poorter, 2004). It is interesting to note that alien plants maintained very similar SLA along the estuarine gradient, while SLA in native populations decreased 5-fold, corresponding to a seaward increase in interstitial soil salinity. In contrast, alien *I.*

FIGURE 5 Relationships between soil electrical conductivity (EC) and plant traits in the introduced range (a, c, e, g, i, k) and native range (b, d, f, h, j, l). Relationships between maximum inundation depth and the number of live leaves per leaf fan for *Iris pseudacorus* in (m) the introduced range, and (n) the native range. Abbreviations of plant traits include specific leaf area (SLA) and leaf water content (LWC). Regression equations for significant relationships: (b) $y = 2.867 - 0.163x$ ($r = -.506$, $p = .001$, $n = 38$); (d), $y = -0.489 + 0.719x$ ($r = .799$, $p < .0001$, $n = 38$); (f) $y = 9.458 - 1.834x$ ($r = -.599$, $p < .0001$, $n = 38$); (g) $y = 3.466 - 0.476x$ ($r = -.396$, $p = .015$, $n = 37$); (h) $y = 4.533 - 0.929x$ ($r = -.663$, $p < .0001$, $n = 38$); (i) $y = 81.891 - 1.001x$ ($r = -.370$, $p = .021$, $n = 39$); (j) $y = 77.680 - 1.193x$ ($r = -.373$, $p = .021$, $n = 38$); (l) $y = 19.432 - 1.602x$ ($r = -.438$, $p = .006$, $n = 38$); (m) $y = 3.733x + 1.391$, $R^2 = 0.289$, $p < .0001$, $n = 39$.



pseudacorus acquired sufficient resources to support robust growth while also allocating 50% more carbon storage reserves in rhizomes than native plants. In this context, the relatively low leaf N concentrations recorded for invading plants could indicate re-translocation of N from leaves to sexual reproduction and subterranean storage

(Sinkkonen, 2006; Wright & Dorken, 2014). Thus, the significantly higher soil N availability observed in the introduced range may likely affect the vigour and reproductive output in alien plants (Pearson et al., 2022). Evolution of traits related to resource uptake can be relevant for alien populations (Burns et al., 2013). SFE has higher

anthropogenic loadings of both N and P concentrations than those in most other global estuaries impaired by nutrient pollution (Cloern et al., 2020). In addition, climate change is also increasing atmospheric nitrogen deposition, enhancing the growth of fast-growing alien plant species (Suddick et al., 2013).

Extreme meteorological events, such as torrential rains, droughts and heat waves, are more frequent now in the actual scenario of climate change (Payne et al., 2020). The water depths we recorded in the introduced range reflected the atmospheric river storm flooding that occurred in SFE in 2017 (Thorne et al., 2022). Even though the year was atypical, if we exclude analysis of the above average data from 2017, maximum inundation depth was still considerably higher in the introduced range when compared to the native range. Even under the extreme conditions which are recurring more frequently, *I. pseudacorus* in the invasive range had greater functional trait capacity to counter environmental stress.

Iris pseudacorus has been experimentally shown to be highly tolerant of inundation (Grewell et al., 2021). In this sense, most expressed functional traits by native plants were independent of inundation period and depth, except the number of dead leaves per leaf fan that increased with increasing inundation. In the introduced range, alien *I. pseudacorus* plants were exposed to deeper inundation than native plants, which illustrated a niche shift between the study areas in the native and introduced ranges. Yuan et al. (2021) also recorded niche shift between intercontinental introduced and native ranges for *Spartina alterniflora* Loisel., also a tidal marsh invader. In this context, alien *I. pseudacorus* plants increased the number of live leaves when exposed to deeper inundation. This response seems to reflect the capacity of *I. pseudacorus* to respond to rising inundation levels since increasing resource allocation to greater leaf biomass production can facilitate carbon acquisition by increasing photosynthetic area (Zhao et al., 2015). In this sense, Grewell et al. (2021) recorded an increase in leaf mass ratio under deeper inundation in a greenhouse experiment. Therefore, *I. pseudacorus*, especially alien plants, would be able to effectively face higher inundation levels derived from SLR. Even so, increasing estuarine salinity derived from climate change and SLR may limit the capacity of *I. pseudacorus* to acclimate to greater inundation (Grewell et al., 2021).

Successful invaders of introduced ranges are thought to “escape” population pressures posed by natural enemies such as herbivores, thereby conserving resources that would otherwise be allocated to defence at a cost to fitness and competitive ability (Enemy Release Hypothesis, Keane & Crawley, 2002). All parts of *Iris pseudacorus* plants have been considered poisonous to livestock due to glycoside concentrations in tissues (Forsyth, 1976), and grazing was considered negligible in British Isle populations (Sutherland & Walton, 1990). Weed profiles and risk assessments have long echoed Sutherland and Walton (1990) (e.g. Tu, 2004; US Fish & Wildlife Service, 2019), which has led to dismissal of grazing as a potential control measure for *I. pseudacorus*. Within and beyond our native study sites in GRE, we observed grazing impacts to *I. pseudacorus* by wild horses, sheep, goats, and cattle. Intense cattle grazing impacts were also observed

on *I. pseudacorus* at Brière wetlands in northwestern France (Authors, pers. obs.). The recorded low values in leaf dimensions at population A5 compared to the more upstream populations (c. -30% leaf width and -60% leaf length), and the lower cover of *I. pseudacorus* (c. -70%) reflected the intense grazing pressure by cattle we observed at this location. In view of these results, herbivory by livestock could be evaluated as a component of integrated management for control of *I. pseudacorus*.

High levels of gene flow and genetic diversity within and among populations of *I. pseudacorus* in the introduced range (Gaskin et al., 2016) are evidence of the importance of sexual reproduction as the primary reproductive mode for this species. Robust reproductive traits such as high seed production which we found for alien *I. pseudacorus* plants may counteract the detrimental effects of genetic bottlenecks often associated with species introductions. Capsule and seed traits such as high seed output and germination rates can be critical for dispersal and establishment success of alien plants (Rejmánek & Richardson, 1996; Pyšek, 1998). In the introduced range, *I. pseudacorus* had 40% more capsules per stem than the native counterparts, suggesting greater propagule pressure. Furthermore, seed viability and seed germination rates were found to exceed 95% for *I. pseudacorus* in our SFE study populations (Gillard et al., 2021, 2022), which should lead to more invasive colonization according to the hypothesis of propagule pressure (Carr et al., 2019).

Some plant traits showing significant differences between geographic ranges were markedly related to variation in environmental conditions and, in contrast, other plant traits were independent of every recorded environmental factor. Ecologically important functional traits of some alien plant species have undergone rapid evolution as they naturalize during range expansion, increasing genetic variation of traits along environmental gradients that may support broadened niche shifts beyond those of founder populations (Colautti et al., 2017). Growing empirical evidence indicates adaptive traits have evolved in introduced plant populations that have become invasive (e.g. Dlugosch & Parker, 2008; Lavergne et al., 2010; Molina-Montenegro et al., 2011, 2013), and some of these evolutionary adaptations have been quite rapid (Colautti & Barrett, 2013; Colautti et al., 2017; Leger & Rice, 2007; Molina-Montenegro et al., 2018). In this sense, our results suggest there are genetic differences in iris populations between the studied biogeographical ranges since six plant traits showed significant differences between ranges only when environmental variables were excluded as covariates. Also, only two plant traits differed between ranges only when the environmental matrix was included in the analysis, which pointed to limited environmental influence on plant trait differences between geographical ranges. Explanatory mechanisms for the differences we documented between ranges of *I. pseudacorus* cannot be fully interpreted without support of common garden experiments and molecular evaluations (Bufford & Hulme, 2021; Colautti & Lau, 2015) to elucidate the potential genetic and environmental contributions to the variation we observed, but our results provide an important foundation for future studies.

5 | CONCLUSIONS

Study of *Iris pseudacorus* through a biogeographic framework in both native and introduced population field sites has provided insights on variation in environmental conditions and functional plant trait responses that support the fitness and spread of invasions in tidal wetlands facing SLR. Our results show that alien *I. pseudacorus* plants in the introduced range were more robust than plants in the native range. Alien *I. pseudacorus* plants were less sensitive to increasing salinity than native plants and were positively affected by higher inundation levels, reflecting a niche shift compared to our study sites in the native range. In summary, our comparative results suggest alien populations in SFE are currently better able to adjust to increasing salinity and inundation with SLR than native populations in GRE. Biogeographic knowledge of these functional trait responses can support improved risk assessments addressing both management of invasive species and conservation of native species in tidal wetland ecosystems vulnerable to impacts of climate change.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be openly available in DRYAD.

“Data: Phenotypic trait differences between *Iris pseudacorus* in native and introduced ranges support greater capacity of invasive populations to withstand sea level rise” (doi:10.25338/B8FP72).

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REFERENCES

- Ackerly, D. D., Dudley, S. A., Sultan, S. E., Schmitt, J., Coleman, J. S., Linder, C. R., Sandquist, D. R., Geber, M. A., Evans, A. S., Dawson, T. E., & Lechowicz, M. J. (2000). The evolution of plant ecophysiological traits: Recent advances and future directions. *Bioscience*, 50, 979–995.
- Adam, P. (2002). Saltmarshes in a time of change. *Environmental Conservation*, 29(1), 39–61. <https://doi.org/10.1017/S0376892902000048>
- AEMET. (2020). AEMET OpenData. <https://opendata.aemet.es/centrodedescargas/inicio>
- Atwater, B. F. (1979). Ancient processes at the site of southern San Francisco Bay: movement of the crust and changes in sea level. In T. J. Conomos (Ed.), *San Francisco Bay: the urbanized estuary* (pp. 31–45). Pacific Division, American Association for the Advancement of Science.
- Bajwa, A. A., Chauhan, B. S., Farooq, M., Shabbir, A., & Adkins, S. W. (2016). What do we really know about alien plant invasion? A review of the invasion mechanism of one of the world's worst weeds. *Planta*, 244(1), 39–57. <https://doi.org/10.1007/s00425-016-2510-x>
- Baldwin, A. H., & Mendelsohn, I. A. (1998). Effects of salinity and water level on coastal marshes: An experimental test of disturbance as a catalyst for vegetation change. *Aquatic Botany*, 61(4), 255–268. [https://doi.org/10.1016/S0304-3770\(98\)00073-4](https://doi.org/10.1016/S0304-3770(98)00073-4)
- Barrett, S. C. (2000). Microevolutionary influences of global changes on plant invasions. In *Invasive species in a changing world* (pp. 115–139). Island Press.
- Beaury, E. M., Patrick, M., & Bradley, B. A. (2021). Invaders for sale: The ongoing spread of invasive species by the plant trade industry. *Frontiers in Ecology and the Environment*, 19(10), 550–556. <https://doi.org/10.1002/fee.2392>
- Bradley, B. A., Blumenthal, D. M., Wilcove, D. S., & Ziska, L. H. (2010). Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, 25(5), 310–318. <https://doi.org/10.1016/j.tree.2009.12.003>
- Bufford, J. L., & Hulme, P. E. (2021). Seed size–number trade-offs are absent in the introduced range for three congeneric plant invaders. *Journal of Ecology*, 109(11), 3849–3860. <https://doi.org/10.1111/1365-2745.13761>
- Burns, J. H., Pardini, E. A., Schutzenhofer, M. R., Chung, Y. A., Seidler, K. J., & Knight, T. M. (2013). Greater sexual reproduction contributes to differences in demography of invasive plants and their noninvasive relatives. *Ecology*, 94(5), 995–1004. <https://doi.org/10.1890/12-1310.1>
- Carr, A. N., Hooper, D. U., & Dukes, J. S. (2019). Long-term propagule pressure overwhelms initial community determination of invader success. *Ecosphere*, 10(8), e02826. <https://doi.org/10.1002/ecs2.2826>
- Castillo, J. M., Grewell, B. J., Pickart, A., Bortolus, A., Peña, C., Figueroa, E., & Sytsma, M. (2014). Phenotypic plasticity of invasive *Spartina densiflora* (Poaceae) along a broad latitudinal gradient on the pacific coast of North America. *American Journal of Botany*, 101(3), 448–458. <https://doi.org/10.3732/ajb.1400014>
- CCH1 Portal. (2023). Biodiversity data provided by the participants of the Consortium of California Herbaria. <https://ucjeps.berkeley.edu/consortium/>
- Chow, P. S., & Landhäusser, S. M. (2004). A method for routine measurements of total sugar and starch content in woody plant tissues. *Tree Physiology*, 24(10), 1129–1136. <https://doi.org/10.1093/treephys/24.10.1129>

- Cloern, J. E., Knowles, N., Brown, L. R., Cayan, D., Dettinger, M. D., Morgan, T. L., Schoellhamer, D. H., Stacey, M. T., van der Wegen, M., Wagner, R. W., & Jassby, A. D. (2011). Projected evolution of California's San Francisco Bay-Delta River system in a century of climate change. *PLoS One*, 6(9), e24465.
- Cloern, J. E., Schraga, T. S., Nejad, E., & Martin, C. (2020). Nutrient status of San Francisco Bay and its management implications. *Estuaries and Coasts*, 43(6), 1299–1317. <https://doi.org/10.1007/s12237-020-00737-w>
- Colautti, R. I., Alexander, J. M., Dlugosch, K. M., Keller, S. R., & Sultan, S. E. (2017). Invasions and extinctions through the looking glass of evolutionary ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1712), 20160031. <https://doi.org/10.1098/rstb.2016.0031>
- Colautti, R. I., & Barrett, S. C. H. (2013). Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science*, 342(6156), 364–366. <https://doi.org/10.1126/science.1242121>
- Colautti, R. I., & Lau, J. A. (2015). Contemporary evolution during invasion: Evidence for differentiation, natural selection, and local adaptation. *Molecular Ecology*, 24(9), 1999–2017. <https://doi.org/10.1111/mec.13162>
- Colautti, R. I., Maron, J. L., & Barrett, S. C. H. (2009). Common garden comparisons of native and introduced plant populations: Latitudinal clines can obscure evolutionary inferences. *Evolutionary Applications*, 2(2), 187–199. <https://doi.org/10.1111/j.1752-4571.2008.00053.x>
- CSIC-Real Jardín Botánico, Castilla F. (2022). CSIC-Real Jardín Botánico-Colección de Plantas Vasculares (MA). Real Jardín Botánico (CSIC). Occurrence Dataset <https://doi.org/10.15468/mug7kr> accessed via GBIF.org on 2023-01-04
- Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, 14(4), 419–431. <https://doi.org/10.1111/j.1461-0248.2011.01596.x>
- Dlugosch, K. M., & Parker, I. M. (2008). Founding events in species invasions: Genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, 17(1), 431–449. <https://doi.org/10.1111/J.1365-294X.2007.03538.X>
- Dong, Y., García Molinos, J., Larson, E. R., Lin, Q., Liu, X., Sarà, G., Cai, Q., Zhang, Z., Helmuth, B., & Bates, A. (2022). Biological traits, geographic distributions, and species conservation in aquatic ecosystems. *Diversity and Distributions*, 28(8), 1516–1523. <https://doi.org/10.1111/ddi.13600>
- Drenovsky, R. E., Grewell, B. J., Dantonio, C. M., Funk, J. L., James, J. J., Molinari, N., Parker, I. M., & Richards, C. L. (2012). A functional trait perspective on plant invasion. *Annals of Botany*, 110(1), 141–153. <https://doi.org/10.1093/aob/mcs100>
- Encyclopedia of Life. (2022). Yellow flag, *Iris pseudacorus* L. Hosted by Smithsonian National Museum of Natural History. <http://eol.org>
- Forsyth, A. A. (1976). *British poisonous plants*. H.M.S.O.
- Gallego-Tévar, B., Grewell, B. J., Whitcraft, C. R., Futrell, J. C., Bárcenas-Moreno, G., & Castillo, J. M. (2022). Contrasted impacts of yellow flag iris (*Iris pseudacorus*) on plant diversity in tidal wetlands within its native and invaded distribution ranges. *Diversity*, 14(5), 326. <https://doi.org/10.3390/d14050326>
- Garnier, E., Shipley, B., Roumet, C., & Laurent, G. (2001). A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, 15(5), 688–695. <https://doi.org/10.1046/j.0269-8463.2001.00563.x>
- Gaskin, J. F., Pokorny, M. L., & Mangold, J. M. (2016). An unusual case of seed dispersal in an invasive aquatic; yellow flag iris (*Iris pseudacorus*). *Biological Invasions*, 18(7), 2067–2075. <https://doi.org/10.1007/s10530-016-1151-0>
- Gervazoni, P., Sosa, A., Franceschini, C., Coetzee, J., Falthäuser, A., Fuentes-Rodríguez, D., Martínez, A., & Hill, M. (2020). The alien invasive yellow flag (*Iris pseudacorus* L.) in Argentinian wetlands: Assessing geographical distribution through different data sources. *Biological Invasions*, 22(11), 3183–3193. <https://doi.org/10.1007/s10530-020-02331-4>
- Gillard, M. B., Castillo, J. M., Mesgaran, M. B., Futrell, C. J., & Grewell, B. J. (2021). High aqueous salinity does not preclude germination of invasive *Iris pseudacorus* from estuarine populations. *Ecosphere*, 12(5), e03486. <https://doi.org/10.1002/ecs2.3486>
- Gillard, M. B., Castillo, J. M., Mesgaran, M. B., Futrell, C. J., & Grewell, B. J. (2022). Germination niche breadth of invasive *Iris pseudacorus* (L.) suggests continued recruitment from seeds with global warming. *American Journal of Botany*, 109(7), 1108–1119. <https://doi.org/10.1002/ajb2.16026>
- Grewell, B. J., Espeland, E. K., & Fiedler, P. L. (2013). Sea change under climate change: Case studies in rare plant conservation from the dynamic San Francisco estuary. *Botany*, 91(5), 309–318. <https://doi.org/10.1139/cjb-2012-0300>
- Grewell, B. J., Gallego-Tévar, B., Gillard, M. B., Futrell, C. J., Reicholf, R., & Castillo, J. M. (2021). Salinity and inundation effects on *Iris pseudacorus*: Implications for tidal wetland invasion with sea level rise. *Plant and Soil*, 466(1–2), 275–291. <https://doi.org/10.1007/s11104-021-04997-8>
- Guo, Q. (2006). Intercontinental biotic invasions: What can we learn from native populations and habitats? *Biological Invasions*, 8(7), 1451–1459. <https://doi.org/10.1007/s10530-005-5834-1>
- Hamilton, M. A., Murray, B. R., Cadotte, M. W., Hose, G. C., Baker, A. C., Harris, C. J., & Licari, D. (2005). Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters*, 8(10), 1066–1074. <https://doi.org/10.1111/j.1461-0248.2005.00809.x>
- Hayasaka, D., Fujiwara, S., & Uchida, T. (2018). Impacts of invasive *Iris pseudacorus* L. (yellow flag) establishing in an abandoned urban pond on native semi-wetland vegetation. *Journal of Integrative Agriculture*, 17(8), 1881–1887. [https://doi.org/10.1016/S2095-3119\(17\)61831-8](https://doi.org/10.1016/S2095-3119(17)61831-8)
- Hierro, J. L., Maron, J. L., & Callaway, R. M. (2005). A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. *Journal of Ecology*, 93(1), 5–15. <https://doi.org/10.1111/j.0022-0477.2004.00953.x>
- IPCC. (2022). In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegria, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate change 2022: Impacts, adaptation, and vulnerability. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press.
- Jelbert, K., Stott, I., McDonald, R. A., & Hodgson, D. (2015). Invasiveness of plants is predicted by size and fecundity in the native range. *Ecology and Evolution*, 5(10), 1933–1943. <https://doi.org/10.1002/ece3.1432>
- Keane, R., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17(4), 164–170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0)
- Kimmerer, W. J. (2004). Open water processes of the San Francisco estuary: From physical forcing to biological responses. *San Francisco Estuary and Watershed Science*, 2(1), 1. <https://doi.org/10.15447/sfews.2004v2iss1art1>
- Lambers, H., & Poorter, H. (2004). Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. *Advances in Ecological Research*, 34, 283–362. [https://doi.org/10.1016/S0065-2504\(03\)34004-8](https://doi.org/10.1016/S0065-2504(03)34004-8)
- Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, 41(1), 321–350. <https://doi.org/10.1146/annurev-ecolsys-102209-144628>
- Leger, E. A., & Rice, K. J. (2007). Assessing the speed and predictability of local adaptation in invasive California poppies (*Eschscholzia californica*). *Journal of Evolutionary Biology*, 20(3), 1090–1103. <https://doi.org/10.1111/j.1420-9101.2006.01292.x>

- Lehan, N. E., Murphy, J. R., Thorburn, L. P., & Bradley, B. A. (2013). Accidental introductions are an important source of invasive plants in the continental United States. *American Journal of Botany*, 100(7), 1287–1293. <https://doi.org/10.3732/ajb.1300061>
- Light, T., Grosholz, T., & Moyle, P. (2005). *Delta ecological survey (phase I): Nonindigenous aquatic species in the Sacramento-san Joaquin Delta, a literature review*. US Fish and Wildlife Service.
- Marchini, G. L., Sherlock, N. C., Ramakrishnan, A. P., Rosenthal, D. M., & Cruzan, M. B. (2016). Rapid purging of genetic load in a metapopulation and consequences for range expansion in an invasive plant. *Biological Invasions*, 18(1), 183–196. <https://doi.org/10.1007/s10530-015-1001-5>
- Mathiventhan, T., Gorman, D., & Jayasingam, T. (2022). Sea-level rise, coastal salinity and vegetation changes in Sri Lanka. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 380(2221), 20210142. <https://doi.org/10.1098/rsta.2021.0142>
- Miatta, M., Bates, A. E., & Snelgrove, P. V. R. (2021). Incorporating biological traits into conservation strategies. *Annual Review of Marine Science*, 13(1), 421–443. <https://doi.org/10.1146/annurev-marine-032320-094121>
- Minuti, G., Stiers, I., & Coetzee, J. A. (2022). Climatic suitability and compatibility of the invasive *Iris pseudacorus* L. (Iridaceae) in the southern hemisphere: Considerations for biocontrol. *Biological Control*, 169, 104886. <https://doi.org/10.1016/j.biocntrl.2022.104886>
- Molina-Montenegro, M. A., Acuña-Rodríguez, I. S., Flores, T. S. M., Hereme, R., Lafon, A., Atala, C., & Torres-Díaz, C. (2018). Is the success of plant invasions the result of rapid adaptive evolution in seed traits? Evidence from a latitudinal rainfall gradient. *Frontiers in Plant Science*, 9, 1–15. <https://doi.org/10.3389/fpls.2018.00208>
- Molina-Montenegro, M. A., Palma-Rojas, C., Alcayaga-Olivares, Y., Oses, R., Corcuera, L. J., Cavieres, L. A., & Gianoli, E. (2013). Ecophysiological plasticity and local differentiation help explain the invasion success of *Taraxacum officinale* (dandelion) in South America. *Ecography*, 36(6), 718–730. <https://doi.org/10.1111/j.1600-0587.2012.07758.x>
- Molina-Montenegro, M. A., Quiroz, C. L., Torres-Díaz, C., & Atala, C. (2011). Ecophysiological traits suggest local adaptation rather than plasticity in the invasive *Taraxacum officinale* (dandelion) from native and introduced habitat range. *Plant Ecology & Diversity*, 4, 36–42. <https://doi.org/10.1080/17550874.2011.577459>
- Mopper, S., Wiens, K. C., & Goranova, G. A. (2016). Competition, salinity, and clonal growth in native and introduced irises. *American Journal of Botany*, 103(9), 1575–1581. <https://doi.org/10.3732/ajb.1600075>
- Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., & Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea level. *Ecology*, 83(10), 2869–2877. [https://doi.org/10.1890/0012-9658\(2002\)083\[2869:ROCWTR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2869:ROCWTR]2.0.CO;2)
- Nelson, D. W., & Sommers, L. E. (1996). Total carbon, organic carbon, and organic matter. In *Methods of soil analysis, agronomy series* (pp. 961–1010). Soil Science Society of America. <https://doi.org/10.2136/sssabookser5.3.c34>
- Ng, V. K. Y., & Cribbie, R. A. (2017). Using the gamma generalized linear model for modeling continuous, skewed and heteroscedastic outcomes in psychology. *Current Psychology*, 36(2), 225–235. <https://doi.org/10.1007/s12144-015-9404-0>
- Palacio-López, K., & Gianoli, E. (2011). Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: A meta-analysis. *Oikos*, 120(9), 1393–1401. <https://doi.org/10.1111/j.1600-0706.2010.19114.x>
- Payne, A. E., Demory, M.-E., Leung, L. R., Ramos, A. M., Shields, C. A., Rutz, J. J., Siler, N., Villarini, G., Hall, A., & Ralph, F. M. (2020). Responses and impacts of atmospheric rivers to climate change. *Nature Reviews Earth & Environment*, 1, 143–157. <https://doi.org/10.1038/s43017-020-0030-5>
- Pearman, P. B., Guisan, A., Broennimann, O., & Randin, C. F. (2008). Niche dynamics in space and time. *Trends in Ecology & Evolution*, 23(3), 149–158. <https://doi.org/10.1016/j.tree.2007.11.005>
- Pearson, D. E., Eren, Ö., Ortega, Y. K., Hierro, J. L., Karakuş, B., Kala, S., Bullington, L., & Lekberg, Y. (2022). Combining biogeographical approaches to advance invasion ecology and methodology. *Journal of Ecology*, 110(9), 2033–2045. <https://doi.org/10.1111/1365-2745.13945>
- Pyšek, P. (1998). Is there a taxonomic pattern to plant invasions? *Oikos*, 82(2), 282. <https://doi.org/10.2307/3546968>
- Pyšek, P., & Richardson, D. M. (2008). Traits associated with invasiveness in alien plants: Where do we stand? In *Biological Invasions* (pp. 97–125). Springer. https://doi.org/10.1007/978-3-540-36920-2_7
- Quentin, A. G., Pinkard, E. A., Ryan, M. G., Tissue, D. T., Baggett, L. S., Adams, H. D., Maillard, P., Marchand, J., Landhäusser, S. M., Lacoite, A., Gibon, Y., Anderegg, W. R. L., Asao, S., Atkin, O. K., Bonhomme, M., Claye, C., Chow, P. S., Clément-Vidal, A., Davies, N. W., ... Woodruff, D. R. (2015). Non-structural carbohydrates in woody plants compared among laboratories. *Tree Physiology*, 35(11), 1146–1165. <https://doi.org/10.1093/treephys/tpv073>
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Reddy, I. N. B. L., Kim, S. M., Kim, B. K., Yoon, I. S., & Kwon, T. R. (2017). Identification of rice accessions associated with K⁺/Na⁺ ratio and salt tolerance based on physiological and molecular responses. *Rice Science*, 24(6), 360–364. <https://doi.org/10.1016/j.rsci.2017.10.002>
- Reichard, S. H., & White, P. (2001). Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience*, 51(2), 103–113. [https://doi.org/10.1641/0006-3568\(2001\)051\[0103:HAAPO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0103:HAAPO]2.0.CO;2)
- Rejmánek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology*, 77(6), 1655–1661. <https://doi.org/10.2307/2265768>
- Rodríguez-Ramírez, A., Villarías-Robles, J. J. R., Pérez-Asensio, J. N., & Celestino-Pérez, S. (2019). The Guadalquivir estuary: Spits and marshes. In J. A. Morales (Ed.), *The Spanish coastal systems: Dynamic processes, sediments, and management* (pp. 517–541). Springer Nature.
- Sage, R. F. (1994). Acclimation of photosynthesis to increasing atmospheric CO₂: The gas exchange perspective. *Photosynthesis Research*, 39(3), 351–368. <https://doi.org/10.1007/BF00014591>
- Scheiner, S. (2001). Multiple response variables and multi-species interactions. In S. M. Scheiner & J. Gurevitch (Eds.), *Design and analysis of ecological experiments* (2nd ed., pp. 99–115). Oxford University Press. [https://books.google.es/books?hl=es&lr=&id=AgstDAAAQBAJ&oi=fnd&pg=PA99&dq=Scheiner+SM+\(2001\)+MANOVA:+multiple+response+variables+and+multi-species+interactions.+In:+Scheiner+SM,+Gurevitch+J+\(eds\)+Design+and+analysis+of+ecological+experiments,+2nd+edn.+Oxf](https://books.google.es/books?hl=es&lr=&id=AgstDAAAQBAJ&oi=fnd&pg=PA99&dq=Scheiner+SM+(2001)+MANOVA:+multiple+response+variables+and+multi-species+interactions.+In:+Scheiner+SM,+Gurevitch+J+(eds)+Design+and+analysis+of+ecological+experiments,+2nd+edn.+Oxf)
- Schlaepfer, D. R., Glättli, M., Fischer, M., & van Kleunen, M. (2010). A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. *New Phytologist*, 185(4), 1087–1099. <https://doi.org/10.1111/j.1469-8137.2009.03114.x>
- Schrieber, K., & Lachmuth, S. (2017). The genetic paradox of invasions revisited: The potential role of inbreeding × environment interactions in invasion success. *Biological Reviews*, 92(2), 939–952. <https://doi.org/10.1111/brv.12263>
- Sinkkonen, A. (2006). Sexual reproduction advances autumn leaf colours in mountain birch (*Betula pubescens* ssp. *czerepanovii*). *Journal of Evolutionary Biology*, 19(5), 1722–1724. <https://doi.org/10.1111/j.1420-9101.2005.00991.x>
- Suddick, E. C., Whitney, P., Townsend, A. R., & Davidson, E. A. (2013). The role of nitrogen in climate change and the impacts of nitrogen-climate interactions in the United States: Foreword to thematic issue. *Biogeochemistry*, 114(1–3), 1–10. <https://doi.org/10.1007/s10533-012-9795-z>

- Sutherland, W. J., & Walton, D. (1990). The changes in morphology and demography of *Iris pseudacorus* L. at different heights on a saltmarsh. *Functional Ecology*, 4(5), 655. <https://doi.org/10.2307/2389733>
- Thorne, K., Jones, S., Freeman, C., Buffington, K., Janousek, C., & Guntenspergen, G. (2022). Atmospheric river storm flooding influences tidal marsh elevation building processes. *Journal of Geophysical Research: Biogeosciences*, 127, e2021JG006592. <https://doi.org/10.1029/2021JG006592>
- Thorne, K., MacDonald, G., Guntenspergen, G., Ambrose, R., Buffington, K., Dugger, B., Freeman, C., Janousek, C., Brown, L., Rosencranz, J., Holmquist, J., Smol, J., Hargan, K., & Takekawa, J. (2018). U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. *Science Advances*, 4(2), 3270. <https://doi.org/10.1126/sciadv.aao3270>
- Thuiller, W., Lavorel, S., & Araujo, M. B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, 14(4), 347–357. <https://doi.org/10.1111/j.1466-822X.2005.00162.x>
- Torrey Botanical Club. (1888). Preliminary catalog of Anthophyta and Pteridophyta, reported as growing spontaneously within one hundred miles of new York City, New York, USA.
- Tu, M. (2004). *Iris pseudacorus* L.-yellow flag iris, water iris. Element stewardship abstract, Global Invasive Species Team Management library: control methods-plants. Wildland Invasive Species Team, The Nature Conservancy, Arlington, Virginia, U.S.A. <https://www.invasive.org/gist/esadocs/documnts/irisipse.pdf>
- UNESCO (2022). <http://www.ioc-sealevelmonitoring.org/station.php?code=bon2>; <http://www.ioc-sealevelmonitoring.org/station.php?code=sev2>
- US Fish & Wildlife Service. (2019). *Yellow flag iris* (*Iris pseudacorus*). Ecological Risk Screening Summary. <https://www.fws.gov/sites/default/files/documents/Ecological-Risk-Screening-Summary-Yellow-Flag-Iris.pdf>
- van Kleunen, M., Schlaepfer, D. R., Glaetli, M., & Fischer, M. (2011). Preadapted for invasiveness: Do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range? *Journal of Biogeography*, 38(7), 1294–1304. <https://doi.org/10.1111/j.1365-2699.2011.02495.x>
- van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13(2), 235–245. <https://doi.org/10.1111/j.1461-0248.2009.01418.x>
- Vicente, O., & Boscaiu, M. (2020). Will halophytes in Mediterranean salt marshes be able to adapt to climate change? *Agrolife Scientific Journal*, 9, 369–376.
- Vitousek, P. M., D'Antonio, C. M., Loope, L., Rejaneck, M., & Westbrooks, R. (1997). Introduced species; a significant component of human-caused global change. *New Zealand Journal of Ecology*, 21, 1–16. <https://doi.org/10.2307/24054520>
- Wells, E. F., & Brown, R. L. (2000). An annotated checklist of the vascular plants in the forest at historic Mount Vernon, Virginia: A legacy from the past. *Castanea*, 65(4), 242–257.
- Wright, V. L., & Dorken, M. E. (2014). Sexual dimorphism in leaf nitrogen content but not photosynthetic rates in *Sagittaria latifolia* (Alismataceae). *Botany*, 92(2), 109–112. <https://doi.org/10.1139/cjb-2013-0246>
- Yuan, Y., Tang, X., Liu, M., Liu, X., & Tao, J. (2021). Species distribution models of the *Spartina alterniflora* Loisel in its origin and invasive country reveal an ecological niche shift. *Frontiers in Plant Science*, 12, 738769. <https://doi.org/10.3389/fpls.2021.738769>
- Zedler, J. B., & Kercher, S. (2004). Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences*, 23(5), 431–452. <https://doi.org/10.1080/07352680490514673>
- Zhao, H., Wang, F., & Ji, M. (2015). Brackish eutrophic water treatment by *Iris pseudacorus* L.-planted microcosms: Physiological responses of *Iris pseudacorus* L. to salinity. *International Journal of Phytoremediation*, 17(9), 814–821. <https://doi.org/10.1080/15226514.2014.981240>
- Zong, J. W., Zhang, Z. L., Huang, P. L., Chen, N. Y., Xue, K. X., Tian, Z. Y., & Yang, Y. H. (2021). Growth, physiological, and photosynthetic responses of *Xanthoceras sorbifolium* Bunge seedlings under varying degrees of salinity. *Frontiers in Plant Science*, 12, 730737. <https://doi.org/10.3389/fpls.2021.730737>

BIOSKETCH

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Author contributions: BJG and JMC led research design with contributions from CRW, BJG, CRW, JMC, GB-M, KMT, and KJB executed data collection in the field research. BJG, JMC, BG-T, GB-M, and KJB performed data analyses. BJG, BG-T, and JMC drafted the manuscript. All co-authors contributed to and approved the final manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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