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Seed source regions drive fitness differences in invasive macrophytes

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PREMISE: Worldwide, ecosystems are threatened by global changes, including biological invasions. Invasive species arriving in novel environments experience new climatic conditions that can affect their successful establishment. Determining the response of functional traits and fitness components of invasive populations from contrasting environments can provide a useful framework to assess species responses to climate change and the variability of these responses among source populations. Much research on macrophytes has focused on establishment from clonal fragments; however, colonization from sexual propagules has rarely been studied. Our objective was to compare trait responses of plants generated from sexual propagules sourced from three climatic regions but grown under common environmental conditions, using *L. peploides* subsp. *montevidensis* as a model taxon.

METHODS: We grew seedlings to reproductive stage in experimental mesocosms under a mediterranean California (MCA) climate from seeds collected in oceanic France (OFR), mediterranean France (MFR), and MCA.

RESULTS: Seed source region was a major factor influencing differences among invasive plants recruiting from sexual propagules of *L. peploides* subsp. *montevidensis*. Trait responses of young individual recruits from MCA and OFR, sourced from geographically distant and climatically distinct source regions, were the most different. The MCA individuals accumulated more biomass, flowered earlier, and had higher leaf N concentrations than the OFR plants. Those from MFR had intermediate profiles.

CONCLUSIONS: By showing that the closer a seedling is from its parental climate, the better it performs, this study provides new insights to the understanding of colonization of invasive plant species and informs its management under novel and changing environmental conditions.

KEY WORDS biological invasions; climate change; creeping water primrose; environmental niche; invasion ecology; MERRAclim bioclimatic variables; Onagraceae; plant traits; sexual reproduction.

Climate change and non-native plant invasion into novel ecosystems are pervasive aspects of global environmental change that are simultaneously increasing at unprecedented rates. Global warming, coupled with extreme climatic events, is predicted to exacerbate negative ecological impacts of invasive plant populations (Diez et al., 2012). However, the interaction of non-native species with new environmental drivers, such as a changing climate, may lead to either invasion successes or failures (Buckley and Csergő, 2017). Overall, climatic niche shifts can be common among introduced plants (Atwater et al., 2018, but see Petitpierre et al., 2012)

and can affect population demography and performance of invaders (Broennimann et al., 2007). A frequent assumption in invasion ecology is that most invasive species display enhanced performance when introduced to novel environments, although this idea has been rarely tested. Existing studies have yielded contrasting results, with some invasive species performing better in their new range, whereas others perform similarly across ranges (Firn et al., 2011; Parker et al., 2013; Lemoine et al., 2016). Some non-native species are able to establish in environmental conditions quite different from those in their native range and become invasive (Broennimann

and Guisan, 2008), although underlying mechanisms may vary by species and are not fully understood. In particular, it is still unclear if invasive species performance is driven by ecological processes, evolutionary processes, or both (Estoup and Guillemaud, 2010; Colautti and Lau, 2015; Pearson et al., 2018).

Plant functional traits (measurable characteristics indirectly impacting fitness via their effects on growth, reproduction and survival; Violle et al., 2007) can be used to evaluate species' responses to environmental factors. For example, specific leaf area (SLA) is a key functional trait representing the amount of light-capturing surface area and thus is used widely to estimate plant carbon acquisition efficiency (Milla and Reich, 2007) and leaf thickness (Vile et al., 2005). Examining functional traits and other fitness components of an invasive species from contrasting environments provides a useful framework to assess invasive plant responses to climate change and the variability of these responses among source populations (Díaz et al., 1998; Lavorel et al., 2007; Drenovsky et al., 2012; Colautti and Barrett, 2013). Across demographic life stages, trait responses of a colonizer will influence the success or failure of a new population in newly invaded sites (Ridley and Ellstrand, 2010). Understanding trait variation in individual growth, and ultimately the process of population establishment, can improve predictions of colonization success and expansion of invasions into distant novel habitats and therefore can be used to improve invasion risk assessments and management strategies.

Aquatic ecosystems are greatly threatened by biological invasions (Reid et al., 2019), including those by invasive macrophytes. Indeed, non-native aquatic plants have been widely introduced by humans all over the world, and their dispersal is facilitated by flows and flooding events that connect water bodies (Gherardi, 2007; Nilsson et al., 2010). Among them, the genus *Ludwigia* represents one of the greatest threats to freshwater ecosystems globally (Gassmann et al., 2006; Thouvenot et al., 2013). These aquatic macrophytes can spread rapidly and degrade ecological functions throughout watersheds in their naturalized ranges (Thouvenot et al., 2013; Grewell et al., 2016a). *Ludwigia peploides* subsp. *montevidensis* (Sprengel) P.H.Raven (creeping water primrose, floating primrose-willow, hereafter *L. p.* subsp. *montevidensis*) is an emergent, perennial, floating-leaved macrophyte considered native to South America (Wagner et al., 2007; Hoch et al., 2015). Its global occupied range includes populations disjunct from this likely origin, with naturalized populations occupying a wide range of aquatic habitats and environmental conditions. *Ludwigia* spp. have long been favored by horticulturists given their attractive yellow flowers, and the history of introduction of the different species is difficult to disentangle given their morphological similarity. *Ludwigia* spp. were introduced as ornamental plants to the Lez River in southeastern France in 1830 (Martins, 1866). A naturalization experiment by a botanical garden near Bordeaux in 1882 (Guillaud, 1883) and growing popularity of *Ludwigia* taxa as ornamental water garden plants are believed to have accelerated their expansion throughout much of France in the 20th century (Dandelot et al., 2005). In northwestern France, *L. p.* subsp. *montevidensis* arrived in the Loire River watershed by the end of the 1970s and spread rapidly among water bodies (Riaux et al., 2009). In recent years, the European expansion of *L. p.* subsp. *montevidensis* beyond France includes established populations in Belgium, the Netherlands, the United Kingdom, Italy, Spain, Greece, and Turkey with high risk for further spread (Zotos et al., 2006; Eppo, 2011; Robert et al., 2013; Thouvenot et al., 2013). *Ludwigia p.* subsp. *montevidensis* is subjected to regulation in

France, where its import has been banned since 2007. In addition, the species was included in the list of 37 invasive species adopted by the European Commission in July 2016 with the aim to mitigate the adverse impact of these species across the European Union. The invasion history of *L. p.* subsp. *montevidensis* in the United States is believed to be relatively recent, similar to its naturalization in Europe. Verified invasions of the populations in California are most prevalent in the Great Central Valley (Sacramento and San Joaquin), inner North Coast Range and San Francisco Bay subregions of the California Floristic Province, with some scattered populations in the northern Sierra Nevada foothills (Baldwin et al., 2012; Calflora, 2019). In 2010, new invasive populations of *L. p.* subsp. *montevidensis* were recognized in Oregon.

It has been assumed that the rapid and prolific spread of this taxon has been driven by clonal reproduction and hydrochorous dispersal of fragments (Thouvenot et al., 2013). Therefore, most empirical studies have focused on growth from clonal fragments and the role of plant traits on clonal invasiveness of diploid *L. p.* subsp. *montevidensis* and polyploid congeners (Rejmánková, 1992; Haury et al., 2014; Smida et al., 2015; Thiébaud and Martinez, 2015; Grewell et al., 2016b). However, the taxon has both asexual and sexual reproductive modes and is self-compatible. Okada et al. (2009) found high genotypic variation of *L. p.* subsp. *montevidensis* in highly disturbed sites, inferring recruitment from seedbanks. Recent studies also have revealed significant resource allocation to early flowering and seed production (Riaux et al., 2009; Grewell et al., 2016b; B. J. Grewell, personal observations), suggesting sexual reproduction of *L. p.* subsp. *montevidensis* represents an important mechanism in the potential spread of the species. Gillard et al. (2017a, b) found that seed germination of the taxon will be sustained under rising global temperatures predicted in climate change models. All of these factors suggest a need for increased understanding of traits underlying the survival, first season's growth, and success of *L. p.* subsp. *montevidensis* established from sexual propagules.

While historic records of *Ludwigia* occurrence and invasions exist, repeated and recent introductions from the native range into novel environmental niches are probable. The environmental niche breadth of *L. p.* subsp. *montevidensis* in Europe appears to be limited by hydrologic conditions, with observations suggesting standing biomass production is reduced with decreased inundation and soil moisture (Hussner, 2009; Haury et al., 2014). Recent modeling efforts using CLIMEX (Eppo 2011) and species distribution models (Gillard et al., 2017c) to inform invasive species risk assessments under climate change scenarios predict future changes in the spread of *Ludwigia* spp. For example, the distribution of aquatic *Ludwigia* spp. may decrease by up to 55% in the native South American range, while in Europe and North America the species has the potential to spread invasively into higher latitudes, if warming climate model predictions are realized (Gillard et al., 2017c). Given the importance of sexual propagules in the spread of some invasive plant species, improving our understanding of their growth in relation to seed source is needed to predict their performance in novel environments and to support management strategies.

In the present study, we performed a common garden experiment to evaluate how plant trait responses to environmental factors may contribute to the success of invasive plants that establish from sexual propagules in their new, non-native range. We germinated *L. p.* subsp. *montevidensis* seeds collected from three different invaded regions located in one oceanic climate zone (northwestern

France) and two mediterranean climate zones (southeastern France and northern California) and established a common garden experiment in the mediterranean California climate, beginning with the seedling life stage. We explored whether trait values varied among these source populations when grown in a common garden and if seed source regions and parental environmental niche characteristics could explain potential differences. We hypothesized that (1) individuals of *L. p.* subsp. *montevidensis* from different invaded seed source regions would exhibit variation in plant traits during the first season of growth (that conditions the success of population establishment) when grown in common garden; (2) populations grown from seeds from the two mediterranean climate zones would display traits more similar than those from the oceanic climate zone; (3) mediterranean climate zone populations would perform better than those from oceanic climate under the mediterranean conditions of the common garden; and (4) the environmental niche distance would be smaller for populations from the same climate zone type. Trait responses of invasive macrophyte populations for plants grown from seedlings through reproductive life stages are rarely studied. Our results should contribute to improved understanding of recruitment of *L. p.* subsp. *montevidensis* and can inform invasion risk assessment planning and management.

MATERIALS AND METHODS

Source regions

We selected six invasive populations of *L. p.* subsp. *montevidensis* from three source regions (northwestern France, southeastern France, and northwestern California), with two populations per region (Table 1). In southeastern France and northwestern California (hereafter mediterranean France and mediterranean California, respectively), the populations were located in Köppen climate zone Csa, corresponding to a hot-summer mediterranean climate, with a dry season. In contrast, the two populations in northwestern France (hereafter oceanic France) experienced a temperate oceanic climate, with a warm summer and no dry season, categorized as Cfb according to the Köppen climate classification.

The two oceanic populations of *L. p.* subsp. *montevidensis* were located in northwestern France, in oxbows of the Loire River approximately 20 km from each other, at Ile Joli Coeur (LRJC) and Port de Vallières (LRPV) (Table 1). In the warmer mediterranean climate region of southeastern France, two populations separated by 4 km were selected. The first was a small drained pond with emergent wetlands known as Marais de Coute (MACO), and the second was Canal des Capettes (CCAP), a tributary artificial channel to the Petit Rhône River (Table 1). In California, one of the populations was in the inner Northern Coast Range at Sage Creek, immediately upstream of impounded Lake Hennessey (LHSC) (Table 1). The

second donor population was established 50 km inland in the Great Central Valley in the Putah Creek Riparian Preserve at University of California, Davis (PCRP). Within the three regions, selected populations are likely to be connected by gene flow to some extent, although there is no existing information to confirm whether they spread from a similar genotype.

Capsule collection and seedling production

In each source region, collection sites were characterized by dense perennial stands of *L. p.* subsp. *montevidensis*. Mature capsules were collected between August and October 2017 from two populations from each of the three source regions (Table 1), from ramets separated by at least 10 m in population patches, where possible, to increase probability of collection from distinct individual ramets. Capsules were dried at ambient temperature and then stored at 4°C in the dark. Capsules from populations in France were imported to the Davis, California lab under conditions of Permit 3405 issued by the California Department of Food and Agriculture Plant Health and Pest Prevention Services, Sacramento, California. Mid-March 2018, 15 capsules of each population were soaked in water at 4°C for a week, and then dissected to extract seeds. For each population, 150 seeds (10 seeds from each of the 15 capsules) were weighted by lots ($n = 25$), and sown at 1 cm depth in Leach Cone-tainers (Stuewe and Sons, Tangent, OR, USA; 14 cm high, 4 cm diameter) filled with a potting soil mix, Seed Starter Mix (E.B. Stone Organics, Suisun, CA, USA) composed of Canadian sphagnum peat moss, perlite, dolomite lime, and gypsum. Cone-tainers were placed in shallow fiberglass tanks outdoors to produce seedlings for our experiment. These tanks were immediately adjacent to the Putah Creek Riparian Reserve at the USDA-ARS Aquatic Weed Research Facility at the University of California, Davis. Therefore, the climatic conditions of the research site correspond to the home environment of population PCRP, with this population serving as control in the experiment. Cone-tainers were arranged within trays in two fiberglass tanks (1.95 × 1.21 m) filled with 13 cm of tap water, with the bottom 7 cm of the pots immersed in water. Seedling emergence (Appendix S1) and seedling growth were monitored for ≈12 weeks. Water was changed weekly to avoid eutrophic conditions due to algal proliferation. The water level was increased by 2 cm for the last 3 weeks of growth to support seedling survival and growth.

Seedling selection

Beginning in early June, the length of the primary stem of the largest seedlings was monitored approximately every other day, and all seedlings were grown until there were at least a dozen individuals from each population that had primary stem lengths of at least 4 cm. In mid-June, a stratified random selection was applied, based on primary stem length, to select 10–12 individuals from each population

TABLE 1. Location of populations from which the capsules of *Ludwigia peploides* subsp. *montevidensis* were collected.

Seed source region code	Population code	Name of waterbody, population location	GPS coordinates
MCA	LHSC	Sage Creek tributary to Napa River	38.489926, -122.347039
MCA	PCRP	Putah Creek at Riparian Reserve	38.524286, -121.783758
MFR	MACO	Marais de Coute	43.584092, 4.366019
MFR	CCAP	Canal des Capettes	43.606264, 4.336035
OFR	LRJC	Loire River at Ile Joli Coeur	47.318086, 0.405323
OFR	LRPV	Loire River at Port de Vallières	47.386011, 0.608789

MCA = mediterranean California, MFR = mediterranean France, OFR = oceanic France.

for the experimental garden. The seedlings were transplanted individually into 4.2 L pots (18.5 cm high, 20 cm diameter) filled with a 1:1 (v/v) mixture of fine sand and potting soil with initial nitrogen (N), phosphorus (P), and potassium (K) at 14-10-18 by soil mass. After transplanting, plants were maintained in tanks in subirrigated conditions (water at the surface level of the soil) for 5 days. The primary stem length was measured again, and within each population we selected for the experiment six individuals that were most similar in primary stem length. The other 4–6 individuals remaining per population were harvested, dried at 70°C for 72 h, and weighed to obtain an estimation of initial dry biomass (Appendix S2).

Experimental design

A full factorial experiment was arranged in a randomized complete block design (2 individuals \times 2 populations \times 3 source regions \times 3 blocks) to test the effects of source population origin on growth and trait responses of *L. p.* subsp. *montevidensis* grown in uniform climate conditions in a common garden. The rapid biomass increase of the focal species combined with the available tank space limited the experiment to comparing two populations per region; this limitation ensured each individual would have sufficient space to grow to sexual maturity without competing with others. Potted individual plants (total $n = 36$; $n = 12$ per mesocosm) were placed on submersed concrete blocks, to achieve a water depth of 30 cm above the soil surface within the pots, within each of three large fiberglass aquatic mesocosms (blocks; 9500 L volume; 0.9 m depth \times 3.7 m diameter). Total water depth within each mesocosm was maintained at 80 cm with a standpipe drainage system set to maintain constant circulation of freshwater inflow and drainage, allowing water oxygenation. Water and air temperature were recorded hourly with HOBO U22 Water Temp Pro v2 and HOBO Pro v2 loggers (Onset Computer Corp., Pocasset, MA, USA), respectively. The 36 individuals were grown for 9 weeks and monitored to track phenological changes. After 9 weeks of growth in the pools, leaf biomass of the mediterranean California populations was starting to senesce, and capsules were maturing. If the experiment continued, the risk that organs would detach from the mother plant was increasing. These observations led to the termination of the experiment to ensure the measurability and comparability of important traits. During the 9-week duration of the experiment in the common garden mesocosms, plants experienced an average temperature of $26.7^\circ\text{C} \pm 1.3$ in water, $26.2^\circ\text{C} \pm 8.6$ in the air, and a relative humidity of $63.5\% \pm 24.6$. A transparent insect exclusion netting (Combined Clear Net 13%; Green-Tek, Visalia, CA, USA; hole size = $2 \times 11\text{mm}$) was placed above and secured down the sides of each mesocosm when the first flower buds were visible but not open, to prevent pollen introduction in local field populations. From measurement of photosynthetically active radiation above the water surface, under and over the net with a Li-Cor LI-250A light meter (Li-Cor, Lincoln, NE, USA), the presence of the net reduced ambient light by $\approx 14\%$, from 1770 to $1525 \mu\text{mol m}^{-2} \text{s}^{-1}$. Plants of *Ludwigia p.* subsp. *montevidensis* in field and experimental populations frequently support aphid infestations. As aphids appeared, they were controlled by hand removal and foliar application of organic insecticidal soap (Safer Brand, Lititz, PA, USA) from small hand spray bottles.

In late August, after plants grew for 9 weeks in the mesocosms, we measured the maximum canopy height for each individual

before harvesting each plant. Upon removal of each pot from the mesocosm, shoots were separated from sediment roots at the soil surface. The total stem length, number of stem internodes, and basal diameter of the primary stem were measured and recorded. Sediment roots, stems, leaves, floating roots, pneumatophores, and reproductive organs (flower buds, flowers, capsules) were separated and placed in paper bags by structure, dried at 70°C for 72 h, and then weighed. Mass data were used to calculate clonal and sexual reproductive effort, i.e., the proportion of total biomass allocated to clonal reproduction (mass of stems, leaves, and floating roots) and sexual reproduction (mass of flower buds, flowers, or capsules). The relative growth rate (RGR) was calculated as $\text{RGR} = (\ln w_2) - (\ln w_1) / (t_2 - t_1)$, where w_1 and w_2 are biomass at initial time t_1 (beginning of the experiment) and final time t_2 (end of the experiment). Specific leaf area (SLA; leaf area per unit leaf mass) was calculated for a subset of 200 leaves per individual, using mass and leaf area of the subsamples, with leaf area determined using the image analysis software WinFOLIA (2009a, Regent Instruments, Quebec City, Quebec, Canada). Leaves were analyzed for total N concentration using a Perkin Elmer 2400 CHNS/O analyzer (Perkin Elmer, Waltham, MA, USA). Specific leaf area and leaf mass ratio (LMR; fraction of a plant's total leaf mass to the entire biomass of the plant) are important functional traits (Shipley, 2006; Lambers et al., 2008), and with leaf N content, they are notably related to plant palatability (Elger and Willby, 2003; Descombes et al., 2017; Wilson et al., 2018).

Response variables from the common garden experiment were either functional traits or fitness components, and here we also refer to all these measurements as traits. These response variables were classified into four trait categories: (1) growth strategy (functional traits), (2) reproductive effort (fitness components), (3) leaf traits (functional traits), and (4) adaptation to shallow water conditions (functional traits). (1) Growth strategy: biomass accumulated and RGR are two traits related either to the extent and/or to the speed of growth, a determinant of plant competitiveness. To evaluate the spatial exploration of individuals, we used two architectural traits, mean internode length of primary stem and maximum canopy height, to reflect lateral and vertical colonization, respectively. (2) Reproductive effort: Time to anthesis represents the phenology of sexual reproduction. Although plants reproducing clonally can spread without investing energy in sexual reproduction, some combine both reproductive strategies to ensure plant regeneration success under various conditions (Silvertown, 2008). The timing of flowering is crucial for sexual reproduction success, especially in environments that require species to complete their life cycle in a timely manner to avoid or synchronize with particular abiotic or biotic conditions. Thus, inadequate flowering timing may not impact population establishment of clonal plants, but could influence population persistence over time, by impeding some genetic adaptations and by decreasing seed bank inputs, and important hedge against changing conditions. Sexual and clonal reproductive efforts are an estimation of how much energy plants allocate to each reproduction type. Given that branching and rooting occurs at nodes, each stem section with a node represents a potential clone. (3) Leaf traits: SLA, LMR, and N concentration in leaves are proxies for carbon acquisition and allocation and are thus related to plant growth (Appendix S3). (4) Adaptation to shallow water conditions: Basal diameter of primary stem reflects an increase of

stem diameter due to production and expansion of aerenchyma tissues. Pneumatophores are spongy, gas-filled, upward-growing roots that transport oxygen down to submersed nodes (Ellmore, 1981), so measuring pneumatophore biomass indicates acclimation to hypoxic conditions under water.

Environmental niche characterizations

To represent environmental niches in species' range size studies, climate and edaphic variables are often used because variables such as temperature, soil water availability, and nutrient availability represent important parameters that limit the growth and distribution of plants (Yu et al., 2017). We collected five soil core samples (4.7 or 7.0 cm diameter, 10 cm depth) from random points within all six population sites in October 2018. Loss on ignition (LOI) was used to estimate soil organic matter content. Soils samples were oven dried at 70°C for 48 h, weighed for mass loss to determine soil moisture content, and ground to pass through a 40-mesh sieve. Samples were then analyzed for total nitrogen (N) concentration by micro Dumas combustion using a Perkin Elmer 2400 CHN/O elemental. We then quantified Olsen's extractable phosphorus (P) using the molybdenum–ascorbic acid method (Murphy and Riley, 1962).

For assessing variation in climatic differences between populations, MERRAclim data (Vega et al., 2017), which includes 19 bioclimatic variables (Appendix S4), were downloaded at 2.5 arc min resolution (≈ 4.6 km at the considered latitudes), using mean data for BIO12 to BIO19. We extracted the data corresponding to each of our six study population sites. The MERRAclim data set covers the decade of the 2000s, rather than the 1970–2000 decades like the widely used data set of WorldClim (Fick and Hijmans, 2017). Considering the changes of climate over the past decades, we estimated that the MERRAclim data would be a better fit to describe the environmental niches in which our parental plants grew. From these 19 bioclimatic variables, we kept the seven variables shown to be of importance for the distribution of *L. p.* subsp. *montevidensis* and two closely related congeners (Appendix S4; Gillard et al., 2017c).

The number of growing degree days is an important index for climate studies with plants, and the presence and growth of *L. p.* subsp. *montevidensis* has been shown to be limited below 10°C (Yen and Myerscough, 1989; Gillard et al., 2017c). Thus, we obtained the accumulated number of growing degree days $>10^\circ\text{C}$ (GDD10) for the year 2017, from the USA National Phenology Network for the two populations in the U.S., and we calculated it for the populations located in France, from the minimum and maximum daily temperature data provided by Météo France for nearby meteorological stations.

Finally, day length is one integrative factor that strongly influences temperature, the amount of light received by plants for growth, and plant phenological development (Cleland et al., 2007) and thus can have strong impacts on plant life cycles. We calculated the yearly average day length from latitude for each of our populations, using the geosphere package in R 3.5.1 (Hijmans, 2017).

Statistical analyses

All analyses were performed using statistical R 3.5.1 (R Core Team, 2018). We applied linear mixed effect models on the different individual variables, using package lme4 (Bates et al., 2015), with population and seed source region as fixed effects (population being nested in the corresponding seed source region), average seed mass

and plant age as a covariate, and pool (or block) as a random effect, i.e., $Y \sim \text{Source/Population} + \text{Seed mass} + \text{Plant age} + (1|\text{pool ID})$. Plant age corresponds to the number of days from individual seedling emergence day to the day when the individual was collected. Model assumptions were checked with Shapiro–Wilk and Levene's tests and graphically, and there was no need of data transformation for any response variable. The impact of fixed effects was tested with an analysis of deviance performed on the output of the models with package car (Fox and Weisberg, 2011). The differences among populations and among seed source regions were established by comparing the overlapping of 95% confidence intervals from the predicted values of the models. In addition, the variability explained by the models was calculated for fixed and random effect with the method developed by Nakagawa and Schielzeth (2013) implemented in the package MuMin (Barton, 2018).

To assess environmental niche space, we centered and standardized the data and conducted a principal component analysis (PCA) with the ade4 package (Dray and Dufour, 2007) and the factoextra package (Kassambara and Mundt, 2016) in R 3.5.1 (R Core Team, 2018) using the seven selected MERRAclim variables, GDD10, day length, and soil data (Appendices S5, S6). The three first principal components (PCs) accounted for 99% of the variation and were used to calculate the Euclidian distance between each source population (Appendix S7) with the pdist package (Wong, 2013), as an estimate of the environmental niche distance (see Wei et al., 2018). The environmental niche distance represents the difference between environmental niches of the source populations based on the climatic and edaphic characteristics experienced in situ by plants.

We applied the same methodology for the plant trait data by conducting a PCA with centered and standardized values of the 12 measured traits (Appendix S8). The first four PCs, accounting for 97.1% of the variation, were used to calculate the Euclidian distance between source populations (Appendix S7), as an integrative value to estimate the distance among populations based on traits. We then calculated the association between environmental niche and trait distance with a Mantel test (permutations = 999), using the package ade4 (Dray and Dufour, 2007). Plots were generated with ggplot2 (Wickham, 2016).

RESULTS

Population-level trait response

Growth strategy—In the common climate conditions in California, the two populations from oceanic France accumulated ≈ 1.6 -fold less biomass than the populations from mediterranean California and from mediterranean France (Fig. 1A), and this biomass accumulation was highly correlated with clonal reproduction biomass (Appendix S2). Differences among populations from the same source regions were observed for RGR (Appendix S9), with individuals from the population LRPV (oceanic France) growing significantly slower than the five other populations, and with populations from mediterranean France and population LRJC (oceanic France) growing faster than populations from mediterranean California (Fig. 1B). Fixed effects also explained 43.1% and 44.6% of the biomass accumulated and of the RGR of biomass, respectively (Appendix S10), mainly driven by population and seed source regions, while the random effect explained an additional 20% of the variability for these traits.

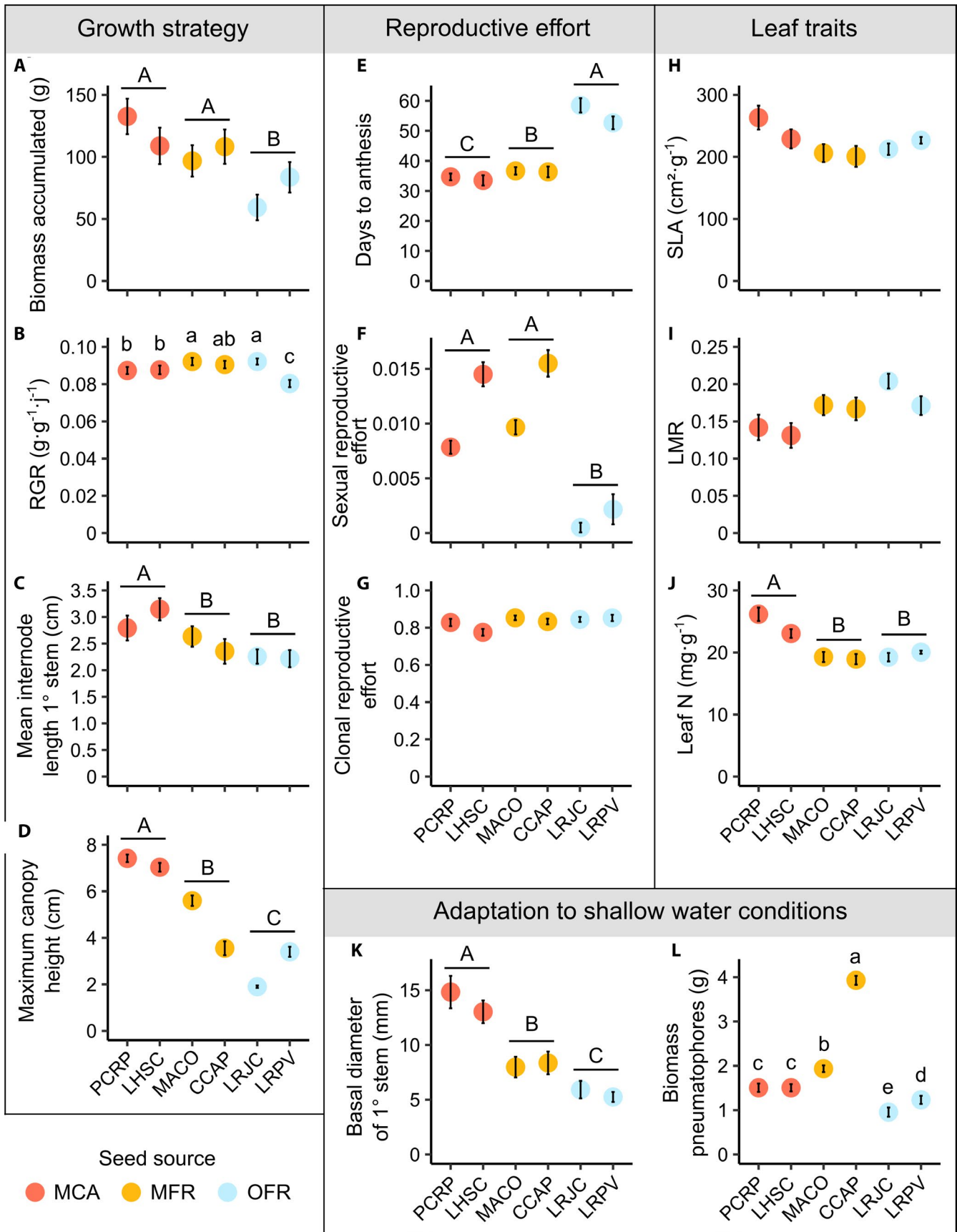


FIGURE 1. Predicted means ($\pm 95\%$ confidence intervals) for functional traits and fitness components related to growth strategy (A–D), reproductive effort (E–G), leaf traits (H–J), and adaptation to shallow water (K, L) for individuals of *Ludwigia peploides* subsp. *montevidensis* grown from seeds from six populations, from three source regions, and exposed to the same climatic conditions in a common garden for 9 weeks. Different capital letters represent significant differences among seed source regions. Different small letters indicate significant differences among populations. LMR = leaf mass ratio. N = nitrogen; RGR = relative growth rate, SLA = specific leaf area. MCA = mediterranean California, MFR = mediterranean France, OFR = oceanic France. See Table 1 for population codes and locations.

Differences in plant architecture were driven by seed source regions (Appendix S9). The primary stems of plants grown from mediterranean California seeds had an average stem internode length 0.73 cm longer than those grown from seeds collected in oceanic France, while stem internode lengths of plants grown from seeds collected in mediterranean France were intermediate in length (Fig. 1C, Appendix S9). The maximum canopy height of populations from California was about twice as high as those of the four populations from France (Fig. 1D, Appendix S9). The effect of block on the variability of maximum canopy height was null; fixed effects alone explained 43.5% of the variability of this trait (Appendix S10). However, the random effect explained 19% of the 64.5% of variability explained by the model for the average internode length. The substantial effect of block on some traits related to growth is likely due to heterogeneous harvesting time among blocks, with plants in one of the blocks having been harvested on average 1.5 days after the others.

Reproductive effort—The two populations from oceanic France (LRJC, LRPV) began anthesis more slowly than plants from the two mediterranean source regions, with anthesis occurring approximately 19 days later (i.e., 65% more time to produce their first flower; Fig. 1E). Sexual reproductive effort of the two populations from oceanic France, highly correlated to sexual reproduction biomass (Appendix S2), was 9-fold lower than that from Mediterranean sources (Appendix S9; Fig. 1F). However, there was no difference among individual study populations or the three population source regions regarding clonal reproductive effort (Fig. 1G, Appendix S9). The linear model explained 22.5% of the variability of clonal reproductive effort, 30.3% of sexual reproductive effort, and 59.9% of the day to anthesis (Appendix S10), largely driven by the fixed effects.

Leaf traits—Differences in SLA and in LMR were driven by the age of plants (Appendix S9), included in the model as a covariate, more than by population or seed source. Seedlings from population PCRP (mediterranean California) were overall older (Appendix S2), due to earlier seedling emergence compared to the other populations (Appendix S1). In addition, seedlings from population LRJC (oceanic France) were slightly younger due to later seedling emergence (Appendices S1 and S2). However, differences in leaf N concentration were explained mostly by seed source region and also by plant age (Appendix S9). Total N concentration in leaves of plants from mediterranean California populations was 1.3-fold greater than in any of those from France (Fig. 1J; Appendix S9). The linear model explained 41.6% of the variability of SLA, 60% of the LMR, and 75.2% of the N concentration in leaves, with 5.1%, 15.6%, and 3.1% that were due to block effect, respectively (Appendix S10).

Adaptations to shallow water conditions—Plants from the two mediterranean California populations had the widest primary stem basal diameter compared to any of the populations from France, due to greater aerenchyma tissue production (Fig. 1K; Appendix S9).

Among individuals grown from seeds collected in France, those from mediterranean France (MACO, CCAP) had a greater primary stem basal diameter than those from oceanic France (LRJC, LRPV). Interestingly, population CCAP from mediterranean France produced, on average, 2.7-fold more pneumatophore biomass than any other population (Fig. 1L; Appendix S9). Among the five other populations, population MACO (mediterranean France) produced significantly more pneumatophore biomass than populations from mediterranean California and oceanic France. Populations from mediterranean California themselves produced more pneumatophore biomass than populations from oceanic France, and the population producing the least pneumatophore biomass was LRJC (oceanic France). Up to 74.2% of the variability of the primary stem basal diameter and 65.1% of the pneumatophore biomass were explained by the model, and thus largely by the fixed factors, while block barely had an impact (Appendix S10).

Environmental niche and trait distances

Among the studied populations, distances between the traits and the environmental niches of two populations were quite variable. Nonetheless, the overall relationship between environmental niche distance and trait distance among populations was strongly positive (Fig. 2): the more population niches presented similar characteristics, the more plants displayed comparable traits. Not surprisingly, populations belonging to the same source region had the shortest environmental niche and trait distances. However, contrary to our expectations, environmental niches and traits of populations from mediterranean California and mediterranean France were quite distant, even though they both belong to the mediterranean climate zone, as defined by the Köppen classification system (Fig. 2). Instead, environmental niches and traits of populations from mediterranean France were closer to those of populations from oceanic France, although the climate between the two regions are typically quite different. The main environmental differences among the two studied mediterranean-climate regions were day length, due to differences in latitude, but also climatic variables related to humidity (Appendix S5). Overall, the mediterranean California study sites are more arid than the population sites in mediterranean France and have lower seasonal variation in specific humidity (Appendix S6). Finally, populations from oceanic France and from mediterranean California were the most distant in terms of environmental niche and of traits displayed when grown in a mediterranean common garden (Fig. 2).

DISCUSSION

In this study, we evaluated whether plants resulting from sexual propagules of *L. p.* subsp. *montevidensis* from three source regions (two with a mediterranean climate and one with an oceanic climate) would have different trait response values when grown in a mediterranean common garden experiment in California. We observed

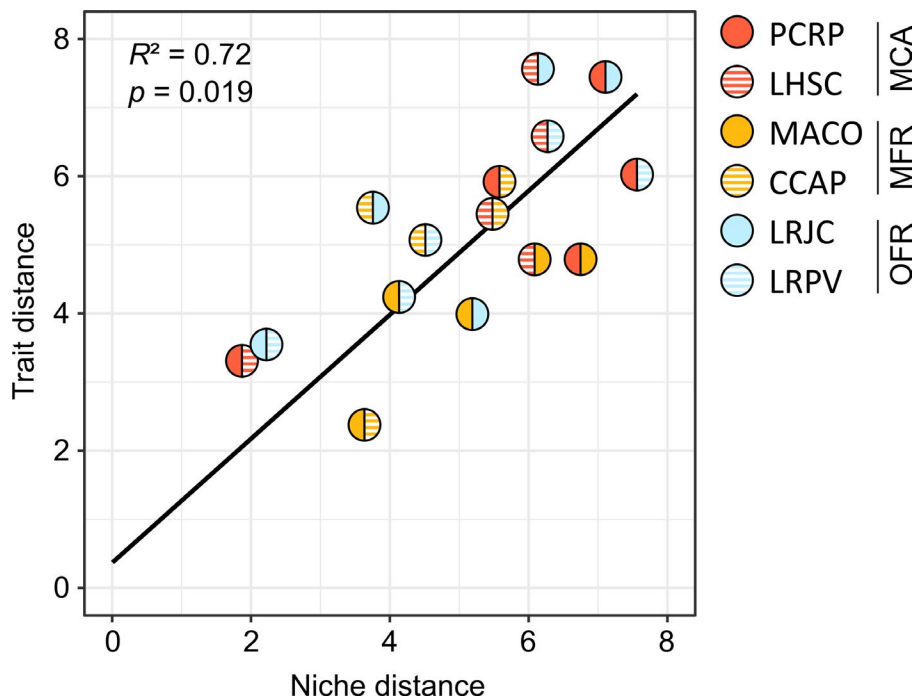


FIGURE 2. Relationship between environmental niche and trait distance based on a Mantel test for six populations of *Ludwigia peploides* subsp. *montevidensis* from three seed source regions. MCA = Mediterranean California, MFR = Mediterranean France, OFR = oceanic France. See Table 1 for population code definitions and locations.

differences in functional traits and fitness components, mainly driven by seed source region, although traits also could be influenced by life history, phenology and genetic diversity. For naturalized invasive *L. p.* subsp. *montevidensis* from multiple source regions, our results demonstrate that the further a population is from its source climate, the worse it performs. Surprisingly, environmental niche distances were not smaller for populations from the same Köppen climate zone type. Instead, similarities among environmental niches were driven by geographical proximity. To a lesser extent, the same trend was observed for plant trait responses, as populations from mediterranean France performed intermediately to that of mediterranean California and oceanic France.

Seed source region drives traits differences away from “home”

Expression of individual functional traits and fitness components differed by seed source region, in support of our first hypothesis. Overall, trait responses and environmental niche characteristics were the most different between mediterranean California and oceanic France populations. However, contrary to our second hypothesis, plants from the two mediterranean climate regions were not the most similar. In fact, individuals from mediterranean France often had traits values intermediate to those sourced from mediterranean California and oceanic France. Even if the two mediterranean source regions are part of the same Köppen climate zone, their environmental niche distance indicated that populations from mediterranean France were more similar in their environmental niche to populations from oceanic France than to those of mediterranean California, which contradicts our fourth hypothesis. This outcome is consistent with recurrent critiques made about the Köppen climate classification, which argue that the classification rules are too

subjective, although the boundaries for the zones are based on vegetation distribution (Belda et al., 2014; Zhang and Yan, 2014). Here, we observed high variation in climate characteristics within a climate classification zone, with these differences likely being affected by ongoing climate change. This relative similarity among environmental niches of the four French populations may explain why populations from mediterranean France had intermediate trait values, as their parents shared environmental characteristics both with the oceanic France populations and the mediterranean California populations. Although day length differences could partially explain variation in environmental niches between the two Mediterranean regions (Appendix S5), these differences also are driven largely by climatic variables related to aridity, with sites in Mediterranean California being more arid and experiencing lower seasonal variation in humidity than those in mediterranean France. The latter may be explained by proximity of the sea to population sites in mediterranean France.

The differences observed among populations based on their trait responses

were essentially explained by seed source regions, and more rarely due to population effects. These trends may be explained by the fact that this study included only two populations per region, which does not encompass significant population-level variance. The two populations from mediterranean California, with PCRP being a control, never differed significantly in trait response from one another, whereas populations from the other two source regions sometimes differed from their paired source population. For example, plants established from seeds from LRJC (oceanic France) had a higher RGR than LRPV (oceanic France). Likewise, population CCAP (mediterranean France) allocated more resources to production of pneumatophore biomass than MACO from the same region. Greater pneumatophore biomass increases oxygen transport and supply to submersed nodes and indicates acclimation to hypoxic conditions under water. This differential response observed among populations was unexpected, as all six populations were grown in the same shallow conditions, yet CCAP had a greater allocation to this adaptive response. The greater similarity between the two populations from California may be explained by their more recent invasion history, whereas French populations, with their longer invasion history, have had more time to differentiate.

Lower performances of populations the farthest from their “home” climate

Overall, under the tested Mediterranean conditions, the populations from the oceanic climate performed poorly compared to those from the two other source regions from mediterranean climates, or similarly to that of mediterranean France, partially supporting our third hypothesis. This outcome may be due to a stronger source population effect for the oceanic France populations than

the other tested populations, due to the larger dissimilarity between their “home” climate and that of the common garden. The oceanic populations (LRJC and LRPV) seem less well adapted to the tested mediterranean climatic conditions compared to the other focal populations, suggesting they would perform poorly at colonizing novel sites under such conditions. Our results may also indicate that these populations could struggle under future climate warming. These results contrast with a study focusing on germination from experimental seedbanks and initial post-emergence traits in young *Ludwigia* seedlings when exposed to two common garden conditions (oceanic climate, mediterranean climate) (Gillard et al., 2017b). In this previous experiment, young seedlings from the same populations of *L. p.* subsp. *montevidensis* (LRJC and LRPV, oceanic France) had higher germination fractions, faster emergence of germinants, lower survivorship, and greater total biomass when grown under warmer conditions (mediterranean climate) rather than in their source population conditions (oceanic climate). Also, the populations from oceanic France did not underperform under mediterranean conditions compared to populations from California. These results were quite different from what we observed in the present experiment on plants sourced from three climate regions, and grown from seedlings to maturity through first season of growth in a hot mediterranean climate. While the experiments are not directly comparable, several hypotheses may explain these observed differences in trait responses: (1) For Loire River populations, the trait response differences induced by warmer temperatures on germinants at early stages are not maintained at later stages of growth. (2) *Ludwigia p.* subsp. *montevidensis* did not perform as well in shallow water conditions (current experiment) as compared to performance in moist/subirrigated conditions (previous experiment). In contrast, populations from mediterranean France performed intermediately, despite being grown in a different environment from where their seeds were produced, potentially because their parents descended from populations that were naturalized, possibly for centuries, in climatic conditions closer to that of the common garden in mediterranean California climate, whereas the parental populations more recently naturalized in oceanic France had experienced quite different climate conditions. Indeed, the environmental conditions experienced by parents can be translated into phenotypic variation in offspring (Mousseau and Fox, 1998; Matesanz and Valladares, 2014). Thus, maternal effects, although too rarely studied and dissociated from other genotype \times environment effects in plants, can influence the life history of offspring (Galloway, 2001, 2002; Li et al., 2018) and may have primed offspring responses to the common garden conditions for those propagules originating from mediterranean climates. Even though propagule size is heavily dependent on maternal investment and can influence propagule resources and performance (Mousseau and Fox, 1998; Larios and Venable, 2015, but see Lacey et al., 1997), the differences in average initial seed mass in our experiment (Appendix S2) did not correspond with other traits differences. In addition, the strength of plant maternal effects typically weakens with age of the offspring (Maruyama et al., 2016). Although our study was not designed to control for maternal effects, these factors suggest that maternal effects were not the sole source of variation among our populations.

The observed variability of traits between source populations indicates phenotypic differentiation that could be adaptive. Our results are similar to those in a recent meta-analysis indicating that locally sourced plants present higher survival and reproductive fitness in their home environment, harboring adaptations that

facilitate their establishment success in these environmental conditions (Baughman et al., 2019). The species response to environmental conditions that differ from that of their home environment can be explored through the lens of other adaptive and non-adaptive mechanisms that were not tested in the present study. Invasive species or genotypes that overcome climatic differences in their non-native habitat may express pre-adapted trait differences, facilitating their establishment and spread (Pyšek and Richardson, 2007; van Kleunen et al., 2010). Non-native plants often present high phenotypic plasticity enabling them to rapidly cope with changing conditions, particularly at the colonization stage (Theoharides and Dukes, 2007), which can be revealed using reciprocal transplant experiments. Furthermore, distribution models can be used to detect potential niche shift of invasive populations between the native range and invasive range (Ebeling et al., 2008; Peña-Gómez et al., 2014; González-Moreno et al., 2015). Combining trait data and niche modeling results in mechanistic models that allow for prediction of population range, i.e., the performance of any population when growing in any climate, can be useful for assessment of the establishment potential of propagules that move into new environmental conditions (Wang et al., 2010; Chapman et al., 2017; Richardson and Chaney, 2018). Identifying the evolutionary mechanism(s) underlying invasiveness is important to disentangle whether the characteristics displayed by invaders to cope with different environmental conditions are due to existing genetic variation in the colonizing population or were acquired through adaptation.

Impact of life history and phenology on traits

Plants from oceanic France transitioned to flowering life stage later than other source populations when grown in the mediterranean climate of our experiment. Unlike plants sourced from the other regions, plants from the oceanic source populations also did not develop capsules by the end of the experiment. This late phenological shift relative to the other study populations could ultimately lead to lower seed production and hence, lower fitness of plants from oceanic France. Thus, the differences in sexual reproductive effort we report among plants from different seed source region are essentially due to the absence of capsule production by populations from oceanic France. Populations from oceanic France may have a different life history in their home environment, compared to the mediterranean common garden conditions. Unlike populations from mediterranean climates, which likely implement a fast but shorter reproductive period as a strategy to cope with the warm season (Sherry et al., 2007; Hedhly et al., 2009), populations from oceanic France may have a delayed reproductive period due to cooler temperatures. The evidence of shifted reproduction phenology among populations of *L. p.* subsp. *montevidensis* from different invasive ranges would support Dietz and Edwards' (2006) assumption that changes in species' life history are expected during the secondary phase of plant invasion, when species extend their ecological range to occupy a greater range of habitats, as shown for example by Moloney et al. (2009) for *Lythrum salicaria*. In addition, species and populations with flexible phenologies, such as flowering time shifts, would be the most successful invaders in new or changing environments (Wolkovich et al., 2013).

To date and to our knowledge, there has been no experiment comparing responses of sexual versus asexual propagules of *L. peploides* subsp. *montevidensis*. Thus, the outcome of the present experiment performed with clonal fragments or with rhizomes is

uncertain. Asexual fragments would likely grow faster than seedlings due to greater carbon resources available. Nonetheless, the two propagules types may have different dispersal potential and differential responses to herbivory and pathogens, and sexual propagules could benefit from genetic variation. In addition, sexual propagules allow populations of invasive *Ludwigia* spp. to grow back from seed banks after a drawdown (Grewell et al., 2019). Thus, sexual and asexual propagules may be complementary for the species spread and persistence, independently of their growth strategies.

This study highlighted that population sites belonging to the same climate type do not systematically lead to similar environmental niches. For our study populations, differences in precipitation and precipitation seasonality were major drivers of niche differentiation, with the intensity and duration of the dry season under Mediterranean conditions generating major differences in environmental niche characteristics. We also showed that the plants resulting from sexual propagules of *L. p.* subsp. *montevidensis* from different seed source regions expressed different trait values, when grown to reproductive stage in a common garden. Geographically distant populations from two different climate zones had the most distinct responses (oceanic France versus mediterranean California). The two populations from mediterranean France were intermediate in their responses, being exposed to a mediterranean climate and belonging to same Köppen climate zone as the mediterranean California populations and a closer geographical region to the oceanic France populations. Our results indicate that the more similar the climate in the source region and the newly invaded region, the better plants can establish and perform. While source populations of a new invasion are seldom known, *L. p.* subsp. *montevidensis* is clearly able to adjust to new environments and establish. With its high capacity for sexual reproduction, the potential for rapid evolution to improve performance under new conditions is also high, suggesting the need for rapid management responses to new invasions of this species. Current management options of invasive *Ludwigia* species consist mainly of biomass removal efforts of extant vegetation as addressed by Grewell et al. (2019). Management must consider the existence of seed banks and target the removal of biomass before the filling of seed capsules to limit new seed dispersal, coupled to detection strategies of new populations.

Given the observed variation in functional trait response, plants from some source regions may be more suited than others to cope with current and future environmental changes, although we recognize that documented differences among populations are not disentangled from the possible complexity of invasion history or from interactions between genetic differences and maternal effects. Further studies should address these aspects for a better characterization and understanding of the strategies and abilities of invasive populations of *L. p.* subsp. *montevidensis* to grow and reproduce in novel environments. This understanding is essential to improve management plans, particularly in the context of changing environmental conditions.

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AUTHOR CONTRIBUTIONS

B.G., G.T., and M.G. conceived the original idea. All authors contributed to the experimental design. M.G. and C.F. implemented the experiment and did the trait measurements. C.F. performed the chemical analysis on soil and leaves. M.G. analyzed the data and wrote the first draft of this manuscript with input from B.G. and R.D. All authors contributed to completion of the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Cumulative seedling emergence percentage of *Ludwigia peploides* subsp. *montevidensis* over time for populations from three seed sources.

APPENDIX S2. Raw means of different additional traits measured.

APPENDIX S3. Correlation between leaf traits and traits related to plant growth.

APPENDIX S4. List of the 19 bioclimatic variables from MERRAclim.

APPENDIX S5. PCA and hierarchical clustering based on niche characteristics.

APPENDIX S6. Values of environmental variables used for the six studied population sites to build the PCA in Appendix S5.

APPENDIX S7. Euclidian distances among populations for environmental niches and functional traits.

APPENDIX S8. PCA and hierarchical clustering based on 12 measured functional traits.

APPENDIX S9. Analysis of deviance.

APPENDIX S10. Variability in plant functional traits explained by the model for fixed and random effects.

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