Biol Invasions (2024) 26:1425–1436
https://doi.org/10.1007/s10530-024-03253-1

ORIGINAL PAPER

Some like it hot: small genomes may be more prevalent under climate extremes

Laura A. Meyerson · James T. Cronin · Magdalena Lučanová · Carla Lambertini · Hans Brix · Jasmin G. Packer · Jan Čuda · Jan Wild · Jan Pergl · Petr Pyšek

Received: 10 November 2022 / Accepted: 14 January 2024 / Published online: 9 February 2024
© The Author(s) 2024

Abstract Changing climates can influence species range shifts and biological invasions, but the mechanisms are not fully known. Using the model species *Phragmites australis* (Cav.) Trin. ex Steud. (*Poaceae*), we conducted a global analysis of climate and plant native and introduced cytotypes to determine whether this relationship influences population distributions, hypothesizing that smaller genomes are more common in regions of greater environmental stress. First, we identified 598 *Phragmites australis* field-collected native and introduced genome size variants using flow cytometry. We then evaluated whether temperature and precipitation were associated with *P. australis* monoploid genome size (Cx-value) distributions using Cx-value and Worldclim data. After accounting for potential spatial autocorrelation among source populations, we found climate significantly influenced Cx-value prevalence on continents. The relationships of Cx-value to temperature and precipitation varied according to whether plants were native or introduced in North America and Europe, and Cx-values were strongly influenced by precipitation during the

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-024-03253-1.

L. A. Meyerson (✉)
Department of Natural Resources Science, The University of Rhode Island, Kingston, RI 02881, USA
e-mail: lameyerson@uri.edu

J. T. Cronin
Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

M. Lučanová · J. Čuda · J. Wild · J. Pergl · P. Pyšek
Institute of Botany, Czech Academy of Sciences, 252 43 Průhonice, Czech Republic

M. Lučanová
Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic

C. Lambertini · H. Brix
Department of Bioscience, Aarhus University, Ole Worms Alle 1, 8000 Aarhus C, Denmark

C. Lambertini
Department of Bioscience, Università degli Studi di Milano, Via Celoria 26, 20133 Milan, Italy

J. G. Packer
Environment Institute, University of Adelaide, North Terrace, Adelaide, SA 5005, Australia

J. G. Packer
School of Biological Sciences, University of Adelaide, Adelaide, SA 5005, Australia

P. Pyšek
Department of Ecology, Faculty of Science, Charles University, Prague, Viničná 7, 128 44 Prague, Czech Republic

dry season. Smaller plant monoploid genome size was associated with more stressful abiotic conditions; under extreme high temperatures and under drought, plants had smaller Cx-values. This may influence genome dominance, biological invasions, and range expansions and contractions as climate change selects for genome sizes that maximize fitness.

Keywords Climate change · Cx-value · Genome size · Invasive Species · Plant traits · Range shift

Introduction

Genome size, i.e., the quantity of nuclear DNA in a cell (Doležel et al. 1998), varies within and among species and can influence traits from the subcellular to whole organism levels regardless of encoded genomic information (i.e., the nucleoptypic effect, Bennett 1971). In terms of heredity, DNA stores information about organismal development and function but also seems to have a nucleotypic function where it defines the thresholds within which the genes can operate and independently constrains functional traits (Suda et al. 2015).

The genomes of invasive plants are generally smaller (i.e., < 5pg) than plants that are not invasive, a trait hypothesized to contribute to successful invasions because smaller genomes are thought to undergo faster cell division allowing more rapid growth (Suda et al. 2015) with lower energy costs (Petrov 2001). Small genomes can be particularly advantageous for invasive plants to rapidly establish in new environments where resources may be limited because they can allocate more energy to growth rather than replication or repair. For example, when opportunity is limited by rapidly changing climate-related stressors (Bennett et al. 1998), small genomes may allow for faster replication and cell division than plants with larger genome sizes (Bennett and Leitch 2005). Leitch and Leitch (2013) posited that plants with larger genome sizes may have a greater potential than plants with smaller genomes to adapt and evolve, possibly due to higher frequencies of polyploidization which increase genetic diversity and evolution of novel traits. Across vascular plants in general, small genome size favors naturalization (ability to reproduce in the wild) but when invading (spreading and competing in invaded communities), large genomes are better because small genome constrains invasions (Pyšek et al. 2023). In addition, larger genomes may buffer DNA damage caused by environmental stressors, such as heat, by absorbing and repairing more mutations than plants with smaller genomes (Leitch and Leitch 2013). Conversely, the costs associated with larger genomes may constrain where plants are able to grow when environmental variation exerts selective pressure on nuclear DNA (i.e., the Large Genome Constraint Hypothesis [LGCH], Knight et al. 2005), although these costs may be minor in some cases (Lynch and Marinov 2015).

Global scale plant genome size studies can offer insights into how both native and invasive plant genomes can vary in their interactions with environmental change over space, particularly introductions of non-native species to new regions and range expansions associated with climate change for both native and invasive species. This can provide additional information to predictive models on species range changes (Anderson 2016). *Phragmites australis* is a cosmopolitan macrophyte with functional trait variations across populations and lineages (Cronin et al. 2015) and genome size variation (i.e., monoploid genome size, chromosome base number x, i.e. Cx-value) that influences invasiveness (Pyšek et al. 2018), plant traits (Suda et al. 2015; Meyerson et al. 2016; Pyšek et al. 2018), and phenotypic plasticity (Meyerson et al. 2020). In North America, native and invasive *P. australis* have overlapping ranges. These two lineages could have parallel evolutionary histories, but it is more likely that their response to climate differs due to divergent evolutionary histories (e.g., drift, selection) as the invasive lineage has been spreading for only ~ 150 years in North America (Chambers et al. 1999). Supporting this, Cronin et al. (2015) and Bhattarai et al. (2016) found non-parallel latitudinal clines in native and invasive *P. australis* traits such as defence and nutritional condition, suggesting recent evolution of the invasive genotype in its introduced range. Other studies have also confirmed these findings for other species (e.g., Oke et al. 2019; Yang et al 2021; Liu et al. 2021; Heckley et al. 2022).

Larger genome sized plants seem to be more constrained in the variability of functional traits whereas small genomes demonstrate greater variability (Knight and Beaulieu 2008) in traits such as photosynthetic rates (Knight et al. 2005),

aboveground biomass (Pyšek et al. 2019), and plasticity (Meyerson et al. 2020), possibly increasing stressor tolerance and resulting in greater population prevalence under extreme climates, including those amplified by global change (Suda et al. 2015). Interspecific genome size variation comparisons are well-documented, but few studies focus on intraspecific genome size variation, partly because early attempts suffered from methodological artefacts rather than real intraspecific differences (Suda et al. 2015). However, very small differences in intraspecific genome size (i.e., 2%) are reliably detected by employing best practices (Dolezel et al. 2007). Focusing on intraspecific rather than interspecific genome size increases phylogenetic control and avoids species-level differences that can confound results. Mixed cytotypes are common in nature and genome size variants within a population can have distinct abiotic and biotic interactions (Thompson and Merg 2008). In North America, mixed stands of native and invasive *P. australis* are relatively common (Cronin et al. 2015). Failing to account for intraspecific phenotypic variation that buffers climate change could overestimate impacts but ignoring this variation and its effects on interactions could underestimate climate change impacts on factors such as cytotype diversity or plant traits, if range dominance were to shift according to genome size under new climate conditions.

Investigations into the ecological significance of genome size variation, including interactions with climate, remain uncommon (e.g., Ohri 2005; Garcia et al. 2008; Carta and Peruzzi 2016; Meyerson et al. 2016; Gomes et al. 2018), and we are unaware of any global scale phylogenetically controlled studies. No studies that we are aware of have conducted a global scale investigation that compares how environmental variables interact with native and invasive lineages of the same species. Our global study of plant intraspecific genome size variation tests whether Cx-values interact with bioclimatic factors such as temperature and drought. We developed a comprehensive global genome size data set for a single plant species that spans multiple lineages, a wide range of latitudes, and diverse bioclimatic conditions analysing 598 populations sampled from field surveys on six continents and from our living collections to quantify Cx-values. By controlling for phylogenetic differences in Cx-value and evolution, we tested whether some variants were especially prevalent under certain bioclimatic conditions.

Based on the Large Genome Constraint Hypothesis (LGCH), we hypothesized that plants with large genomes would be excluded from higher stress climates (e.g., high temperatures, drought) and plants with smaller genomes (e.g., invasive *P. australis*) would be more common in regions of high environmental stress. We further hypothesized that clines in Cx-values would be less apparent as species undergo range expansions causing relationships between Cx-value and climate to differ in native and introduced ranges. In support of this second hypothesis where species are rapidly expanding their range, species may not have been present long enough to adapt to the new climate or be filtered out by an unsuitable climate and therefore the relationship might be weaker than in an established range (Cronin et al 2015). For example, Cronin et al (2015) found that clines in traits associated with growth and defense may not be fully formed in the invaded range and here we apply the same to the sorting of genome size along a new climatic gradient. To test these hypotheses, we compared genome size relative to climate variables in (i) all populations globally; (ii) European populations in their native (Europe and North Africa) and introduced (North America) ranges; (iii) native North American populations and native European populations; and, focusing only on North America, (iv) invasive European and native North American population.

Materials and methods

Phragmites australis (Cav.) Trin. ex Steud. (*Poaceae*) is a cosmopolitan grass with high genetic variation (Saltonstall 2002; Lambertini et al. 2006) growing from the tropics to cold temperate and arid regions in both hemispheres (Packer et al. 2017). Cx-values vary up to 22% which is associated with phenotypic variation (Meyerson et al. 2016; Pyšek et al. 2018). Lineages included in this study were European native, Asian native, African native, North American native, North American Gulf (cryptic), and the introduced lineage from Europe which is invasive in North America hereafter referred to as Invasive. Populations were defined to lineage according to the phylogenetic study of Lambertini et al. (2012) that resolved the nuclear DNA relationships among the chloroplast

DNA haplotypes used to classify *Phragmites* (Saltonstall 2016).

Flow cytometry analysis

We collected fresh leaf tissue from 598 unique *P. australis* clones representing all lineages described above and with distinct populations from field surveys and living collections curated at our institutions that included clones from Europe, Asia, Africa, North and South America, and Australia (see SI 1, Meyerson et al. 2023 in Dryad for complete database). Nuclear genome size was determined by DNA flow cytometry in a single laboratory using best practices (methods detailed in SI 7) to ensure small differences fell within detection limits (Dolezel et al. 2007).

Climatic variables

We used 19 bioclimatic WorldClim database global variables to express climate in the geographic origins of all 598 clones. From the original 19 variables, we extracted three principal components (PCs) using R v 4.0.0 AND PACKAGE 'PRCOMP' (R Core Team 2020) explaining nearly 85% of total variation (Dupin et al. 2011). Original variables included minimum, maximum, and mean temperature and precipitation data for the past 50 years broken out in biologically relevant ways (e.g., precipitation seasonality or mean temperature during the wettest or driest quarters; see http://www.worldclim.org; (Fick and Hijmans 2017). The first PC (ClimPCTemp) was attributed mainly to mean annual temperature, the second (ClimPCWet) mainly to precipitation during wet or warm periods, and the third (ClimPCDry) to precipitation during dry periods (Dupin et al. 2011, PCA loadings in SI 1 and deposited with full data set in Dryad, https://doi.org/10.5061/dryad.6t1g1jx1d).

Statistical analyses

Phragmites australis is a wind-pollinated, outcrossing, interbreeding, and long-distance dispersed species (Lambertini et al. 2008) making spatial autocorrelation in the data possible, i.e., continental populations closer together are more likely to have similar genome sizes than intercontinental populations. As such, we needed to account for non-independence among samples in our statistical tests for the effect of climatic variables on genome size. We used eigenvector spatial filtering (Moran's eigenvector mapping, MEM) to encapsulate spatial variation and account for potential autocorrelation in the distribution of source populations as eigenvectors (i.e., set of orthogonal spatial filters). Detailed methods are provided in Dray et al. (2006), Griffith and Peres-Neto (2006) and Murakami and Griffiths (2015) and in SI 7. Briefly, a distance matrix for Phragmites source populations was created using R package 'Geosphere' (R Core Team 2021) with the World Geodetic System (WGS84) as the reference coordinate system. The matrix was scaled by the maximum minimum spanning-tree distance between sites. Spatial filters are the eigenvectors computed from the distance matrix and were determined using packages 'Ade4' and 'adespatial.' Spatial filters were deemed informative if eigenvalues were positive and at least 25% of the maximum eigenvalue (Tiefelsdorf and Griffith 2007). Spatial filters (eigenvectors) meeting these criteria were included in our statistical models (below), allowing us to test for the effects of the bioclimatic variables on Cx-value independent of the spatial autocorrelation of P. australis populations.

Next, we used a generalized linear mixed model (GLMM) to evaluate the effects of these spatial filters (random effects) and three climatic PCAs (ClimPCTemp, ClimPCWet and ClimPCDry) on Cx-values across the entire global dataset. ClimPCTemp was strongly negatively correlated with the absolute value of latitude ($R = -0.72$, $P < 0.001$, $n = 598$) and latitude was therefore excluded. Analyses were conducted using R PACKAGE 'LME4' (Bates et al. 2015), goodness-of-fit was computed in package 'MuMIn' (Nakagawa and Schielzeth 2012). The proportion of variance explained was divided into two components: (1) marginal R^2 (R^2m) measuring the variance explained by all fixed effects combined and (2) conditional R^2 (R^2c) measuring the variance explained by the model, i.e., all fixed and random effects (spatial filters) combined.

Subsequent analyses focused on lineages in North America and Europe. In North America, lineage was a fixed factor (Native, Gulf, and Invasive). Finally, we assessed whether Cx-values for the European lineage in its native (Europe, northern Africa) and invaded (North America) ranges differed in response to climate; the fourth compared Cx-values for native *P. australis* in Europe and North America. For

statistically significant predictor variables, we performed spatially filtered quantile regression analyses to assess whether the slope of the relationship between the predictor and Cx-value changes over the range of Cx-values. We expected that plants with the smallest and largest genome sizes would be most responsive to climatic variability—e.g., the slope of the relationship between Cx-values and temperature would be more strongly positive or negative than plant with intermediate Cx-values. Using quantile regression analysis, we divided rank-ordered genome sizes into quantiles (0.1 increments) and estimated the slope of the relationship and 95% CIs for each quantile. The analysis was performed using package *adespatial* in R.

Results

Global distribution of cytotypes

For the full global dataset, Cx-values are presented in Fig. 1. The Moran Eigenvector Mapping (MEM) procedure identified two spatial filters (eigenvectors) that represent important spatial variation in the data. Spatial filter 1 (Moran's $I = 0.83$, $P < 0.001$) and filter 2 ($I = 0.79$, $P < 0.001$) accounted for data clustering at the continental and regional scales, respectively (SI 2). Including these two spatial filters as random effects in a GLMM, we found no significant relationship ($P \leq 0.05$) between Cx-value and our climatic variables (SI 1). Overall, Cx-value variance explained by the fixed factors in the GLMM, i.e., climatic variables, was only 0.8% (based on the marginal R^2) whereas the full model, which included both fixed (lineage and climate) and random effects (spatial data), explained 53.9% of Cx-value variation.

Cx-value, and climate—European lineage in its native and invasive range

Comparing the European lineage in its native and introduced ranges, the MEM revealed one important and obvious spatial filter that separated northern Africa and Europe from North America (SI 3A). Based on a GLMM with spatial filter 1 as a random effect, ClimPCTemp (mean annual temperature) and ClimPCWet (precipitation during wet or warm periods) were significantly related to Cx-value (SI 2). Importantly, the relationship involving both bioclimatic variables was strongly dependent upon the provenance of the European lineage (native European or invasive European in North America). In both cases, there were strong climate × provenance interactions (SI 2). For natives, Cx-values increased from 0.48–0.51 (6.2%) across the range of ClimPCTemp (least-squares regression: $R^2 = 0.04$, $P = 0.029$), whereas for invasive plants, Cx-value decreased from 0.52 to 0.49 (5.7%) across the same range of ClimPCTemp ($R^2 = 0.04$, $P = 0.004$; Fig. 2a). Similar

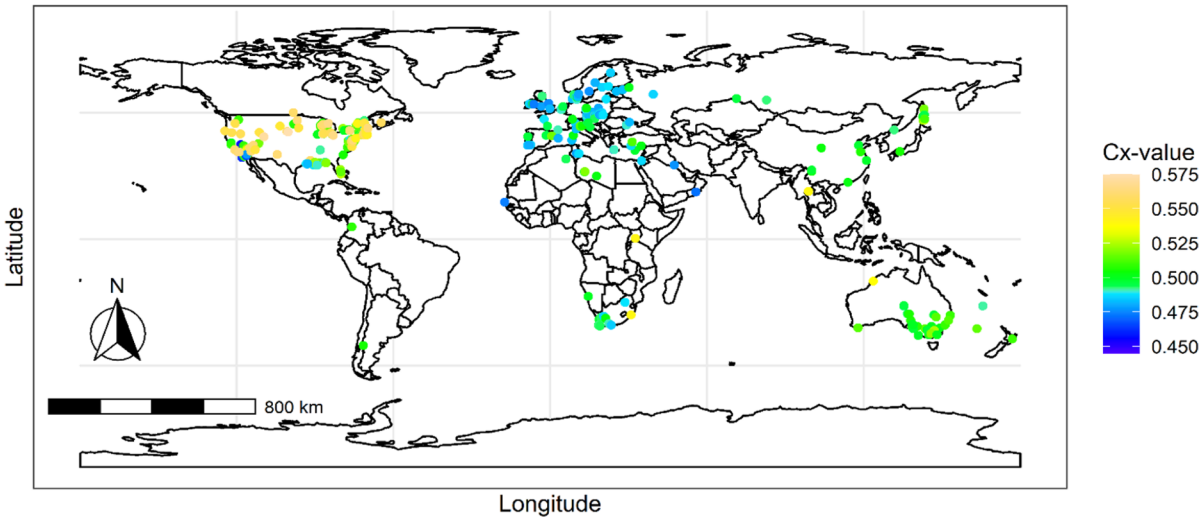

Fig. 1 Global variation in monoploid genome size (Cx-value) for *P. australis*

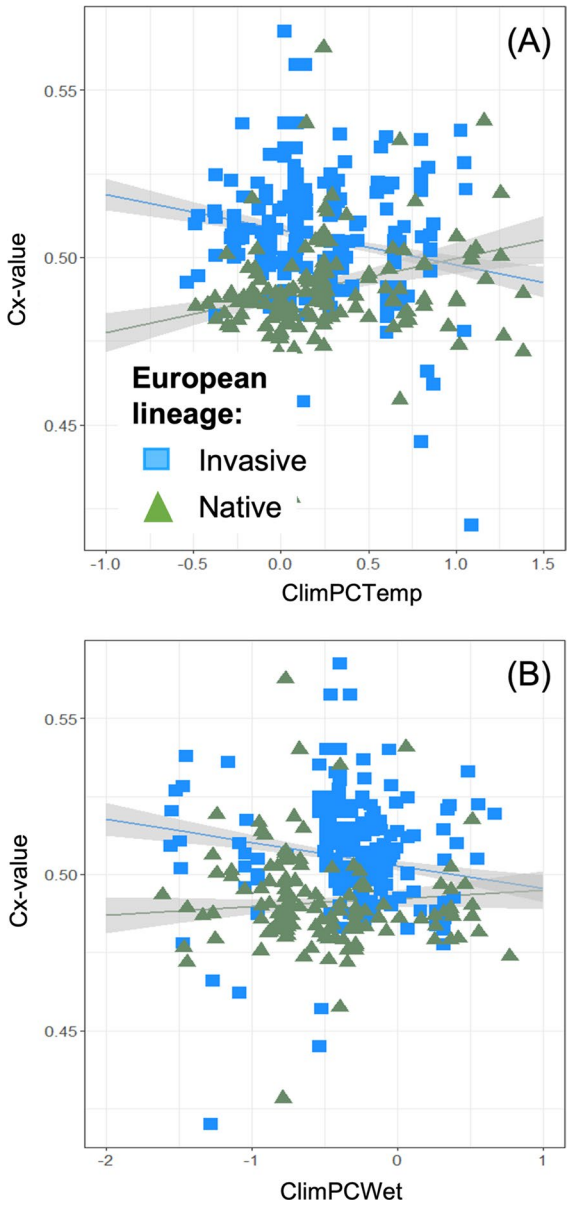

Fig. 2 Relationship between Cx-value and **a** ClimPCTemp and **b** ClimPCWet for the European lineage in its native and invasive range. ClimPCTemp represents mean annual temperature and is strongly correlated with latitude and ClimPCWet represents the amount of precipitation during wet or warm periods. Points further to the right on the ClimPCTemp axis and further to the left on the ClimPCWet axis indicate harsher conditions. Regression lines and SE bands based on estimates from the GLMM. Raw data for the invasive and native lineages are included

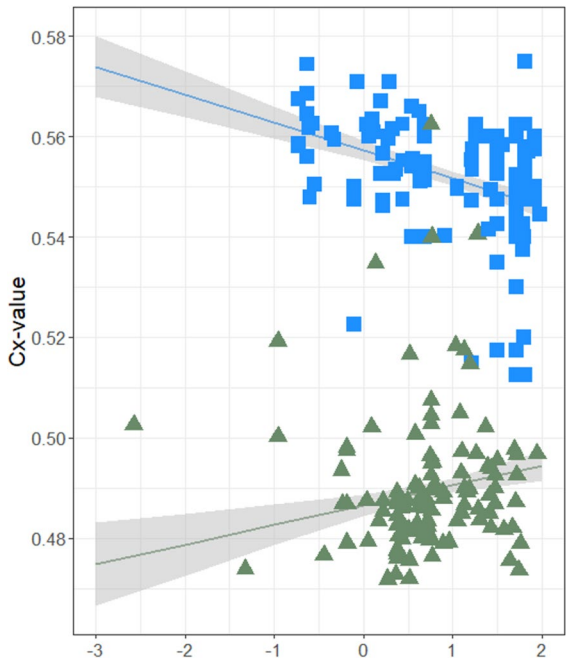

Fig. 3 Relationship between ClimPCDry and Cx-value for native *P. australis* in North America and Europe/North Africa. ClimPCDry represents the amount of precipitation during drought; further right on the *x*-axis = greater rainfall and lower drought stress. Regression lines and SE bands based on estimates from the GLMM. Raw data for native plants on each continent included

results were observed for ClimPCWet and the native European or invasive North American *P. australis* populations (Fig. 2b), but the slopes of the individual least-squares lines weren't significant ($R^2 < 0.01$, $P > 0.25$) (Figs. 3, 4). Finally, quantile regression analyses of relationships between ClimPCTemp and Cx-value revealed slopes were more negative at lower quantiles of Cx value (Fig. 5) suggesting that irrespective of provenance, plants in lower quantiles with larger Cx-values are favoured by colder temperatures. This correlation was reported in the original PCA for the bioclim variables, see Dupin et al. 2011, PCA loadings deposited with full data set in Dryad, https://doi.org/10.5061/dryad.6t1g1jx1d). Quantile regression for the relationship between ClimPCWet and Cx-value produced significantly negative slopes for intermediate Cx-values, quantiles between 0.2 and 0.8 (Fig. 6), suggesting that for plants with intermediate Cx-values, drier conditions during wet or warm periods favour the occurrence of plants with larger genomes, irrespective of provenance. Note, additional

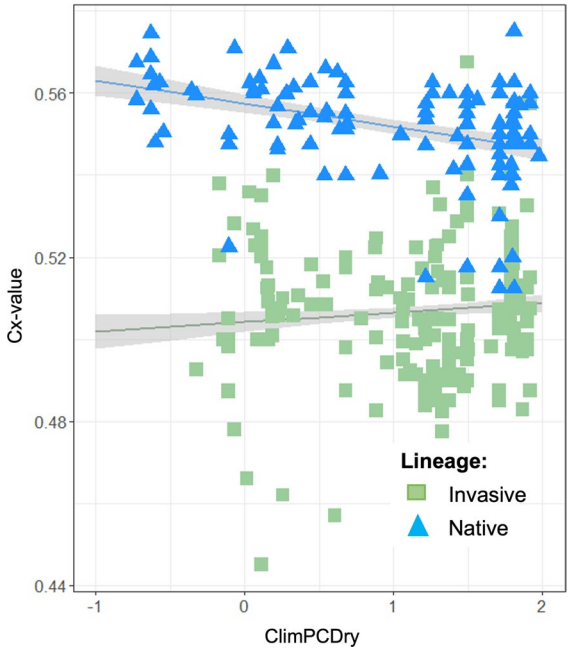

Fig. 4 Relationship between ClimPCDry and Cx-value for *P. australis* in North America. ClimPCDry represents the amount of precipitation during drought; further right on the *x*-axis = greater rainfall and lower drought stress. Regression lines and SE bands based on estimates from the GLMM. Raw data for the invasive and native lineages included

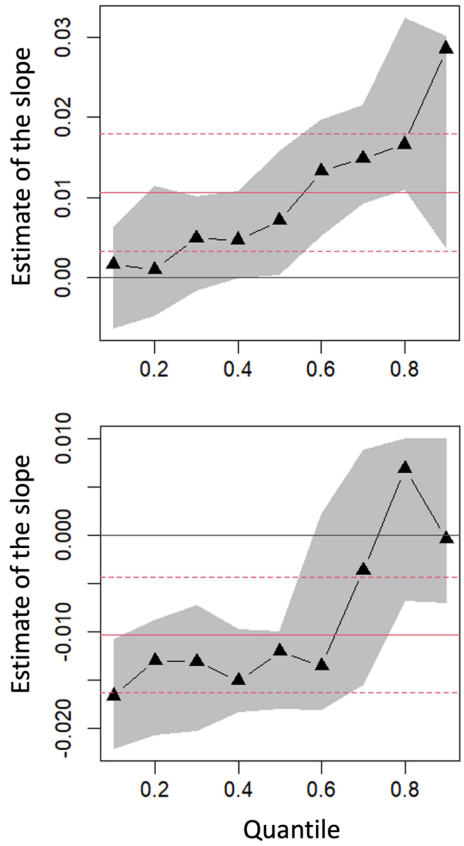

Fig. 5 ClimPCTemp for the European lineage in its native and invasive range. Each black dot is the slope for the quantile indicated on the x axis and grey bands are 95% confidence intervals. Solid red line is the least-squares estimate of the slope and the dashed red lines are the 95% confidence intervals

quantile regression results can be found in the supplementary materials.

Cx-value and climate—native lineages in Europe versus North America

North American, European and Northern Africa populations of native *P. australis* are widely distributed. MEM revealed one important spatial filter separating North America from Europe (SI 5)—North American native plants have a Cx-value 11% larger than European natives (0.55 ± 0.001 and 0.49 ± 0.001; mean ± SE; SI 1, $P < 0.001$). Cx-value was also strongly influenced by ClimPCDry and continent × ClimPCDry interaction (SI 2, Fig. 3). For North American native plants, Cx-values decreased from 0.562 to 0.546 (2.8%) across the range of ClimPCDry (least-squares regression: $R^2 = 0.15$, $P < 0.001$), whereas for the European/northern African plants, Cx-value exhibited no significant change across the range of ClimPCDry ($R^2 = 0.003$, $P = 0.109$; Fig. 3). For both lineages, the slopes of relationships between ClimPCDry and Cx-value did not change depending on Cx-value quantile (SI 5c). Overall, fixed effects in the model explained 85% of Cx-value variation.

Cx-value and climate—distribution of North American native and invasive lineages

Native and invasive *P. australis* lineages broadly overlap over much of the contiguous United States and southern Canada whereas the Gulf lineage inhabits the Gulf of Mexico and southwestern states. Focusing only on the widely distributed and overlapping native and invasive *P. australis* lineages, we found that Cx-value was strongly affected by lineage and ClimPCDry and the lineage × ClimPCDry interaction (SI 2, Fig. 5). One spatial filter was included

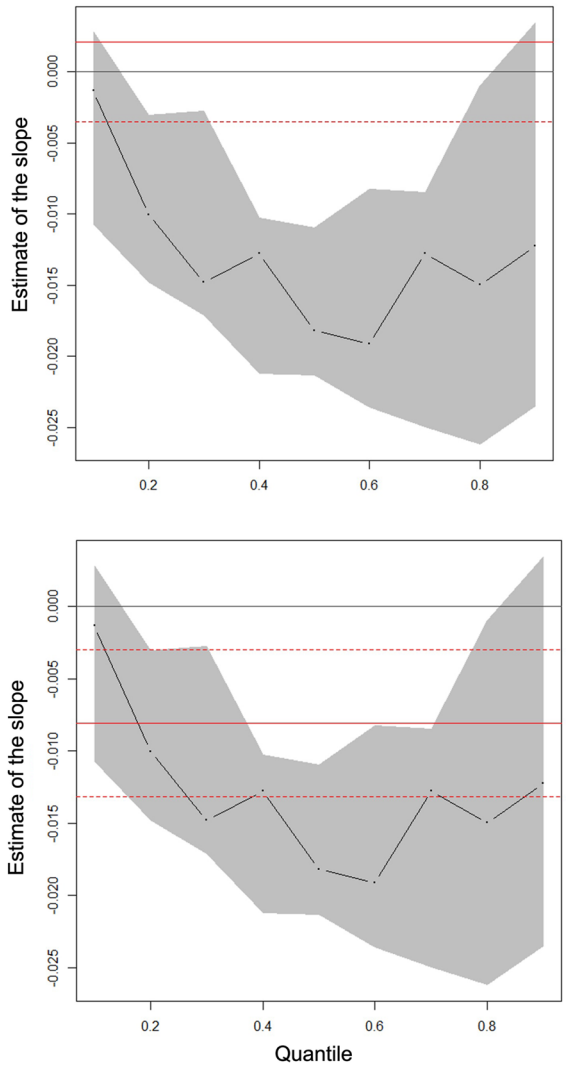

Fig. 6 ClimPCWet for the European lineage in its native and invasive range. Each black dot is the slope for the quantile indicated on the x axis and grey bands are 95% confidence intervals. Solid red line is the least-squares estimate of the slope and the dashed red lines are the 95% confidence intervals

as a random effect in the GLMM (SI 3b). Cx-values for the native lineage decreased from 0.563 to 0.545 (3.2% change) as rainfall during drought periods increased. In contrast, Cx-values for the invasive lineage increased very little, from 0.512 to 0.515 (a 0.5% change) over the same range of precipitation during dry periods. Focusing on each lineage separately, we found no evidence that slopes of the relationship between ClimPCDry and Cx-value changed significantly for different quantiles of the Cx-values (SI 5d).

Overall, Cx-value variance was mostly explained by the model's fixed factors (marginal $R^2 = 0.69$). Variance explained by the full model only slightly increased when considering both fixed and random effects (conditional $R^2 = 0.74$). The one spatial filter included in the model represented regional structure in the data (SI 4b).

Discussion

Using the most comprehensive intraspecific genome size database that we know of for any single plant species, we demonstrated relationships between Cx-value spatial distribution and climate. Our initials analyses were at the global scale and ignored continent and lineage to reveal patterns at a global scale *Phragmites australis* genome size. Subsequent analyses were narrowed to focus in on cross-continent and lineage analyses. We found that Cx-variants significantly (though weakly) covary with climate which suggests genome size is likely a key trait for predicting plant range shifts. We identified important relationships between Cx-values and three climate variables – temperature (ClimPCTemp), precipitation during the warm/ wet season (ClimPCWet), and precipitation during the dry season (ClimPCDry). Both ClimPCTemp and ClimPCDry reflect stressful conditions when high values represent very high temperatures, aridity and/or drought, whereas conditions under ClimPCWet are mesic unless scores are very low indicating drought during the wet period. While bioclimatic variables at the global scale explained little variation in global-scale Cx-values (Fig. 1), the importance of climate variables emerged as key factors explaining Cx-value variation in the higher resolution analysis focused on North America and Europe where most our samples originated. This result supports the large genome constraint hypothesis by suggesting plants with larger genomes are less likely to be found in very hot and/or droughty environments. Overall, our results suggest that genome size variability may confer greater functional flexibility that increases fitness and facilitates adaption to a wider range of competitive and abiotic conditions (Levin 2002). However, despite weak overall fits to the relationship between Cx-value and climate, such a coarse analysis isn't effective at identifying what's happening at the extreme ends of the genome size spectrum.

Cx-values and climate

Natural conditions often impose multiple interacting stressors and understanding how coincident stressors affect fitness is critical to predicting how plants will redistribute under global change (Mittler 2006), i.e., the imposition of a single experimental stressor might not predict actual plant responses in the field (Suzuki et al. 2014). We used global scale bioclimatic variables to test how simultaneous stressors (high temperature and drought) interact with monoploid genome size (Cx-value). We began with 19 bioclimatic variables (Hijmans et al. 2005; Dupin et al. 2011), ultimately using three PCAs based on temperature and precipitation which explained most of the variation. These two variables are critically important in determining how species distributions and range shifts under climate change are diverging from historical patterns (Trenberth 2011). Because genome size influences physiological relationships between cells and whole plants via plant tolerance to stressors (Roddy et al. 2020), it is a key driver of plant invasion success, setting range limits in response to climate change including in regions where dryland climates are expanding (Chen and Chen 2013; Koutroulis 2019).

Are relationships between Cx-values and climate the same in native and introduced ranges?

Temperature

We found weak but significant relationships between temperature and Cx-values for the European lineage in both its native (Europe) and introduced (NA) ranges, and the native North American lineage. The European native Cx-value rose as temperature increased, but the invasive European lineage in North America had an inverse relationship with temperature (Fig. 2a). Though seemingly paradoxical because European populations in both the native and introduced ranges are derived from the same source, the average introduced European Cx-value in North America (0.51 pg) is smaller than the average Cx-value of the European lineage in its native range (0.49 pg). One possibility is that at higher temperatures and regardless of range, the most advantageous or "optimum" genome size (sensu Garcia et al. 2008; Šmarda et al. 2008) for the European lineage lies between the averages for native populations in Europe and invasive populations in North America thereby explaining our result. If an optimum genome size exists for *P. australis*, it is likely constrained by the distinct average genome sizes that have evolved for each lineage (i.e., larger North America native, smaller European native and invasive), but within that constraint, an optimum may exist that increases fitness. Interestingly, the invasive European lineage underwent a bioclimatic niche shift in North America to habitat with temperature fluctuations absent in its native European niche (Guo et al. 2018), a potential explanation for the different relationships of genome size to high temperature found on the two continents. Under this scenario, selection would be exerted by temperature peaks, i.e., unstable, extreme conditions under which small genome plants grow more quickly gaining a greater chance to mature and reproduce despite adverse conditions.

Conversely, using quantile regression to examine the relationship more closely between Cx-value and temperature, we found a negative relationship across most quantiles for the EU lineage in its invasive range, but a positive relationship for all quantiles for EU in its native range. found a negative relationship, regardless of quantile, suggesting that Cx-values decrease as temperature rises. Furthermore, plants in lower quantiles showed an even steeper relationship, i.e., there was a much stronger effect of temperature on smaller Cx-values (Fig. 5). Relative to the whole data set, our results demonstrate a significant relationship between genome size and temperature that is particularly clear for the native European lineage in Europe and the invasive lineage North America likely because most samples these comprised most of our samples.

Precipitation during warm/wet season

The European lineage in Europe and the invasive in North America had relationships to precipitation similar to those for temperature during the growing season (Fig. 2b, ClimPCWet, $P = 0.014$, precipitation during warm/wet season). Relative to arid/drought during the dry season (ClimPCDry), these conditions are mesic and no relationship between Cx-value and ClimPCWet is expected. As precipitation increased in Europe, larger Cx-values became more prevalent,

whereas in North America, smaller Cx-values became more predominant.

Precipitation during the dry season/drought

Our results support the large genome constraint hypothesis (LGCH). Under high temperatures with unlimited water, plants can be highly productive aboveground (Packer et al. 2017) by increasing transpiration to cool leaves and ameliorate heat stress but are less productive under high heat droughty conditions (Rizhsky et al. 2004; Suzuki et al. 2014). The smallest Cx-values are more prevalent where arid or drought conditions exist and salinity often becomes the dominant stressor (Sieben 2019), further supporting LGCH. Interestingly, when we analysed only native and invasive populations in North America, we found that Cx-values decreased for the NA native but increased for the European invasive with worsening drought (Fig. 4), again raising the possibility of an optimal genome size with respect to water availability under drought stress. It also suggests that the invasion potential of the smaller genome European invasive *P. australis* in North America may not be limited by increasing drought, whereas the larger genome North American native may be constrained by drought thereby conferring another advantage to small genome populations that could increase their prevalence.

Given that *P. australis* is a wetland plant, it is unsurprising that drought is an important determinant of genome size prevalence — ClimPCTemp and ClimPCDry reflected the strongest stress gradients relative to ClimPCWet. However, when we compared native and introduced lineages in North America, Cx-values were significantly smaller for the native lineage under drier conditions, but not for the invasive lineage (SI 5d). Further experiments on interactions between Cx-value, fitness, and water stress would illuminate this relationship.

The duration, intensity and frequency of droughts and record-breaking high temperatures are increasing (IPCC 2014). Within evolutionary constraints, we found that plants with smaller genomes have the potential to become more prevalent as regions become hotter and drier. A genome size-based redistribution of plant populations could influence top down species interactions via herbivory and changing plant chemistry across genome sizes (Meyerson et al. 2016) and through bottom up microbial communities processes associated with plant lineages or genome size (Bowen et al. 2017). One recent study found that plastic responses were most important for *P. australis* under heat and salinity stress and were associated with smaller plant genomes (Meyerson et al. 2020). Another recent study (Guo et al. 2023) found that in North America, the invasive lineage of *P. australis* (smaller genome size) was more stress adapted than the native lineage (larger genome size). Quantifying trait responses to emerging stress gradients informs predictions on how communities and ecosystem functions are influenced by population establishment and extinction as some population ranges expand and others contract (van der Putten 2012). How will population-level intraspecific variation, including genome size, drive plant species responses to environmental change (Franklin et al. 2016)? Our results and other research suggest plants respond differently to abiotic stressors such as drought and heat than to a single stressor and highlight the need for more empirical research using different stressor combinations associated with climate change on multiple cytotypes and more species.

Acknowledgements This paper is written in memory of Professor Jan Suda who worked with the authors to develop the ideas and analyze samples in this manuscript. We thank all technicians and gardeners who helped duplicate the Aarhus *Phragmites* living collection for this study. We also thank the associate editor that handled this manuscript and anonymous reviewers of this manuscript. LAM and JTC were supported by National Science Foundation DEB Awards 1049914 and 1050084. Additional funding to LAM was provided by the Fulbright Commission of the United States and the Czech Republic, and the University of Rhode Island College of Environment and Life Sciences Agricultural Experiment Station Project RI00H-332, 311000-6044 and to JTC by USDA-APHIS Grant APP-6585. PP and JP were supported by EXPRO Grant No. 19-28807X (Czech Science Foundation), PP, JP, JČ, JW, and ML by long-term research development project RVO 67985939 (Czech Academy of Sciences).

Funding Funding was provided to LAMand JTC by National Science Foundation DEB Awards 1049914 and 1050084. Additional funding to LAM was provided by the Fulbright Commission of the United States and the Czech Republic, and the University of Rhode Island College of Environment and Life Sciences Agricultural Experiment Station Project RI00H-332, 311000-6044.

Data availability Data has been deposited in Dryad (https://doi.org/10.5061/dryad.6t1g1jx1d) and will be made publicly available upon acceptance of this manuscript.

Declarations

Competing interests The authors have no competing interests.

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

References

Anderson JT (2016) Plant fitness in a rapidly changing world. New Phytol 210:81–87

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Bennett MD, Leitch IJ (2005) Genome size evolution in plants. In: Gregory T (ed) The evolution of the genome. Elsevier, San Diego, pp 89–162

Bennett MD, Leitch IJ, Hanson L (1998) DNA amounts in two samples of angiosperm weeds. Ann Bot 82:121–134

Bhattarai GP, Meyerson LA, Anderson J, Cummings D, Allen WJ, Cronin J (2016) Biogeography of a plant invasion: genetic variation and plasticity in latitudinal clines for traits related to herbivory. Ecol Monogr 87:57–75. https://doi.org/10.1002/ecm.1233

Bowen JL, Kearns PJ, Byrnes JEK, Wigginton S, Allen WJ, Greenwood M, Tran K, Yu J, Cronin JT, Meyerson LA (2017) Lineage overwhelms environmental conditions in determining rhizosphere bacterial community structure in a cosmopolitan invasive plant. Nat Commun 8:433

Carta A, Peruzzi L (2016) Testing the large genome constraint hypothesis: plant traits, habitat and climate seasonality in Liliaceae. New Phytol 210:709–716

Chambers RM, Meyerson LA, Saltonstall K (1999) Expansion of *Phragmites australis* into tidal wetlands of North America. Aquat Bot 64:261–273

Cronin JT, Bhattarai GP, Allen WJ, Meyerson LA (2015) Biogeography of a plant invasion: plant-herbivore interactions. Ecology. https://doi.org/10.1890/14-1091.1

Dolezel J, Greilhuber J, Suda J (2007) Estimation of nuclear DNA content in plants using flow cytometry. Nat Protoc 2:2233–2244

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Model 196:483–493

Dupin M, Reynaud P, Jarošík V, Baker R, Brunel S, Eyre D, Pergl J, Makowski D (2011) Effects of the training dataset characteristics on the performance of nine species distribution models: application to diabrotica virgifera virgifera. PLoS ONE 6:e20957

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315

Franklin J, Serra-Diaz JM, Syphard AD, Regan HM (2016) Global change and terrestrial plant community dynamics. Proc Natl Acad Sci 113:3725–3734

Garcia S, Canela MÁ, Garnatje T, McArthur ED, Pellicer J, Sanderson SC, VallÈS J (2008) Evolutionary and ecological implications of genome size in the North American endemic sagebrushes and allies (Artemisia, Asteraceae). Biol J Lin Soc 94:631–649

Gomes SSL, Vidal JD, Neves CS, Zorzatto C, Campacci TVS, Lima AK, Koehler S, Viccini LF (2018) Genome size and climate segregation suggest distinct colonization histories of an orchid species from Neotropical high-elevation rocky complexes. Biol J Lin Soc 124:456–465

Griffith DA, Peres-Neto PR (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. Ecology 87:2603–2613

Guo W-Y, Lambertini C, Pyšek P, Meyerson LA, Brix H (2018) Living in two worlds: evolutionary mechanisms act differently in the native and introduced ranges of an invasive plant. Ecol Evol 8:2440–2452

Guo W-Y, Čuda J, Skálová H, Lučanová M, Lambertini C, Pierce S, Brix H, Meyerson LA, Pyšek P (2023) In Revision. Genome size and climate shape the intraspecific variation in ecological adaptive strategies of a cosmopolitan grass species. Oecologia

Heckley AM, Pearce AE, Gotanda KM, Hendry AP, Oke KB (2022) Compiling forty years of guppy research to investigate the factors contributing to (non)parallel evolution. J Evol Biol 35:1414–1431. https://doi.org/10.1111/jeb.14086

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva

Knight CA, Molinari NA, Petrov DA (2005) The large genome constraint hypothesis: evolution, ecology and phenotype. Ann Bot 95:177–190

Koutroulis AG (2019) Dryland changes under different levels of global warming. Sci Tot Environ 655:482–511

Lambertini C, Gustafsson MHG, Frydenberg J, Lissner J, Speranza M, Brix H (2006) A phylogeographic study of the cosmopolitan genus Phragmites (Poaceae) based on AFLPs. Plant Syst Evol 258:161–182

Lambertini C, Gustafsson MHG, Frydenberg J, Speranza M, Brix H (2008) Genetic diversity patterns in *Phragmites australis* at the population, regional and continental scales. Aquat Bot 88:160–170

Leitch IJ, Leitch AR (2013) Genome size diversity and evolution in land plants. In: Greilhuber J, Dolezel J, Wendel J (eds) Plant genome diversity, vol 2. Springer, Vienna. https://doi.org/10.1007/978-3-7091-1160-4_19

Levin DA (2002) The role of chromosomal change in plant evolution. Oxford University Press, Oxford

Liu M, Pan Y, Pan X, Sosa A, Blumenthal DM, Van Kleunen M, Li B (2021) Plant invasion alters latitudinal pattern of plant-defense syndromes. Ecology 102(12):e03511. https://doi.org/10.1002/ecy.3511

Lynch M, Marinov GK (2015) The bioenergetic costs of a gene. Proc Natl Acad Sci 112:15690

Meyerson LA, Cronin JT, Bhattarai GP, Brix H, Lambertini C, Lučanová M, Rinehart S, Suda J, Pyšek P (2016) Do ploidy level and nuclear genome size and latitude of origin modify the expression of *Phragmites australis* traits and interactions with herbivores? Biol Invasions 18:2531–2549

Meyerson LA, Pyšek P, Lučanová M, Wigginton S, Tran C-T, Cronin JT (2020) Plant genome size influences stress tolerance of invasive and native plants via plasticity. Ecosphere 11:e03145

Mittler R (2006) Abiotic stress, the field environment and stress combination. Trends Plant Sci 11:15–19

Murakami D, Griffith DA (2015) Random effects specifications in eigenvector spatial filtering: a simulation study. J Geogr Syst 17:311–331

Nakagawa S, Schielzeth H (2012) The mean strikes back: mean-variance relationships and heteroscedasticity. Trends Ecol Evol 27:474–475

Ohri D (2005) Climate and growth form: the consequences for genome size in plants. Plant Biol 7:449–458

Oke KB, Motivans E, Quinn TP, Hendry AP (2019) Sexual dimorphism modifies habitat-associated divergence: evidence from beach and creek breeding sockeye salmon. J Evol Biol 32:227–242. https://doi.org/10.1111/jeb.13407

Packer JG, Meyerson LA, Skálová H, Pyšek P, Kueffer C (2017) Biological Flora of the British Isles: *Phragmites australis*. J Ecol 105:1123–1162

Petrov DA (2001) Evolution of genome size: new approaches to an old problem. Trend Genet 17:23–28

Pyšek P, Skalova H, Čuda J, Guo W, Doležal J, Kauzal O, Lambertini C, Pyšková K, Brix H, Meyerson L (2019) Physiology of a plant invasion: biomass production, growth and tissue chemistry of invasive and native *Phragmites australis* populations. Preslia 91:51–75

Pyšek P, Skálová H, Čuda J, Guo W-Y, Suda J, Doležal J, Kauzál O, Lambertini C, Lučanová M, Moravcová L, Pyškova K, Meyerson L (2018) Small genome separates native and invasive populations in an ecologically important cosmopolitan grass. Ecology 99:79–90

Pyšek P, Lučanová M, Dawson W, Essl F, Kreft H, Leitch I, Maurel N, Meyerson LA, Pergl J, van Kleunen M, Weigelt P, Winter M, Guo W-Y (2023) Small genome size and variation in ploidy levels support the naturalization of vascular plants but constrain their invasive spread. New Phytol 239:2389–2403. https://doi.org/10.1111/nph.19135

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

Rizhsky L, Liang H, Shuman J, Shulaev V, Davletova S, Mittler R (2004) When defense pathways collide. The response of arabidopsis to a combination of drought and heat stress. Plant Physiol 134:1683

Roddy AB, Théroux-Rancourt G, Abbo T, Benedetti JW, Brodersen CR, Castro M, Castro S, Gilbride AB, Jensen B, Jiang G-F, Perkins JA, Perkins SD, Loureiro J, Syed Z, Thompson RA, Kuebbing SE, Simonin KA (2020) The scaling of genome size and cell size limits maximum rates of photosynthesis with implications for ecological strategies. Int J Plant Sci 181:75–87

Saltonstall K (2016) The naming of Phragmites haplotypes. Biol Invasions 18:2433–2441. https://doi.org/10.1007/s10530-016-1192-4

Saltonstall K (2002) Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proc Natl Acad Sci USA 99:2445–2449

Sieben EJJ (2019) Zonal and azonal vegetation revisited: How is wetland vegetation distributed across different zonobiomes. Austral Ecol 44:449–460. https://doi.org/10.1111/aec.12679

Šmarda P, Bureš P, Horová L, Rotreklová O (2008) Intrapopulation genome size dynamics in *Festuca pallens*. Ann Bot 102:599–607

Suda J, Meyerson LA, Leitch IJ, Pyšek P (2015) The hidden side of plant invasions: the role of genome size. New Phytol 205:994–1007

Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R (2014) Abiotic and biotic stress combinations. New Phytol 203:32–43

Team RC (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Thompson JN, Merg KF (2008) Evolution of polyploidy and the diversification of plant-pollinator interactions. Ecology 89:2197–2206

Trenberth KE (2011) Changes in precipitation with climate change. Climate Res 47:123–138

van der Putten WH (2012) Climate change, aboveground-belowground interactions, and species' range shifts. In: Futuyma DJ (ed) Annual review of ecology, evolution, and systematics, vol 43, pp 365–383

Yang Y, Liu M, Pan Y, Huang H, Pan X, Sosa A, Hou Y, Zhu Z, Li B (2021) Rapid evolution of latitudinal clines in growth and defence of an invasive weed. New Phytol 230:845–856. https://doi.org/10.1111/nph.17193

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