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ORIGINAL ARTICLE

Links of ploidy with other traits and distributions of non-native plants in North America

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• **Background and Aim** Polyploidization is becoming an increasingly important subject in ecology and invasion biology. To date, the role of polyploidy in the success of species invasions remains unclear. Here, we explore the associations between ploidy levels and seed size, reproductive mode, life form, time after introduction and range size of non-native plants introduced to North America, and whether polyploidization is related to invasion success.
• **Methods** Using data on 1804 non-native plant species in continental North America with information on chromosome numbers, we conducted comparative, correlation and regression analyses to investigate the possible links among ploidy level, multiple life-history traits and geographical distribution.
• **Key Results** Among the 1804 species, 54 % were polyploids. The proportion of plants with three or more levels of ploidy was much higher in herbaceous species than in woody species. Species in aquatic, forb and graminoid forms had higher proportions of species that exhibit multiple ploidy levels than trees and shrubs. Range size was also positively related to levels of ploidy. We also observed clear differences in seed size among ploidy levels, but no correlation between chromosome number and seed size.
• **Conclusions** Our findings demonstrate that: (1) polyploidy is linked to other life-history traits at varying degrees or intensities; and (2) the level of ploidy appears to be important in regulating plant traits and distribution. The relationships of levels of ploidy to other traits and range size are useful in predicting species invasiveness and spread potential. Our findings thus have strong implications for invasion biology and management.

Key words: Chromosome number, life-history trait, growth form, polyploidy, species invasion.

INTRODUCTION

Chromosome number and level of ploidy, which vary significantly among species, especially plants, are being increasingly recognized as a key characteristic of species (Hijmans *et al.*, 2007; Ramsey and Ramsey, 2014; Rice *et al.*, 2015; Soltis *et al.*, 2016). Changes in chromosome numbers regularly serve as an indication of major genomic events, most notably polyploidy and dysploidy (Carta *et al.*, 2022). Polyploidy is a result of the acquisition of one or more complete chromosome sets to the genome or whole genome duplication, a process called polyploidization (te Beest *et al.*, 2012; Soltis *et al.*, 2016; Van de Peer *et al.*, 2017; Rice *et al.*, 2019). Some polyploid species exhibit autopolyploidy, formed through identical or duplicated genomes from a single species, whereas many others exhibit allopolyploidy, formed through hybridization among closely related species (Soltis *et al.*, 2016). Thus, a polyploid species means that it has multiple sets of chromosomes, leading to a higher overall chromosome count.

Polyploidy has also been linked with speciation and divergence rate (Wood *et al.*, 2009; Van de Peer *et al.*, 2017). Many studies have found that polyploidization is responsible for many successful plant invasions because it leads to many advantages, such as increased genetic diversity, larger cell size and enhanced tolerance to environmental stresses (Pyšek *et al.*, 2023). For example, polyploid species usually have higher within-species diversity and greater plasticity (Pyšek *et al.*, 2023) and are more resistant to environmental stresses and diseases (Comai, 2005).

Many life-history traits of plants, such as seed size, leaf size, reproductive modes and life forms, are related to one another, and some are strongly linked to species invasiveness (e.g. Rejmánek and Richardson, 1996; Pyšek, 1998;

Ricklefs *et al.*, 2008; Nunez-Mir *et al.*, 2019). Specifically, increasing evidence suggests that a high level of ploidy might be a contributing factor to species invasiveness, thereby influencing their spread (Pandit *et al.*, 2011; Pyšek *et al.*, 2023). Additionally, earlier studies have shown that polyploid plants are more successful in disturbed habitats and fluctuating environments, in addition to colder or drier places (e.g. temperature at higher latitudes or elevations and disturbances; te Beest *et al.*, 2012).

Knowing whether and how a species trait, such as ploidy level, is related to other traits (e.g. seed size), distribution and associated abiotic factors (e.g. climate) is crucial for predicting species invasiveness and future spread. Although some studies have linked polyploidy or levels of ploidy to some other traits, such as life form or growth form, and distribution (Rice *et al.*, 2019), it is important to note that species in a flora can be classified into various categories using different traits. Understandably, different plant categories exist primarily owing to data availability or special interests. However, different classifications can have varying meanings and sometimes yield highly useful results for both basic ecology and management. For example, most living plants can be classified into C_3, C_4 and Crassulacean acid metabolism (CAM) plants, based on their photosynthetic pathways (Guo *et al.*, 2026). Based on reproductive mode, however, plants can be categorized into sexual, asexual and both sexual/asexual species. Furthermore, some traits are easier to measure or quantify than others. For these reasons, including more traits to examine their possible correlations and interactions, when possible, would be more desirable (Küster *et al.*, 2008).

Although the role of polyploidy has been recognized as an important trait regarding speciation, invasiveness and distribution (te Beest *et al.*, 2012; Rice *et al.*, 2019), the reasons behind it are still far from being fully realized. First, it is unclear how frequently and to what extent polyploidy is linked to other plant traits. Second, information is lacking regarding the degree to which the ploidy level of a species affects its performance and invasiveness (Moura *et al.*, 2021; Pyšek *et al.*, 2023). Third, whether species exhibiting different ploidy levels also show similar (latitudinal) distribution and climate space use between native regions and non-native regions remains elusive. To date, the vast majority of related studies have focused on individual species (or small species groups), and the results vary and are often taxon or region specific (Treier *et al.*, 2009; Green *et al.*, 2013; Wan *et al.*, 2020; Moura *et al.*, 2021).

In this study, we use all 1804 non-native seed plant species introduced to continental North America (NAM; the USA and Canada) that have chromosome data to test the following hypotheses: (1) the level of ploidy varies across plant life and growth forms (e.g. herbaceous vs. woody species, evergreen vs. deciduous, graminoids vs. forbs) and reproductive modes (i.e. sexual, asexual or both); (2) the level of ploidy affects species performance, and species invasiveness measured by range size increases with the level of ploidy; and (3) species exhibiting different ploidy levels also show different levels of match/mismatch in distribution and climate-space use between native regions and non-native regions in NAM. We focus on NAM because this region has one of the largest numbers (and fractions) of naturalized non-native plants, and related data are relatively more complete than in many other world regions (Pyšek *et al.*, 2017).

MATERIALS AND METHODS

Among the >2441 non-native vascular plant species naturalized in continental North America (hereafter, NAM), we were able to collect data on chromosome numbers (based on direct counts) for 1822 species. We then removed fern species ($N = 18$), because the role of polyploidy in ferns is different from the role in seed plants, and classified the 1804 species of seed plants into three ploidy levels based on the number of chromosome sets ($2n$) that had been reported, i.e. one, two and three or more sets corresponding to levels I, II and III, respectively. We did not use the strictly defined 'ploidy level', which usually means diploid vs. tetraploid vs. pentaploid, etc., because this was not always clear based on the originally reported chromosome numbers; however, more sets of chromosome numbers usually indicate higher ploidy levels. The naturalized species in NAM were introduced from the rest of the world to the USA and Canada; that is, they were all considered 'foreign' (Pyšek *et al.*, 2004; Pyšek, 2011). We included all species with three or more sets of chromosomes in level III for statistical purposes and to facilitate meaningful comparisons, because the number of species with more than three sets of chromosomes was very small.

To examine how ploidy level might be linked with other life-history traits and distribution, we compiled and collated the life-history data from numerous sources, including literature, online traits databases (https://plants.usda.gov/home and http://ccdb.tau.ac.il/ The Chromosome Counts Database: CCDB, version web/CCDB_1.66.6), regional floras such as the Flora of North America (Flora of North America Editorial Committee, 1993) and the Centre for Agriculture and Bioscience International (CABI), with more comprehensive life-history data for >2441 species (for additional data sources, see also the Supplementary Data). We then classified the 1804 species into different categories according to: (1) life form (herbaceous vs. woody); (2) leaf duration (evergreen vs. deciduous); (3) growth form (aquatic, forb, graminoid, subshrub, shrub, tree and vine/liana); and (4) reproductive mode (sexual vs. asexual vs. both).

To investigate whether the number of ploidy levels is constrained by the phylogenetic relationships of species, we used Pagel's λ (Pagel, 1999) to assess whether there is a significant phylogenetic signal in the number of ploidy levels, using the function phylosig in the package phytools (Kembel *et al.*, 2010). A value of zero indicates no phylogenetic signal in the number of ploidy levels across the phylogeny, whereas a value of one indicates a strong phylogenetic signal, which matches expectations under the Brownian motion model. We used the megatree 'GBOTB.extended.WCVP.tre' as a backbone and the functions build.nodes.1 and Scenario 3 in the package U.PhyloMaker (Jin and Qian, 2023) to add species to the megatree, and we pruned the resulting phylogeny to retain only the 1804 species examined in this study.

The distribution data (e.g. latitude and range size data in both native regions and NAM) of these species were obtained from van Kleunen *et al.* (2019) and the World Checklist of Vascular Plants (Brown *et al.*, 2023). The operational geographical units (following the Global Administrative Areas Database; http://www.gadm.org/) used to document species distributions are geographical

units at level 3 of the scheme of the International Working Group on Taxonomic Databases for Plant Sciences (Brummitt, 2001). Oceanic islands and Antarctica were excluded. We used the package U.Taxonstand (Zhang and Qian, 2023; Zhang *et al.*, 2025) to standardize botanical nomenclature according to the World Checklist of Vascular Plants. Native and non-native range sizes of each species were estimated according to the operational geographical units where the species was present (i.e. the total area of the operational geographical units in which the species occurred in either case).

To test whether the non-native species at the three levels of ploidy were occupying similar climate space between the native regions and NAM and among the three ploidy levels, we acquired climate data [bio1 and bio12 for mean annual temperature (MAT) and mean annual precipitation (MAP), respectively] from the CHELSA climate database (https://chelsa-climate.org) (Karger *et al.*, 2017). We chose these two key variables because they are fundamental and most influential in determining the distributions of plants, and they are the sole variables used to delineate biomes. We calculated the average value of either climatic variable based on all pixels at the 30-arc-second resolution located within the distributional range of a species within each geographical region defined by van Kleunen *et al.* (2019).

All comparisons (e.g. seed size, range size, latitude and climate) among ploidy levels were initially made using ANOVA, which effectively tested whether there was a significant difference among the means of the three levels. When a significant difference was detected but the data normality test failed, we used Mann–Whitney rank sum tests to pinpoint which specific ploidy levels differ. We conducted phylogenetic regressions, which account for evolutionary relatedness among species, to examine the relationship between ploidy level and range size (Ho and Ané, 2014*a*, *b*). We used the function 'phylolm' in the R package 'phylolm' (Ho and Ané, 2014*a*) to conduct the phylogeny-based models.

RESULTS

Among the 1804 non-native plant species in North America with at least one chromosome number reported, 1174, 348 and 282 species were assigned to ploidy level I, II and III, respectively, based on the number of chromosome sets ($2n$) that had been reported, i.e. one, two and three or more sets. Most species had a small number of chromosomes ($2n$), ranging from 10 to 50 (peak $2n = 14$ and mean $2n = 29$; Supplementary Data Fig. S1).

There was a weak, albeit statistically significant, phylogenetic signal in the distribution of polyploid plants among the 1804 naturalized species in NAM (Pagel's $\lambda = 0.257$, $P < 0.001$). Species with the same level of ploidy tended, to some degree, to be clustered in the phylogeny (Fig. 1).

The proportion of plants with levels of ploidy of three or more was much higher in herbaceous species (28.15 %) than that in woody species (2.96 %) (Table 1), but no significant difference was found among shrubs, subshrubs and trees, and between deciduous and evergreen species (in these cases, *t*-test, $P > 0.05$). Among the seven growth forms and taxonomic groups, aquatic, forb and graminoid had higher proportions of species with two and three levels of ploidy than others, especially trees and shrubs (Fig. 2).

Seed size decreased with increasing number of ploidy levels, i.e. level I > II: $U = 187\,636$, $P = 0.004$; level I > III: $U = 141\,590$, $P < 0.001$; although the difference between ploidy II and III was not significant; Fig. 3A). Species range size also varied significantly among the three ploidy levels in NAM: Mann–Whitney rank sum test: level I vs. II: $U = 250\,251$ ($P < 0.001$); II vs. III: $U = 62\,806$ ($P = 0.018$); I vs. III: $U = 185\,654$ ($P < 0.001$) (Fig. 3B). Similar results were also observed in the native regions of species (Supplementary Data Fig. S2). All the four phylogenetic regression models showed that regression coefficients were positive and statistically significant ($P < 0.001$ in all cases; Table 2), implying that a larger non-native range in North America was associated with a higher level of ploidy. This result was consistent with that based on ANOVA (Fig. 3B).

For species that exhibited all three ploidy levels, the proportion (percentage) of polyploid species with either sexual (37.53 %) or asexual (44.85 %) reproductive mode was much higher than the proportion of polyploid species with both sexual and asexual reproductive modes (17.62 %; Table 3).

In the native regions, the maximum latitudes of species that exhibit multiple ploidy levels were significantly higher than species with fewer ploidy levels (i.e. level II > I: $U = 188\,764$, $P = 0.009$; III > I: $U = 132121$, $P < 0.001$; and III > II, $U = 43346$, $P = 0.007$). However, in all other paired comparisons (Fig. 4A), no difference among the three ploidy levels was detected using the mean and minimum latitudes. Likewise, in the non-native region of NAM, the maximum latitudes of species at levels II and III were significantly higher than the species at level I ($U = 182\,856$, $P = 0.001$ and $U = 139\,138$, $P < 0.001$, respectively, but no difference between levels II and III, $U = 46\,480$, $P = 0.178$). In addition, in all paired comparisons (Fig. 4B), no difference among the three ploidy levels was detected using mean and minimum latitudes.

The mean values of latitudes and longitudes for most species exhibiting multiple ploidy levels were located at higher latitudinal regions, such as Europe and temperate Asia (Supplementary Data Fig. S3, top). However, it is surprising that the mean values of latitudes and longitudes for the species with two and three ploidy levels were generally located in the Midwest of the USA (Supplementary Data Fig. S3, bottom).

Most of the polyploid species among the 1804 species examined here occupied an annual temperature between 5 and 17 °C and a mean precipitation of 400–2500 mm in their native regions. In NAM, however, the 1804 species used a much smaller two-dimensional climate space, and the concentration of these species occupied a similar annual temperature range but a smaller precipitation range (700–1500 mm; Fig. 5A, B). Almost half of the paired comparisons (17 of 36) in maximum, mean and minimum temperature and precipitation showed that the species at the three ploidy levels occupy different climate spaces (envelopes), especially between the species at level I vs. III (10 of 12).

Paired comparisons among species with different levels of ploidy also clearly showed that species with more ploidy levels occupied significantly broader ranges of both MAT

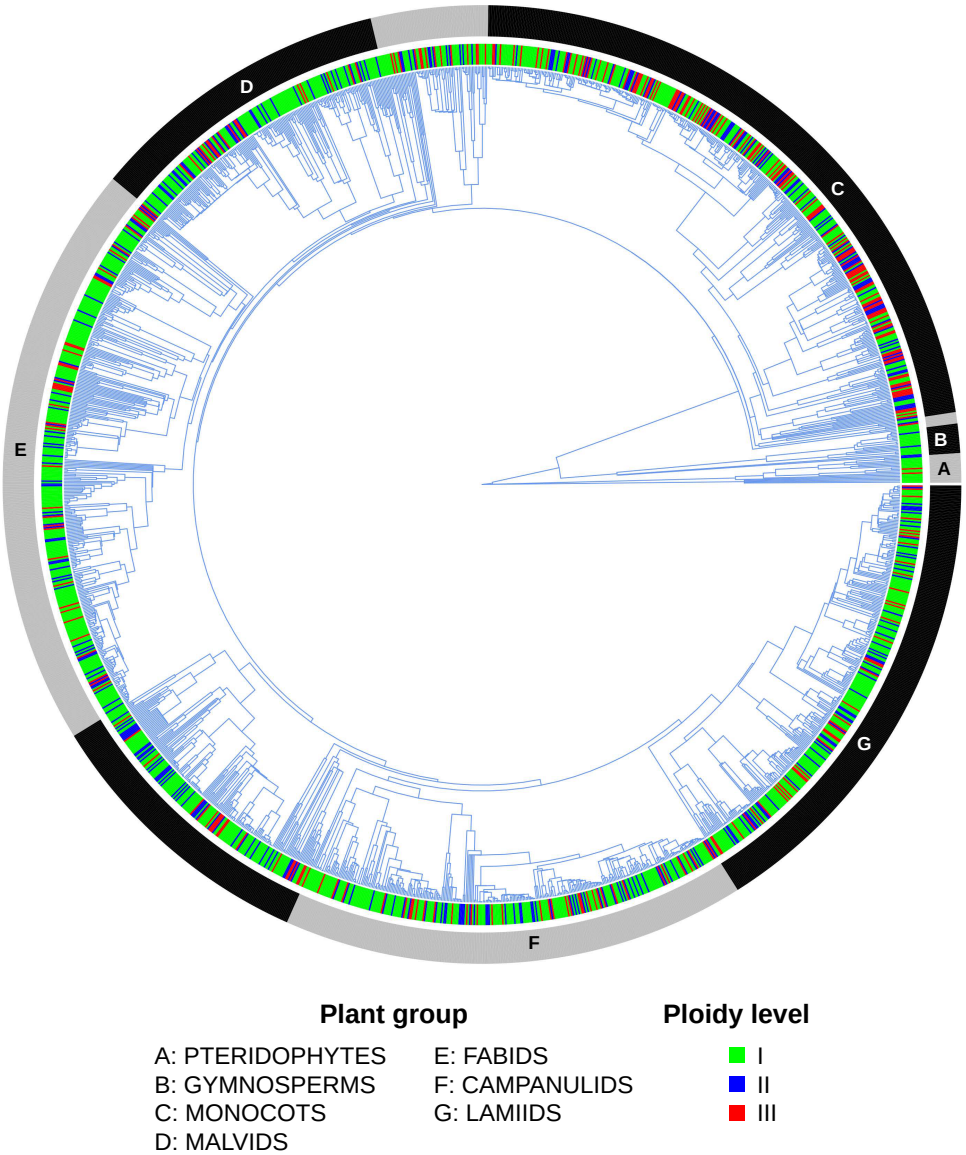

FIG. 1. Distribution of the three ploidy levels and six plant groups across the phylogeny of the 1804 naturalized plant species in North America (NAM). The nine segments along the outermost circle (alternatively marked as black and grey) represent different groups of plants. Six of the nine segments represent named clades of plants (A–F), and the other three are not named clades.

TABLE 1. Contingency table showing the proportion (percentage) of the woody vs. herbaceous species with different numbers of ploidy levels among the non-native plant species in North America.

Growth form	Level of ploidy			
	I	II	III	Total
Herbaceous	31.18	21.32	28.15	**80.65**
Woody	12.23	4.16	2.96	**19.35**
Total	**43.41**	**25.48**	**31.11**	**100.00**

Bold values are the sums of the corresponding rows or columns.

(Fig. 5C, D) and MAP (Fig. 5E, F). Detailed statistical results from these comparisons are given in Supplementary Data Table S1. The maximum and minimum MAT and MAP at all three ploidy levels (I, II and III) were all significantly different between the native regions and NAM (i.e. $P < 0.05$; Fig. 5).

Finally, the time since introduction played an important role in the levels of ploidy, as shown by their positive correlation; that is, the species with longer history since introduction to North America had a greater chance to be polyploid (Mann–Whitney rank sum test: level I vs. II: $U = 169\,392$, $P = 0.138$; level II vs. III: $U = 38\,553$, $P = 0.013$; level I vs. III: $U = 118\,081$, $P < 0.0001$; Fig. 6).

DISCUSSION

Our results clearly support our first two hypotheses, which suggest that the level of ploidy varies across plant growth forms and reproductive modes, and that this variation affects species performance and invasiveness. There are three

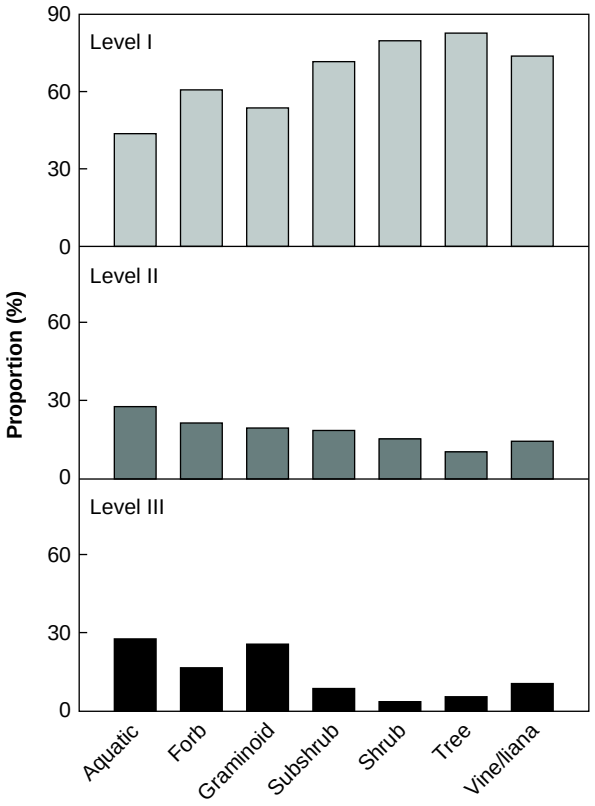

FIG. 2. Proportion (percentage) of the species with different numbers of ploidy levels among the seven growth forms of the non-native plant species in North America.

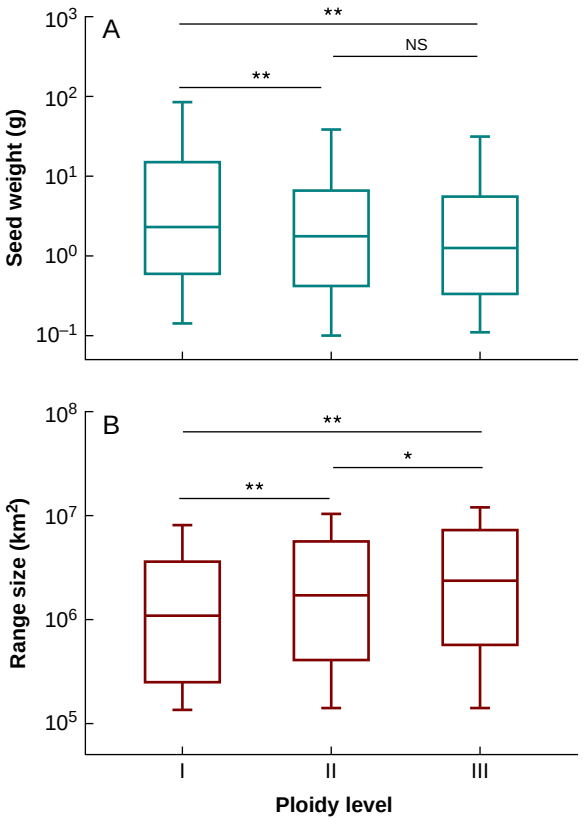

FIG. 3. (A) The differences in seed size (weight, in grams) among the 1804 naturalized seed plant species in North America (NAM) that exhibit different numbers of ploidy levels. Mann–Whitney rank sum test, level I > II: $U = 187\,635$, $P = 0.004$; level I > III: $U = 141\,590$, $P < 0.001$; and the difference between ploidy II and III was not significant (NS). For each box plot, the box represents the 25th and 75th percentiles, with the line in the box being the median, and the whiskers represent the 95 % confidence interval. (B) Comparison of non-native range size in North America (NAM) of the 1804 naturalized seed plant species among the three ploidy levels. Mann–Whitney rank sum test: level I vs. II, $U = 250\,251$, $P < 0.001$; level II vs. III: $U = 62\,806$, $P = 0.018$; level I vs. III: $U = 185\,654$, $P < 0.001$. For each box plot, the box represents the 25th and 75th percentiles, with the line in the box being the median, and the whiskers represent the 95 % confidence interval. *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$.

possibilities about the links between ploidy level and other life-history traits. First, ploidy level regulates species spread, which, in turn, alters the ploidy level (Larkin *et al.*, 2016). Second, an increase in ploidy level can influence life-history variation, such as increased cell size, potential growth rate, enhanced diversity and asexual reproduction, leading to greater adaptive ability, thus increased stress tolerance and resistance (Pyšek *et al.*, 2023). Finally, ploidy level and related life-history traits might change simultaneously owing to possible effects from human disturbance (e.g. land use) and other abiotic drivers, such as climate fluctuation.

Our findings also partly support our third hypothesis that ploidy level indeed plays an important role in the success of species invasions, as shown by species at different ploidy levels that occupy different latitudes and climate niches. For example, species that exhibit multiple ploidy levels show larger range sizes. This holds true even when phylogenetic relatedness among species is accounted for. In addition, the number of ploidy levels is clearly linked to many other life-history traits of the naturalized plants in North America (e.g. Guo *et al.*, 2026). About 54 % of these species are polyploids, much higher than the corresponding figures for the world native floras (33–35 %) reported by Wood *et al.* (2009), Rice *et al.* (2019) and Barker *et al.* (2024). The peak ($2n = 14$) and mean ($2n = 29$) number of chromosomes were highly similar to the reported corresponding figures for world native flora (roughly $2n = 14$–40 in angiosperms, peak $2n = 14$, mean $2n = 28$) by Rice *et al.* (2015) and Guerra (2008).

TABLE 2. Results of regressions of the $\log_{10}$-transformed non-native range size against ploidy level for the 1804 non-native plant species in North America based on four phylogenetic regression models: Pagel's λ (PL) model, Brownian motion (BM) model, Ornstein–Uhlenbeck (OU) model with fixed root, and logistic (LG) model.

Model	Coefficient	Standard error	*t*	*P*-value
PL	0.148	0.0219	6.757	<0.001
BM	0.231	0.0215	10.775	<0.001
OU	0.191	0.0218	8.752	<0.001
LG	0.529	0.0638	8.295	<0.001

The finding that species that exhibit more ploidy levels occupy higher maximum latitudes than other species (e.g. III vs. I) is consistent with other recent studies (Rice *et al.*, 2019). Particularly, species exhibiting three ploidy levels are better adapted to drier and colder regions, in comparison

TABLE 3. Contingency table showing the proportion (percentage) of sexual, asexual (including apomixes) and both reproductive modes among the non-native plant species with different ploidy levels in North America.

Reproductive mode	Level of ploidy			
	I ($N = 230$)	II ($N = 48$)	III ($N = 37$)	Total ($N = 315$)
Sexual only	19.91	8.70	8.92	**37.53**
Asexual only	21.28	10.53	13.04	**44.85**
Both sexual and asexual	11.44	2.75	3.43	**17.62**
Total ($N = 315$)	**52.63**	**21.97**	**25.40**	**100.00**

Bold values are the sums of the corresponding rows or columns.

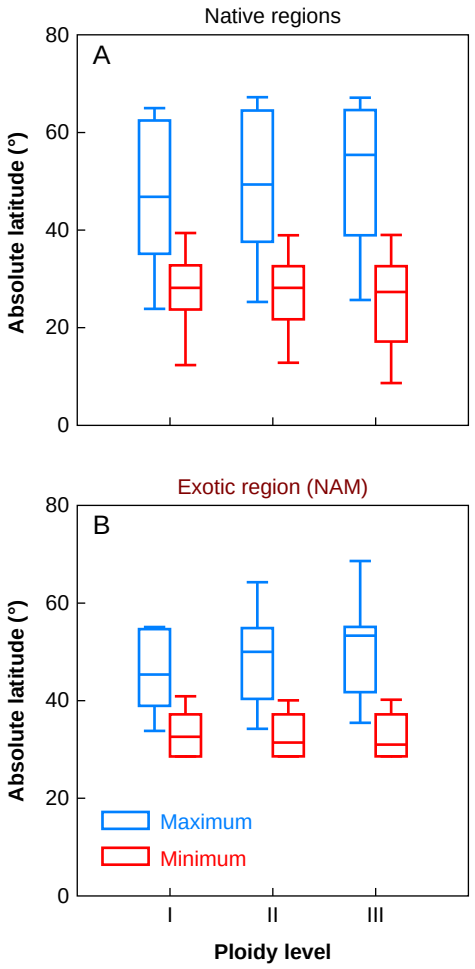

FIG. 4. Comparison of the maximum and minimum absolute latitudinal distribution of the 1804 naturalized seed plant species at the three ploidy levels in both native regions and in non-native regions in North America (NAM). For each box plot, the box represents the 25th and 75th percentiles, with the line in the box being the median, and the whiskers represent the 95 % confidence interval. The maximum latitudes were significantly different across the three ploidy levels, and this is true in both native regions and in non-native regions in NAM.

to species with fewer ploidy levels (especially level I), and could spread to new and harsher ecological niches because of the enhanced species tolerance and resistance to stress (e.g. at higher latitudes) (Chao *et al.*, 2013; Van de Peer *et al.*, 2017). This pattern is mostly attributable to the contribution of perennial herbs that have a slow growth rate and can better tolerate colder conditions at higher elevation or latitude, and most polyploid species are perennial. Also, the mean and minimum latitudes might be less different among different ploidy levels, mostly because the floras in warmer places are mixed with both woody and herbaceous species at all three ploidy levels.

Mean values of latitudes and longitudes for most species that exhibit multiple ploidy levels are located in Europe and temperate Asia (Supplementary Data Fig. S3, top). However, it is surprising that mean values of latitudes and longitudes for the species with two and three ploidy levels are mostly located in the interior lowlands between the eastern Great Plains and western Appalachia of the USA (Supplementary Data Fig. S3, bottom). There are several possible reasons for it. First, this region has a continental climate characterized by great climate fluctuation (cold winters, warm summers, low precipitation and sometimes severe drought). These harsh or disturbed environmental conditions can promote polyploidization that can increase genetic diversity and enhance stress tolerance (Stebbins, 1985; Wan *et al.*, 2020). Second, the retreat of glaciers (deglaciations), deforestation and subsequent agricultural development and associated varying species introduction pathways might have facilitated the polyploidization process in the region (Easterling and Karl, 2001; Turbelin *et al.*, 2022). Third, non-native plants cannot disperse further in the far north of North America partly because of reduced human traffic (Takahashi and Park, 2020). With a history of massive human westward colonization and a larger number of non-native species in the USA than in Canada, a core distribution in the east-central part of the continent could be expected (Guo *et al.*, 2012 ; Klein, 2012). Clearly, more work is needed in the future to understand this pattern better.

We found some, albeit weak, phylogenetic signal in ploidy level, that is, certain taxonomic groups (e.g. families or clades within families) exhibit more ploidy levels than others. This is consistent with earlier findings (Van de Peer *et al.*, 2017; Pyšek *et al.*, 2023). Some life-history traits are strongly related to the number of ploidy levels. For example, relative to woody species that have smaller ranges, the fraction of polyploid species is higher in herbs (19.35 vs. 80.65 %; Table 1), which also have much larger ranges, consistent with the notion that polyploid species spread more efficiently and broadly over space and might also spread faster over time.

Patterns on seed size based on the number of ploidy levels are very clear; that is, species exhibiting more ploidy levels have smaller seeds. The finding of smaller seeds associated with higher ploidy level is consistent with the previous observation that smaller-seeded species have larger distribution ranges (Guo *et al.*, 2000; Qiu *et al.*, 2022). This is particularly apparent, because we observed that species that exhibit multiple ploidy levels have larger ranges (Fig. 3) but smaller seeds (Fig. 3), supporting the notion that polyploidization promotes species invasions (te Beest *et al.*, 2012). Likewise, it also holds true that higher ploidy levels and invasion success are more closely associated with asexual reproduction and species (Kolář *et al.*, 2017; Nunez-Mir *et al.*, 2019).

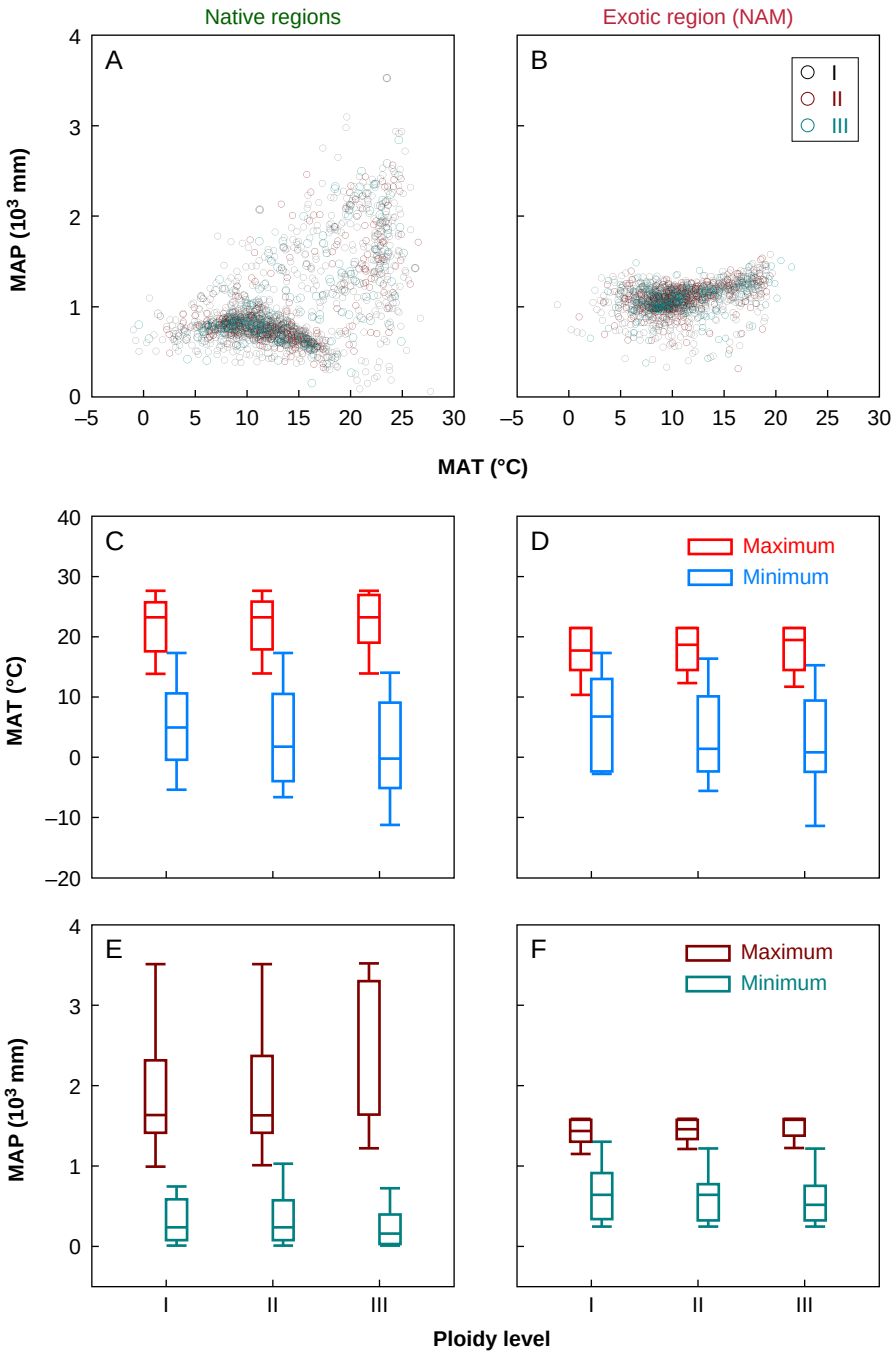

FIG. 5. Top, distribution of the 1804 non-native seed plant species in North America at the three ploidy levels in the two-dimensional space of mean annual temperature (MAT, bio1) and mean annual precipitation (MAP, bio12) in the native regions (A) and in non-native regions across North America (NAM; B). Bottom, comparison in maximum and minimum MAT (C, D) and MAP (E, F) among the three ploidy levels of the 1804 non-native seed plant species in both native regions (C, E) and in NAM (D, F). For each box plot, the box represents the 25th and 75th percentiles, with the line in the box being the median, and the whiskers represent the 95 % confidence interval.

Hybridization between native and non-native species might be one of the factors promoting the overall polyploidization (Alix *et al.*, 2017). It has also, in some ways, homogenized the entire North American flora and those around the world (Qian and Guo, 2010; Qian and Deng, 2023). In the future, it would be very helpful if the number of ploidy levels (and many other traits, such as seed size) could be examined separately and comparatively for native vs. non-native ranges, because it will offer more insights regarding invasion success and further spread potential (Kubátová *et al.*, 2008). The same should also be done for the diploid parents of hybrids (e.g. native × non-native and non-native × non-native congeners that form neo-polyploids) (Guo, 2014).

Consistent with many other studies showing the importance of time since introduction and naturalization (resident time) in invasion biology (Pyšek *et al.*, 2009), we observed that the species with longer history (years) since

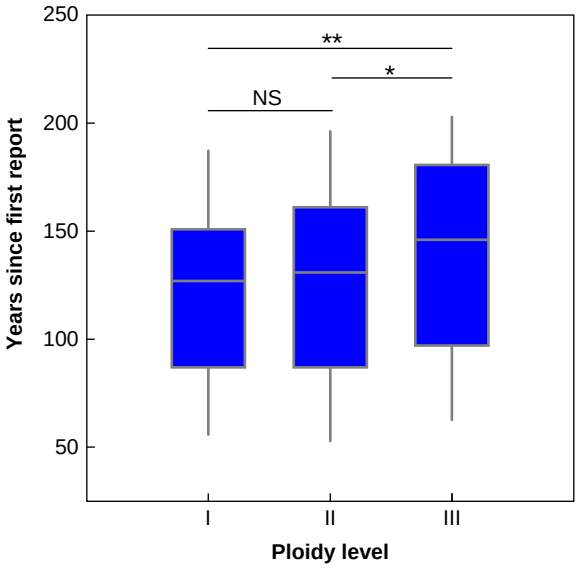

FIG. 6. The species with more levels of ploidy have a longer history (number of years) since the first report in the introduced region, North America (NAM). Mann–Whitney rank sum test: level I ($N = 1100$ species) vs. II ($N = 332$): $U = 169\,392$, $P = 0.138$; level II vs. III ($N = 268$): $U = 38\,553$, $P = 0.013$; level I vs. III: $U = 118\,081$, $P < 0.0001$. For each box plot, the box represents the 25th and 75th percentiles, with the line in the box being the median, and the whiskers represent the 95 % confidence interval. $^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

introduction to North America are more likely to become polyploid. There are three possibilities for this observation. First, polyploid species are indeed formed after the introduction into NAM. Second, some polyploid species were formed in the native regions because they had larger ranges than other species and had a greater chance of being (unintentionally) introduced into NAM earlier. Third, it is also possible that, for whatever reasons, humans might have intentionally introduced species that exhibit multiple ploidy levels earlier than other species. Nevertheless, a more plausible explanation would be the first one; that is, the longer the introduced species have been established, the more chances for the newcomers to explore new habitats and broader environmental conditions, thus becoming polyploid species. Unfortunately, at present, we do not have data to know the answer, especially because, for the vast majority of species, we lack range-wide information about the within-species genetic structure and diversity (e.g. ploidy variations across their geographical ranges). Before such information becomes available from both native and invaded regions, it is difficult to assess the relative contributions of various factors that might be involved.

Given that many species continue to be introduced to non-native regions and more native species and habitats worldwide are increasingly threatened by species invasions, effective conservation depends heavily on how we take early actions to prevent certain species invasions and how to manage invasive species. Knowing what traits might be responsible for species invasiveness and how certain traits are linked to others to predict future invasions is crucial. Our findings with strong implications for basic invasion biology and management could offer more insights into developing future conservation plans. For example, the relationship between ploidy level and range size seems to suggest the importance of polyploidy in its predictability of species invasiveness. This is important, particularly in cases when some traits, such as ploidy information, are relatively easier to achieve than many other traits (Zenil-Ferguson *et al.*, 2017).

Conclusion

The role of polyploidy remains one of the most debated and complex subjects in ecology and biogeography. Overall, our study shows that the level of ploidy appears to be important in determining species invasiveness and spread. It is possible that polyploidy might be related to many more plant traits than previously perceived, but the relationships might vary greatly in different settings (e.g. regions, latitudes) and contexts (e.g. taxonomic groups, natives vs. non-natives). Future studies should further explore the relationships of ploidy level with many other life-history traits and how the relationships are affected by many abiotic factors and human-related disturbances, such as land use, thus advancing our understanding of the role of polyploidy and helping to inform invasion biology and management.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany online* and consist of the following. Figure S1: the frequency distribution of the minimum chromosome number observed for each species among the 1804 naturalized plant species in North America. This (peak $2n = 14$ and mean $2n = 29$) seems to resemble the figure for native plants in the world (i.e. peak $n = 7$, mean $n = 14$) provided by Rice *et al.* (2015) (CCDB: https://tom-e-white.com/datavision/41-plant-chromosome-numbers.html). Figure S2: comparison in species range size of the 1804 naturalized plant species in North America (NAM) in their native regions among the three ploidy levels. Mann–Whitney rank sum test: level I vs. II: $U = 176\,049$, level I vs. III: $U = 117\,245$, level II vs. III: $U = 98\,729$; in all cases, $P < 0.001$. For each box plot, the box represents the 25th and 75th percentiles, with the line in the box being the median, and the whiskers represent the 95 % confidence interval. Figure S3: the native (top) and non-native (bottom) distribution of the 1804 naturalized plant species in North America based on the species mid-latitude and mid-longitude (green, ploidy level I; blue, ploidy level II; red, ploidy level III). Mean values of the latitudes and longitudes for most species with more ploidy levels are located in higher-latitudinal regions, such as Europe and temperate Asia. However, it is surprising that the mean values of the latitudes and longitudes for the species in ploidy levels II and III are mostly located in the Midwest of the USA. Note that in the native regions (top), a few dots appear in the ocean because the location of each dot represents the centre of a species range (i.e. the mid-point of latitude and longitude). Table S1: paired comparison in maximum (Max), mean and minimum (Min) annual temperature (bio1; in degrees Celsius) and precipitation (bio12; in millimetres) among the three ploidy levels of the 1804 non-native

plant species, both in native regions and in non-native regions in North America (NAM). Only significant *U*-values (Mann–Whitney *U*-test) are given (see also Fig. 5).

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DATA AVAILABILITY

The data used in this study have already been published, and the sources of the data were cited in the manuscript: i.e. http://onlinelibrary.wiley.com/doi/10.1002/ecy.2542/suppinfo, https://powo.science.kew.org/, https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13191, https://idata.idiv.de/DDM/Data/ShowData/257, https://chelsa-climate.org, https://plants.usda.gov/home, http://rs.tdwg.org/wgsrpd/doc/data/, https://ccdb.tau.ac.il/ (The Chromosome Counts Database (CCDB, version web/CCDB_1.66.6) and https://www.sciencebase.gov/catalog/item/66ebaa73d34e0606a9dbe774.

AUTHOR CONTRIBUTIONS

Q.G. initiated the research. H.Q. and S.Q. provided plant and climate data. Q.G., H.Q. and S.Q. analysed the data. Q.G. wrote the first draft, and all authors contributed to developing and writing the manuscript.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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