Journal of Biogeography

WILEY

Journal of Biogeography

RESEARCH ARTICLE

Photosynthetic Pathways and Non-Native Plant Invasions in North America

Qinfeng Guo[1] | Hong Qian[2] | Lixin Wang[3]

[1]USDA FS – Southern Research Station, North Carolina, USA | [2]Research and Collections Center, Illinois State Museum, Springfield, Illinois, USA | [3]Department of Earth and Environmental Sciences, Indiana University Indianapolis, Indianapolis, Indiana, USA

Correspondence: Qinfeng Guo (qinfeng.guo@usda.gov)

Received: 13 October 2025 | **Revised:** 18 February 2026 | **Accepted:** 10 April 2026

Keywords: C_3 and C_4 plants | climate | distribution | life history | phenology | seed size | trait

ABSTRACT

Aim: Previous studies have compared various eco-physiological aspects among C_3, C_4, and Crassulacean Acid Metabolism (CAM) plants, mostly using native species. The variation in key genetic and life-history traits and their distribution among non-native plants with the three photosynthetic pathways remains poorly understood. Here, we examine whether the photosynthetic pathways of non-native plants in North America are linked to several major species traits and their current distributions. Location: North America.

Methods: We collate genetic and life-history data on chromosome number (ploidy levels), leaf size, plant height, seed size, life or growth form, reproductive mode, and phenology for 1977 non-native species from published sources. Native and non-native range sizes of each species are estimated according to the operational geographical units in which the species is present. The associated climatic data are obtained from the CHELSA climate database. We use one-way ANOVA, the pairwise Mann–Whitney *U*-test, and the Kruskal-Wallis test to examine the links among photosynthetic pathways, species traits, and distributions. We also perform linear regressions to examine the role of time (since introduction) in the spread of these non-native species.

Results: Non-native plants with the three photosynthetic pathways show clear differences in several life-history traits (ploidy level, leaf and seed size, plant height, reproductive mode), and phenology. The differences among the three plant types in their current distributions (range size, latitude, and elevation) demonstrate that they occupy distinct climate space across North America, although time (since introduction) also plays a role.

Main Conclusions: Our findings show clear links of photosynthetic pathways with life history and the distribution of regional non-native flora. Such results have strong implications for invasion research and management. Future studies should emphasize the roles of photosynthesis with additional traits and spread potential under projected land use and climate fluctuations.

1 | Introduction

Plant traits have been shown to regulate the structure and dynamics of natural assemblages (Ackerly and Cornwell 2007). However, certain traits are more important than others, depending on specific processes and circumstances (Díaz et al. 2004; Nunez-Mir et al. 2019). For example, seed size (a most stable plant trait) and plant height, leaf size, reproduction, flowering time, and ploidy level are among the most frequently used traits and certainly more important in plant performance and invasion success than many other traits, such as leaf colour, in terms of dispersal power and competition (Cornelissen et al. 2003; Guo et al. 2026; Nunez-Mir et al. 2019; Van der Veken et al. 2007; Whitney and Gabler 2008). Such key plant functional traits also include specific leaf area (SLA) (regulating growth strategy and competition), rooting depth (especially essential in arid habitats), and reproductive modes (Nunez-Mir et al. 2019). Consequently, some traits have received more attention than others, and some

species' traits are more closely related to one another than other traits (Díaz et al. 2004; Grace 1990). For example, previous studies have found that plant leaf area has positive effects on growth, size (height), and overall competitive capacity (Kunstler et al. 2016). For non-native plants, seed size, plant height, and growth rate have been frequently cited as key traits that significantly influence species invasiveness in recipient communities (Iannone et al. 2016; Rejmánek and Richardson 1996).

While species traits are increasingly studied and many critical traits have been extensively examined in the past, the role of photosynthetic pathways in species invasions and their links with other plant traits have rarely been thoroughly investigated. However, to better understand and manage biotic invasions, analyses of multi-trait associations, especially at large spatial scales (e.g., continental-scale), are critically needed. For species with different photosynthetic pathways, changes in climate conditions (e.g., rising CO_2, drought) could lead to very different outcomes in overall species performance (Whitney and Gabler 2008). Plants with C_4 photosynthesis have long been perceived as having evolved in response to warmer, drier conditions and low atmospheric CO_2 concentrations (Ehleringer et al. 1997; Sage and Monson 1998). They are usually more advanced taxa, especially common among monocots, such as grasses, but rare among dicots and woody species (Sage et al. 1999). In contrast, elevated CO_2 concentrations can enhance the photosynthetic rates, water-use efficiency, and biomass production of many C_3 plants, particularly in disturbed habitats (Ainsworth and Rogers 2007), promoting their successful invasion (e.g., shrub encroachment in the deserts/grasslands of the southwestern United States; Peters et al. 2006). CAM photosynthesis occurs in many epiphytes and succulents from very arid regions. The CAM pathway is enhanced through either increased water-use efficiency or increased carbon gain (Bartlett et al. 2014). Thus, under different and varying conditions, plants of the three photosynthetic pathways would show different and ever-changing levels of invasion success over space and time.

Globally, plants using the three pathways are widely distributed, but C_4 and CAM plants are highly aggregated in certain regions, with more C_4 plants in warm regions and more CAM plants in arid regions (Ehleringer and Cerling 2002). However, the increase in atmospheric CO_2 complicates the spatial and temporal distributions of C_3 and C_4 species. For example, in a human-enhanced CO_2 environment, while C_3 plants may benefit directly from higher CO_2, C_4 plants may be outcompeted by C_3 plants (Ehleringer et al. 1997). But elevated CO_2 is also likely to result in warmer, sometimes drier conditions that benefit C_4 and CAM plants, leading to unexpected outcomes in species interactions among the three groups. Under rapidly changing circumstances and given the limited dispersal of some species, plants of the three groups may have to use limited microsites and coexist across large landscapes (Sage and Kubien 2007). The future distribution of existing species is further complicated by the invasion of many non-native species with different proportions of photosynthetic pathways than those of resident species. In continental North America, for example, more than 2440 plant species have been naturalized, and the composition of photosynthetic pathways (proportion of each) and trait–climate–distribution relationships remain interesting but largely unexplored.

Earlier investigations of biotic invasions have commonly focused on dominant species and have used a limited number of life-history traits, such as seed size and reproductive mode (Nunez-Mir et al. 2019). Generally, studies examining a small number of species or traits may overlook opportunities to identify more significant patterns or traits that could shed new light on the invasion mechanisms, especially over large spatial scales (Liu et al. 2019). For example, across continental North America, the relative proportions of C_3, C_4, and CAM plants among the 2441 species in its non-native flora are still unknown. Yet, this information, along with the spatial and temporal variation in the three photosynthetic pathways, is a critical indicator of environmental change. In addition, little information is currently available on the association between photosynthetic pathways and other life-history traits and distributions, despite this knowledge having important implications for ecosystem management.

Plant photosynthesis is highly sensitive to changing climate conditions; plants with different photosynthetic pathways would respond differentially to changing climates (Sage and Kubien 2007). Facing many uncertainties under global change, to better predict future species invasions, we need a better understanding of how the changing climate reshapes the distributions of C_3, C_4, and CAM plants (Guo et al. 2025). Also, despite a steadily growing literature on eco-physiological characteristics, the role of photosynthetic pathways in plant invasions remains a major information gap. Also, the possible differences in morphology, phenology, and biogeography of the three plant types remain poorly understood, especially among non-native plants. Here, we examine the relative performance and invasions of the C_3, C_4, and CAM non-native plants across continental North America using newly compiled data. We test two main hypotheses: (1) in addition to many eco-physiological characteristics, photosynthetic pathways are also closely linked to many other morphological (e.g., leaf size, height, seed size) and phenological traits (e.g., flowering start/ending time and duration in month), and (2) plants of these three photosynthetic pathways show different distribution patterns (latitude, elevation) due to their unique preferences and different sensitivities to climate conditions (mean annual temperature and mean annual precipitation). The goal is to explore and predict the potential for plant invasion in North America, given the available climate space. To our knowledge, this study is the first to focus on the role of photosynthetic pathways in species invasiveness and spread within a large non-native flora across a wide geographic extent (i.e., across a continent).

2 | Methods

Among the over 2441 non-native plant species naturalized in North America (the continental United States and Canada), we had information on photosynthetic pathways for 1977 species: 1709 (86%) C_3 plants, 174 (9%) C_4 plants, and 94 (5%) CAM plants. To investigate whether the photosynthetic pathways may be linked with other life history traits and invasion success, we collated the genetic and life history data on chromosome number (including ploidy level, I, II, and III), leaf size (measured as length × width, cm^2; no correction was made to account for compound and heteromorphic leaves), plant height (cm), seed size (weight, g), life or growth form, reproductive mode (sexual,

asexual, and both), and phenology (flowering start/end time and duration in month) from various sources, including literature, online traits databases (https://plants.usda.gov/home), and numerous national, regional, and local floras. Botanical nomenclature in different sources was standardized during data search and before analysis using the R package U.Taxonstand (Zhang and Qian 2023; Zhang et al. 2025), following the World Checklist of Vascular Plants (Brown et al. 2023). The three ploidy levels based on the number of chromosome sets (2n) that have been reported to date, i.e., 1, 2, and ≥3 sets, correspond to level I, level II, and level III, respectively. To examine whether photosynthetic pathways were related to species distribution, we compiled distribution data (e.g., latitude and range size in both native regions and in North America) for these species based on the Global Naturalized Alien Flora (Glo NAF) database (van Kleunen et al. 2019) and the World Checklist of Vascular Plants (Brown et al. 2023). We used the operational geographical units at level 3 of the International Working Group on Taxonomic Databases for Plant Sciences (Brummitt 2001) to document species distributions. Oceanic islands and Antarctica were excluded from analyses. Native and non-native range sizes of each species were estimated according to the operational geographical units in which the species was present (i.e., the total area of the operational geographical units in which the species occurred in either case). To investigate the possible role of residential time on species distribution, we used the data of first record of observation in North America from Sofaer et al. (2025).

The area of each operational geographical unit was determined using the GIS package of the International Working Group on Taxonomic Databases for Plant Sciences (https://github.com/tdwg/wgsrpd/tree/master/level3), including all habitats within the operational geographical unit. Because a species does not occupy every local site within its distributional range, the actual occupied area of a species would necessarily be smaller than its distributional range. However, this is generally not considered as an issue in macroecological studies, partly because the same method of estimating distributional areas is applied to all species in a particular study and thus there is no systematic bias towards a particular species, or a group of species. The method that we used in this study to measure species distribution ranges has been commonly used in macroecological studies (e.g., Cai et al. 2023; Guo et al. 2024; Qian et al. 2024).

To test whether the non-native species of the three photosynthetic pathways were associated with specific climate conditions, we related them to two major climatic variables (bio1 and bio12 for mean annual temperature (MAT) and mean annual precipitation (MAP), respectively); we obtained the climatic data from the CHELSA climate database version 2.1 at the resolution of 30 arc-seconds (https://chelsa-climate.org) (Karger et al. 2017), which are modelled using observed climatic data for the period from 1979 to 2025. We calculated the average value of each climatic variable for all pixels at 30-arc-second resolution within the distributional range of each species in each geographical region defined by van Kleunen et al. (2019).

In most cases of comparison, since data were not normally distributed and sample sizes were different among the three photosynthetic pathways, we first adopted the Kruskal-Wallis test (a non-parametric method ideal for comparing groups when sample sizes are small or very different) to determine whether there was a statistically significant difference in the median values among C_3, C_4, and CAM non-native plants. When the test was significant, we then performed pairwise Mann–Whitney U tests on life-history traits, including seed and leaf size and distribution (range size, latitude, and elevation) among species of the three photosynthetic pathways.

3 | Results

Among the 1977 studied non-native plant species in North America, several life history traits, as well as climate space and distribution, were clearly different among plants of the three photosynthetic pathways. Among these species, the smallest chromosome number increased from C_3 to C_4 and CAM plants (C_3 vs. C_4: $U = 60{,}172$, $p = 0.023$; C_3 vs. CAM: $U = 24{,}809$, $p = 0.014$; C_4 vs. CAM: $U = 2176$, $p = 0.277$; Figure 1A). However, C_4 plants had the highest proportion of polyploids, followed by C_3 and CAM plants (e.g., 27%, 15%, 14% at level III, respectively; Table 1). C_3 plants had the largest seed sizes (weight, g), followed by CAM plants ($C_3 > C_4$: $U = 34{,}800$, $p < 0.001$; $C_3 >$ CAM: $U = 18{,}513$, $p = 0.011$); no difference in seed size was observed between C_4 and CAM plants ($U = 2118$, $p = 0.25$; Figure 1B).

In terms of reproductive mode, C_3 and C_4 plants had a high proportion of species with sexual-only and sexual-plus-asexual reproductive modes (Table 2). Most C_4 plants adopt sexual reproduction; none totally rely on asexual reproduction, and about one-third use both sexual and asexual reproductive modes. In contrast, CAM plants had a high proportion of species with sexual plus asexual reproductive mode (59%), followed by sexual only and asexual only reproductive modes (Table 2).

No difference in leaf size was observed between C_3 and C_4 plants and between C_4 and CAM plants, but there was a marginal difference between C_3 and CAM plants (Figure 1C). The maximum and mean height of C_3 plants was greater than that of C_4 plants and CAM plants, and greater in C_4 plants than in CAM plants (in all cases, $p < 0.05$). Similarly, the minimum height of the C_3 plants was greater than that of the C_4 and CAM plants, but there was no difference between the C_4 and CAM plants Table 3, (Figure 1D).

The flowering duration was significantly shorter among C_3 than among C_4 plants ($U = 179$, $p = 0.004$) and among CAM plants ($U = 729$, $p = 0.008$), but there was no difference between C_4 and CAM plants ($U = 77$, $p = 0.684$; Figure 1E). C_4 plants flowered later than both C_3 and CAM plants but CAM plants flowered much earlier than C_3 plants. In contrast, C_3 plants ended the flowering period earlier than C_4 plants, but there was no difference in the flowering end time between C_3 and CAM plants and between C_4 and CAM plants (Table 3, Figure 1F).

Across all three photosynthesis pathways, the native ranges were significantly larger than their non-native (or introduced) ranges in North America ($p < 0.001$). In the native regions, C_4 plants had the largest mean range size, followed by C_3 and CAM plants. In North America, C_3 and C_4 plants had similar mean range sizes ($p = 0.482$), which were significantly larger than those of CAM plants. The variation in range size among C_3 species and among C_4 species was larger in North America

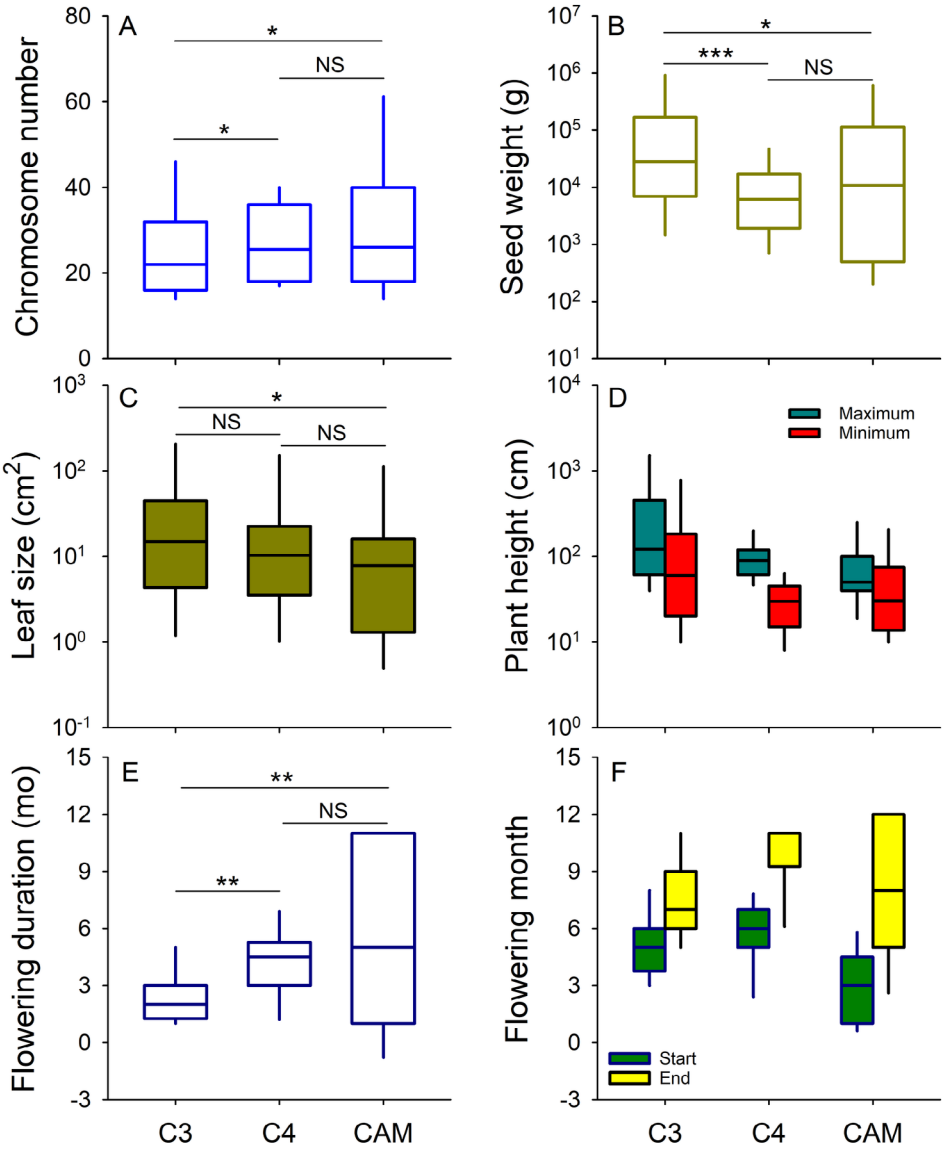

FIGURE 1 | Comparisons of selected life history traits among non-native plants in North America with the three photosynthetic pathways (C_3, C_4, and CAM; in all panels, the boxes represent the median and 25th and 75th percentiles, and whiskers represent the 10th and 90th percentiles). Note that in A, the chromosome number is the lowest chromosome number reported for each species, and in F, the boxes are based on values of 1 through 12 that represent the 12 months from Jan. through Dec. Mann–Whitney Rank Sum Test, $*p < 0.05$, $**p < 0.01$, ***, $p < 0.001$.

TABLE 1 | Comparison of the fraction of species (%) at the three ploidy levels in C_3, C_4, and CAM plants (the three photosynthetic pathways) for all 1488 species with both photosynthetic pathways information and chromosome counts in the non-native North America flora (thus the fraction of species at ploidy-I is 100%).

Photosynthetic pathway	No. species	Ploidy level		
		I	II	≥ III
C_3	1336	100	32	15
C_4	105	100	51	27
CAM	47	100	32	14

TABLE 2 | Proportion (%) of the three reproductive modes (sexual, asexual, and both) among C_3, C_4, and CAM species of the 285 non-native plant species in North America with both photosynthetic pathway information and reproduction data.

Photosynthetic pathway	No. species	Reproductive mode		
		Sexual	Asexual	Both
C_3	233	50	3	47
C_4	23	65	0	35
CAM	29	27	14	59

than in their native regions, but there was no difference among CAM plants between the native regions and North America (Figure 2).

However, when herbaceous and woody species were analysed separately, divergent patterns emerged among C_3, C4, and CAM plants. Among herbaceous species, significant differences in

TABLE 3 | Comparisons of plant height, flowering start/end time (month), latitude (in both native regions and non-native region, North America), and elevation (in North America) among C_3, C_4, and CAM non-native plants in North America based on the Mann–Whitney Rank Sum Tests (*U* values). (see also Figure 1, Figure S1).

		C_3 versus C_4	C_3 versus CAM	C_4 versus CAM
Plant height (cm)	Maximum	14900***	3503***	729**
	Minimum	10974***	3860**	707
Flowering month	Start	298*	355***	254**
	End	168**	583	79
Latitude (°)	Highest	102852***	54500***	7776
Native regions	Mean	72274***	54353***	7067
	Lowest	142,560	80,182	7754
Latitude (°)	Highest	112675***	34482***	7001
North America	Mean	93871***	55747***	8061
	Lowest	99786***	69824*	6338***
Elevation (m)	Highest	1380	704*	102*
North America	Lowest	1006	879	157

Note: *$p < 0.05$, **$p < 0.01$, ***, $p < 0.001$.

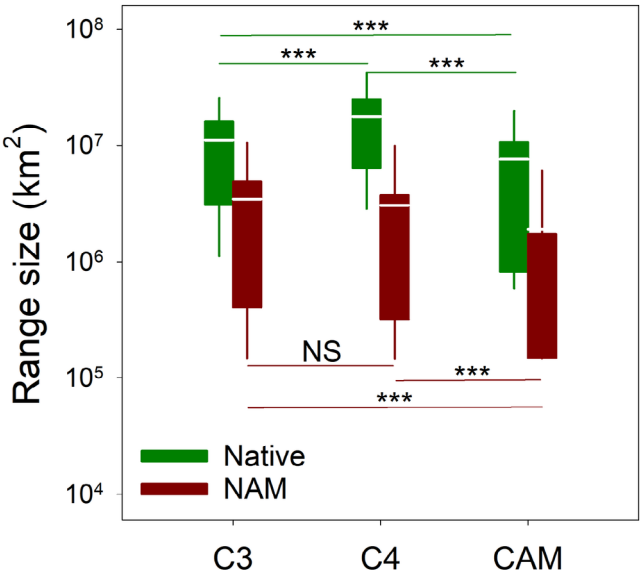

FIGURE 2 | Comparison of the range size of the non-native plants in North America among the three photosynthetic pathways (C_3, C_4, and CAM). Boxes represent the median and 25th and 75th percentiles, and whiskers represent the 10th and 90th percentiles. Mann–Whitney Rank Sum Test, *$p < 0.05$, **$p < 0.01$, ***, $p < 0.001$.

range size were observed in all three pathways, and this was true in both native regions and in North America (Figure S1 A), but no difference among the three pathways in woody species was observed (Figure S1 B). Also, among herbaceous species and in the native regions, C_4 species had the largest ranges; in North America, however, C_3 species had the largest ranges, followed by C_4 and CAM plants (Figure S1A).

In the native regions, both maximum and mean latitudes for C_3 plants were larger than those for C_4 and CAM plants, but no difference in minimum latitudes was detected among all three plant groups (Figure S2A). In North America, similar patterns were observed. However, unlike the patterns observed in the native regions, the minimum latitudes show the following order: $C_3 > C_4$, $C_3 >$ CAM, and $C_4 >$ CAM (Table 3, Figure S2B). There was no difference in maximum elevation between C_3 and C_4 species, but the maximum elevation of these two groups of species was significantly higher than that of CAM species. No difference was observed in the lowest elevation among the three plant groups (Table 3, Figure S2C).

Plants of all three photosynthetic pathways show similar spread rates over time, as shown by similar trends in the relationships between time (yrs) after the first reported date in North America and range size (C_3: $r = 0.59$, $p < 0.001$; C_4: $r = 0.47$, $p < 0.001$; CAM: $r = 0.61$, $p < 0.001$; no difference among the three regression slopes; Figure 3). C_3 and C_4 plants were introduced to North America within a similar timeframe but much earlier than CAM plants. Test based on the time (yr) or first reported date in North America, C_3 versus C_4: $U = 101{,}317$, $p = 0.334$; C_3 versus CAM: $U = 47{,}915$, $p < 0.001$; C_4 versus CAM: $U = 4424$, $p = 0.002$.

All three plant groups occupied a much smaller climate space in North America than in their native regions (Figure S3). The ranges of minimum annual temperature of all three groups (C_3, C_4, and CAM) of non-native species were much larger than the maximum annual temperature in both native regions and in North America (Figure 4A,B). For MAP, the same was true in the native regions; however, the opposite was observed for CAM plants in both native regions and North America, as well as for C_3 and C_4 plants in their native regions only (Figure 4C,D). Across all three plant groups, the medians of both MAT and MAP were higher in the native regions than in North America (in all cases, $p < 0.05$) except for the MAP of C_3 plants (Figure 4E,F). For C_3 and C_4 plants, the differences between maximum and

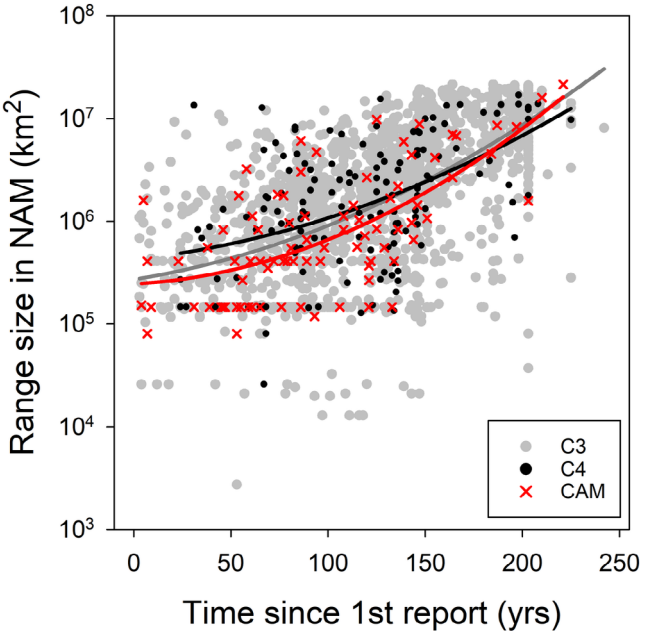

FIGURE 3 | Plants of all three photosynthetic pathways (C_3, C_4, and CAM) show similar trends in the relationships between time (yrs) since the first reported date and range size in North America (km^2).

minimum MAT and MAP were smaller in North America than in the native regions, but no difference was found for CAM plants (Figure 4A–D).

4 | Discussion

Our findings confirm that plants with the three types of photosynthetic pathways exhibit distinctive eco-physiological features and performance (Kumar et al. 2017). Also, many other plant life-history and genetic traits are associated with specific photosynthetic pathways. Most previous studies have focused on native floras. Our study, based on a large non-native flora in North America, also reveals some significant patterns. Some emerging patterns or associations are clear, reflecting both the advantages and disadvantages of each photosynthetic pathway under varying climate and other environmental conditions.

In this study, 86% of the non-native plant species examined in North America are C_3 species, similar to the previously reported estimate that 85%–90% of all plant species on Earth are C_3 plants (Baslam et al. 2020; Kumar et al. 2017). In general, C_4 and C_3 species are believed to be more invasive than CAM plants due to their overall higher rates of growth and resource use (Hartzell et al. 2018). C_4 plants have a significantly higher photosynthetic capacity than C_3 plants and can better cope with higher temperatures and lower water availability. C_4 plants are efficient water users that often adapt to warmer, drier conditions, thereby allowing them to better tolerate heat and drought (Bromham and Bennett 2014; Sage and Monson 1998). Nevertheless, elevated CO_2 would favor more C_3 or woody species over C_4 species unless this effect is counterbalanced by drier, warmer conditions that greatly increase the competitive capacity of C_4 species (Chuine et al. 2012).

On average, C_3 plants are expected to have larger seeds than C_4 and CAM plants, at least among non-native species in North America. A major reason could be that C_3 species exhibit more diverse growth forms (Yamori et al. 2014), including larger plants, and these larger plants (trees and shrubs), on average, have larger seeds (Figure 1B) and leaves (Figure 1C) that could be linked to species invasiveness (Rees and Venable 2007; Rejmánek and Richardson 1996). In our case, C_3 and C_4 plants adopt similar reproductive modes, i.e., the vast majority use sexual or both sexual and asexual modes, and very few totally rely on the asexual mode. In contrast, most (59%) CAM plant species use both sexual and asexual modes, and a few use either sexual or asexual modes. Previous studies show that species with multiple reproductive modes have advantages in invasion (Nunez-Mir et al. 2019; Rejmánek and Richardson 1996). However, in our case, this advantage for CAM plants with both sexual and asexual reproductions may be overshadowed by other limitations such as habitat availability and changing CO_2 levels (see detailed discussion below).

Both photosynthetic pathways and life/growth forms are important factors in determining species' range sizes in both native and nonnative regions. For herbaceous species, the order of range sizes among the three photosynthetic pathways has shifted from native regions ($C_4 > C_3 > CAM$) to nonnative regions in North America ($C_3 > C_4 > CAM$), presumably reflecting species invasiveness and changes in habitat availability. In contrast, for woody species, no difference in range size has been detected among the three species types. This might indicate that species performance of woody plants (e.g., species adaptability and habitat requirements) may be less sensitive to photosynthetic pathways than that of herbaceous species. After all, the vast majority of woody species are C_3 species (Young et al. 2020).

In our case, the range sizes of C_3 and C_4 plants are larger than those of CAM plants in both native regions and in North America. In North America, however, since C_3 and C_4 plants were, on average, introduced earlier than CAM plants, we cannot claim that the observed pattern simply follows that in native regions. If regional or global temperatures continue to rise, C_4 plants are likely to become more invasive, expanding their ranges unless rising CO_2 levels curb their spread (Wang et al. 2020). However, it remains unclear why C_3 and C_4 plants were introduced to North America earlier than CAM plants, which may partly explain the smaller range sizes of CAM plants relative to those of C_3 and C_4 plants in North America (Guo et al. 2025). Another important reason is that CAM plants are mostly prevalent in arid and semi-arid regions of North America (Nobel 1991) with generally lower human population density and a shorter history of massive human settlement (relative to the east, particularly the northeastern US), which reduces the likelihood of successful introduction and naturalization.

The role of residence time is evident in the overall lower elevational distribution of non-native species worldwide compared with native species (Guo et al. 2018). For now, most plants of all three photosynthetic pathways have not yet had enough time to spread (or shift) upward. Thus, their current occupancy of climate space does not reflect niche and dispersal limitation. In our case, it is unclear why the variation in species' maximum temperatures is

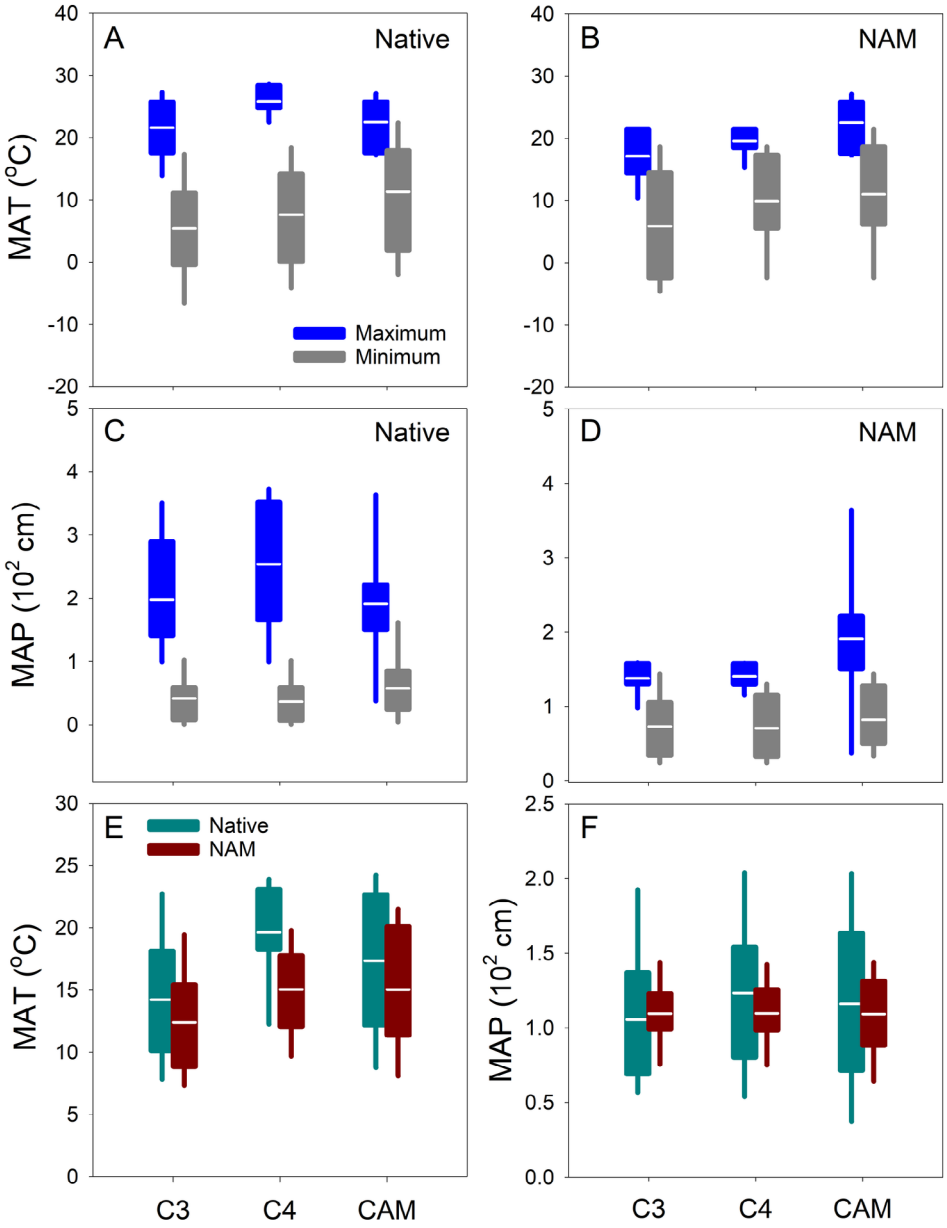

FIGURE 4 | Comparisons in climate space (mean annual temperature, MAT) and mean annual precipitation (MAP) among C_3, C_4, and CAM non-native plants in North America. The boxes represent the median and 25th and 75th percentiles, and whiskers represent the 10th and 90th percentiles.

smaller in native regions than in the non-native regions in North America. For some species, the mismatch in climate space between native and nonnative regions could at least partly be due to enemy release in the invaded habitats (Liu and Stiling 2006). However, the smaller differences between maximum and minimum MAT and MAP in North America compared to those in the native regions simply reflect the climate space limitation in North America, compared to that in the species' native regions. Over time, and as the climate warms, differences in range size, horizontal (across latitude) and vertical (across elevation) span, and many other aspects between the native regions and North America could be drastically altered. More importantly, in the future, as global temperatures and CO_2 levels continue to rise at different rates across world regions and within North America (Grotch and MacCracken 1991), plants of the three photosynthetic pathways may show divergent spread patterns in North America. This is simply because the three plant groups are expected to show different sensitivities and tolerances to climate fluctuations (Bai et al. 2025; Kumar et al. 2017).

The plants using the three photosynthetic pathways clearly adopt different phenological strategies. In our study, the earlier flowering time for C_3 species compared to C_4 species is consistent with the observation by Pereyra Almena et al. (2024). CAM species have a very slow, energy-conserving metabolism designed for survival in arid environments, leading to early flowering and longer flowering time. In this study, the range sizes of CAM plants are mostly restricted by the habitat availability in the southwestern United States. However, future climate warming could significantly alter the strategies of the three plant groups, thereby affecting invasion success and relative abundance in affected regions and habitats (Bai et al. 2025). For example, if the CO_2 level is elevated further in these areas, CAM plants would be further restricted to microhabitats, as

coexisting and invading C_3 species benefit more from high CO_2 (Sage et al. 2023). Also, if global temperature continues to rise, C_4 plants may benefit and become even more invasive, particularly given their smaller seeds with higher abundance (thus more likely to be dispersed) (Howe and Miriti 2004; Rejmánek and Richardson 1996). Warming would advance the flowering time of both C_3 and C_4 plants, but it could significantly reduce the flowering duration for C_3 plants, thereby decreasing the dominance of C_3 plants and creating more favourable conditions for C_4 and CAM plants (Díaz Cando et al. 2025; Yu et al. 2024).

The smaller climate space used by all three plant groups in North America than in their native regions clearly indicates the great potential for them to spread in the future when similar climate niches become available (e.g., under a warming trend) and enough time is given. At the same time, most non-native plants will likely encounter the native plants with the same photosynthetic pathways if the invaded habitat is large. Non-natives that share life histories with resident native species are more likely to invade the same habitat when natives are disturbed, and their abundance is reduced. There is also abundant evidence that some extraordinary invasion successes involve species with competitive traits invading new habitats where resources are still available (Havrilla et al. 2023).

Finally, due to data limitations, our study has not considered the possible role of habitat features in the studied region, such as dominant soil types, vegetation types, and the extent of human disturbance (e.g., urbanization or agricultural land use), in shaping our observed patterns. This remains an important information gap that needs to be filled in the future. Also, our comparisons among three photosynthetic pathways using the univariate analysis are constrained by the inability to identify causal relationships, partly because it cannot account for possible confounding effects. There are many more plant traits and processes (e.g., interactions among the three plant types) that have not been examined but might be related to photosynthetic pathways (Angeli et al. 2025). For example, the potential associations between photosynthetic pathways and various other plant traits (e.g., hybridization, polyploidization) have not been specifically or thoroughly investigated (Liu et al. 2019). Future studies should take the important factors listed above into account to better explain our observed patterns.

Despite the constraints of our analysis, our findings, based on a large number of species, could, to a certain extent, help predict which species types (C_3, C_4, and CAM) may spread and into which habitats under a changing climate. Given ongoing and projected climate fluctuation and land use, it would be very useful to develop a more sophisticated trait-photosynthetic framework that can be integrated with well-designed field experiments to predict where C_3 or C_4 plants may predominate in the future (Raubenheimer et al. 2025). Future research should focus on these aspects, especially given the ever-changing environmental conditions.

Author Contributions

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

Acknowledgements

We thank Josephine Falcone and Jennifer Torgerson for assistance with plant life history data, Jian Zhang for providing climatic data, Jun Wen for assisting with data analysis, and many individuals for their helpful comments and discussions. The authors confirm that no specific permits were required for this study. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in https://onlinelibrary.wiley.com/doi/10.1002/ecy.2542/suppinfo at https://onlinelibrary.wiley.com/doi/10.1002/ecy.2542/suppinfo. These data were derived from the following resources available in the public domain: Species list, https://idata.idiv.de/DDM/Data/ShowData/257; Nonnative status, https://plants.usda.gov/home; Introduction date, https://doi.org/10.5066/P13GAYQA.

References

Ackerly, D. D., and W. K. Cornwell. 2007. "A Trait-Based Approach to Community Assembly: Partitioning of Species Trait Values Into Within-and Among-Community Components." *Ecology Letters* 10, no. 2: 135–145.

Ainsworth, E. A., and A. Rogers. 2007. "The Response of Photosynthesis and Stomatal Conductance to Rising [CO2]: Mechanisms and Environmental Interactions." *Plant, Cell and Environment* 30, no. 3: 258–270.

Angeli, J., D. C. Talora, N. M. Heming, and E. Cazetta. 2025. "Ecological and Historical Drivers of Palm Distributions in the Atlantic Forest." *Global Ecology and Conservation* 62: e03766.

Bai, L., G. Han, L. Jiang, et al. 2025. "Contrasting Responses of Flowering Phenology in C3 and C4 Plants Shape Grassland Community Structure Under Global Change." *Ecology* 106, no. 6: e70139.

Bartlett, M. S., G. Vico, and A. Porporato. 2014. "Coupled Carbon and Water Fluxes in CAM Photosynthesis: Modeling Quantification of Water Use Efficiency and Productivity." *Plant and Soil* 383, no. 1: 111–138.

Baslam, M., T. Mitsui, K. Sueyoshi, and T. Ohyama. 2020. "Recent Advances in Carbon and Nitrogen Metabolism in C3 Plants." *International Journal of Molecular Sciences* 22, no. 1: 318.

Bromham, L., and T. Bennett. 2014. "Salt Tolerance Evolves More Frequently in C4 Grass Lineages." *Journal of Evolutionary Biology* 27, no. 3: 653–659.

Brown, M. J., B. E. Walker, N. Black, et al. 2023. "rWCVP: A Companion R Package for the World Checklist of Vascular Plants." *New Phytologist* 240: 1355–1365.

Brummitt, R. K. 2001. *World Geographical Scheme for Recording Plant Distributions*. 2nd ed. Hunt Institute for Botanical Documentation, Carnegie Mellon University.

Cai, L., H. Kreft, A. Taylor, et al. 2023. "Climatic Stability and Geological History Shape Global Centers of Neo-and Paleoendemism in Seed Plants." *Proceedings of the National Academy of Sciences* 120, no. 30: e2300981120.

Chuine, I., X. Morin, L. Sonié, et al. 2012. "Climate Change Night Increase the Invasion Potential of the Alien C4 Grass Setaria Parviflora (Poaceae) in the Mediterranean Basin." *Diversity and Distributions* Portico. 18, no. 7: 661–672. https://doi.org/10.1111/j.1472-4642.2011.00880.x.

Cornelissen, J. H., S. Lavorel, E. Garnier, et al. 2003. "A Handbook of Protocols for Standardised and Easy Measurement of Plant Functional Traits Worldwide." *Australian Journal of Botany* 51, no. 4: 335–380.

Díaz Cando, P. E., A. Fenesi, J. Sonkoly, P. C. D. Perera, and P. Török. 2025. "Enemy Behind the Gates? Predicted Climate Change and Land-Use Intensification Likely Speed Up C4 Grass Invasions in Europe." *Journal of Vegetation Science* 36, no. 2: e70023.

Díaz, S., J. Hodgson, K. Thompson, et al. 2004. "The Plant Traits That Drive Ecosystems: Evidence From Three Continents." *Journal of Vegetation Science* 15, no. 3: 295–304.

Ehleringer, J. R., and T. E. Cerling. 2002. "C3 and C4 Photosynthesis." *Encyclopedia of Global Environmental Change* 2, no. 4: 186–190.

Ehleringer, J. R., T. E. Cerling, and B. R. Helliker. 1997. "C4 Photosynthesis, Atmospheric CO2, and Climate." *Oecologia* 112, no. 3: 285–299.

Grace, J. B. 1990. "On the Relationship Between Plant Traits and Competitive Ability." *Perspectives on Plant Competition* 2: 51–65.

Grotch, S. L., and M. C. MacCracken. 1991. "The Use of General Circulation Models to Predict Regional Climatic Change." *Journal of Climate* 4: 286–303.

Guo, Q., S. Fei, Z. Shen, B. V. Iannone III, J. Knott, and S. L. Chown. 2018. "A Global Analysis of Elevational Distribution of Non-Native Versus Native Plants." *Journal of Biogeography* 45, no. 4: 793–803.

Guo, Q., H. Qian, and S. Qian. 2025. "Climate Space, Traits, and the Spread of Nonnative Plants in North America." *Plant Diversity* 47, no. 2: 255–263.

Guo, Q., H. Qian, and S. Qian. 2026. "Links of Ploidy With Other Traits and Distribution in Nonnative North American Flora." In *Annals of Botany*. In Press.

Guo, Q., H. Qian, J. Zhang, and P. Liu. 2024. "The Relationships Between Species Age and Range Size." *Journal of Biogeography* 51: 1095–1103. https://doi.org/10.1111/jbi.14809.

Hartzell, S., M. S. Bartlett, and A. Porporato. 2018. "Unified Representation of the C3, C4, and CAM Photosynthetic Pathways With the Photo3 Model." *Ecological Modelling* 384: 173–187.

Havrilla, C. A., J. B. Bradford, C. B. Yackulic, and S. M. Munson. 2023. "Divergent Climate Impacts on C3 Versus C4 Grasses Imply Widespread 21st Century Shifts in Grassland Functional Composition." *Diversity and Distributions* 29, no. 3: 379–394.

Howe, H. F., and M. N. Miriti. 2004. "When seed dispersal matters." *Bioscience* 54, no. 7: 651–660.

Iannone, B. V., K. M. Potter, Q. Guo, et al. 2016. "Biological Invasion Hotspots: A Trait-Based Perspective Reveals New Sub-Continental Patterns." *Ecography* 39: 961–969.

Karger, D. N., O. Conrad, J. Böhner, et al. 2017. "Climatologies at High Resolution for the Earth's Land Surface Areas." *Scientific Data* 4, no. 1: 1–20.

Kumar, V., A. Sharma, J. K. Soni, and N. Pawar. 2017. "Physiological Response of C3, C4 and CAM Plants in Changeable Climate. The Pharma." *Innovation* 6, no. 9: 70.

Kunstler, G., D. Falster, D. A. Coomes, et al. 2016. "Plant Functional Traits Have Globally Consistent Effects on Competition." *Nature* 529, no. 7585: 204–207. https://doi.org/10.1038/nature16476.

Liu, H., and P. Stiling. 2006. "Testing the Enemy Release Hypothesis: A Review and Meta-Analysis." *Biological Invasions* 8, no. 7: 1535–1545.

Liu, H., S. H. Taylor, Q. Xu, et al. 2019. "Life History Is a Key Factor Explaining Functional Trait Diversity Among Subtropical Grasses, and Its Influence Differs Between C3 and C4 Species." *Journal of Experimental Botany* 70, no. 5: 1567–1580.

Nobel, P. S. 1991. "Achievable Productivities of Certain CAM Plants: Basis for High Values Compared With C3 and C4 Plants." *New Phytologist* 119, no. 2: 183–205.

Nunez-Mir, G. C., Q. Guo, M. Rejmánek, B. V. Iannone III, and S. Fei. 2019. "Predicting Invasiveness of Exotic Woody Species Using a Traits-Based Framework." *Ecology* 100, no. 10: e02797.

Pereyra Almena, M., A. E. Ferreras, and M. A. Giorgis. 2024. "Differences in Phenology Between Non-Native C4 Grasses and Native C3 and C4 Grasses in a Seasonally Dry Ecosystem." *Austral Ecology* 49, no. 12: e70017.

Peters, D. P., J. Yao, and J. R. Gosz. 2006. "Woody Plant Invasion at a Semi-Arid/Arid Transition Zone: Importance of Ecosystem Type to Colonization and Patch Expansion." *Journal of Vegetation Science* 17, no. 3: 389–396.

Qian, H., B. D. Mishler, J. Zhang, and S. Qian. 2024. "Global Patterns and Ecological Drivers of Taxonomic and Phylogenetic Endemism in Angiosperm Genera." *Plant Diversity* 46, no. 2: 149–157.

Raubenheimer, S. L., L. Zheng, A. Stefanski, and P. B. Reich. 2025. "Climate-Change-Driven Shifts in C3 and C4 Grass Distributions and Leaf Traits Could Lead to Changes in Community-Level Flammability." *American Journal of Botany* 112: e70081.

Rees, M., and D. L. Venable. 2007. "Why do big plants make big seeds?" *Journal of Ecology* 95, no. 5: 926–936.

Rejmánek, M., and D. M. Richardson. 1996. "What Attributes Make Some Plant Species More Invasive?" *Ecology* 77, no. 6: 1655–1661.

Sage, R. F., I. S. Gilman, J. A. C. Smith, K. Silvera, and E. J. Edwards. 2023. "Atmospheric CO2 Decline and the Timing of CAM Plant Evolution." *Annals of Botany* 132, no. 4: 753–770.

Sage, R. F., and D. S. Kubien. 2007. "The Temperature Response of C3 and C4 Photosynthesis." *Plant, Cell and Environment* 30, no. 9: 1086–1106.

Sage, R. F., and R. K. Monson. 1998. *C4 Plant Biology*. Elsevier.

Sage, R. F., D. A. Wedin, and M. Li. 1999. "The Biogeography of C4 Photosynthesis: Patterns and Controlling Factors." *C4 Plant Biology* 10: 313–376.

Sofaer, H. R., D. A. Williams, C. S. Jarnevich, et al. 2025. "First Records Distribution Models to Guide Biosurveillance for Non-Native Species." *Ecography* 2025, no. 4: e07522.

Van der Veken, S., J. Bellemare, K. Verheyen, and M. Hermy. 2007. "Life-History Traits Are Correlated With Geographical Distribution Patterns of Western European Forest Herb Species." *Journal of Biogeography* 34, no. 10: 1723–1735.

van Kleunen, M., P. Pyšek, W. Dawson, et al. 2019. "The Global Naturalized Alien Flora (Glo NAF) Database." *Ecology* 100, no. 1: e02542.

Wang, F., J. Gao, J. W. Yong, Q. Wang, J. Ma, and X. He. 2020. "Higher Atmospheric CO2 Levels Favor C3 Plants Over C4 Plants in Utilizing Ammonium as a Nitrogen Source." *Frontiers in Plant Science* 11: 537443.

Whitney, K. D., and C. A. Gabler. 2008. "Rapid Evolution in Introduced Species,'Invasive Traits' and Recipient Communities: Challenges for Predicting Invasive Potential." *Diversity and Distributions* 14, no. 4: 569–580.

Yamori, W., K. Hikosaka, and D. A. Way. 2014. "Temperature Response of Photosynthesis in C3, C4, and CAM Plants: Temperature Acclimation and Temperature Adaptation." *Photosynthesis Research* 119, no. 1: 101–117.

Young, S. N., L. Sack, M. J. Sporck-Koehler, and M. R. Lundgren. 2020. "Why Is C4 Photosynthesis So Rare in Trees?" *Journal of Experimental Botany* 71, no. 16: 4629–4638.

Yu, K., P. D'Odorico, A. Novoa, et al. 2024. "Potential Expansion of Plants With Crassulacean Acid Metabolism in the Anthropocene." *Bioscience* 74, no. 7: 478–487.

Zhang, J., and H. Qian. 2023. "U. Taxonstand: An R Package for Standardizing Scientific Names of Plants and Animals." *Plant Diversity* 45: 1–5.

Zhang, J., H. Qian, and X. Wang. 2025. "An Online Version and Some Updates of R Package U. Taxonstand for Standardizing Scientific Names in Plant and Animal Species." *Plant Diversity* 47: 166–168.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Comparisons of range size between the native regions and North America (NAM; non-native region) for herbaceous (A) and woody species (B) among C_3, C_4, and CAM species, respectively. **Figure S2:** Comparisons in latitudinal (highest, mean, and lowest in both native and non-native regions) and elevational (highest, lowest in North America—NAM only) distribution among plants of the three photosynthetic pathways (C3, C4, and CAM). Boxes represent the median and 25th and 75th percentiles, and whiskers represent the 10th and 90th percentiles. **Figure S3:** The comparison of occupied climate space of C3, C4, and CAM non-native plants in their native regions and in North America (NAM). The climate space used by all three plant groups is clearly much smaller in North Amercia than in their native regions. Each dot represents a species.