USING KEY FUNCTIONAL TRAITS TO EXPLAIN VARIATION IN RATES OF SPREAD AMONG INVASIVE PLANTS IN NORTH AMERICA

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Abstract

Invasive plants are major drivers of global change, capable of severely impacting the ecosystems they invade. Consequently, a major aim in invasion ecology has been to understand the dynamics of plant invasions and identify key determinants of spread. One factor hypothesized to explain interspecific variation in rates of invasion are functional traits. Intuitively, species with traits suited to colonization, dispersal, and rapid growth are predicted to spread faster. Despite this, empirical results surrounding the relationship between traits and various aspects of invasiveness remain mixed. Moreover, there is a dearth of research on the influence traits directly have on the rate of spread of a species across a range. To test this relationship, I reconstructed the invasion history of 247 vascular plant species invasive to North America in climate and geographic space. I then tested how well three functional traits (seed dry mass, plant height, and specific leaf area) could be used to predict various metrics of spread rate across these spaces. Of my tested traits, only plant height statistically explained variation in spread rate. However, both native range size and native niche breadth, covariates in my models, showed some predictive value. My results suggest that, when data are aggregated at the continental scale, functional traits are limited estimators of spread rate among invasive plants.

Resumé

Les plantes envahissantes sont des moteurs majeurs du changement mondial, capables d'avoir un impact sévère sur les écosystèmes qu'elles envahissent. Par conséquent, l'un des principaux objectifs de l'écologie des invasions est de comprendre la dynamique des invasions de plantes et d'identifier les principaux déterminants de la propagation. L'un des facteurs supposés expliquer les variations interspécifiques des taux d'invasion sont les traits fonctionnels. Intuitivement, les espèces dont les traits sont adaptés à la colonisation, à la dispersion et à la croissance rapide devraient se propager plus rapidement. Malgré cela, les résultats empiriques concernant la relation entre les traits et les différents aspects de l'envahissement restent mitigés. De plus, il y a une pénurie de recherches sur l'influence directe des traits sur le taux de propagation d'une espèce dans une aire de répartition. Pour tester cette relation, j'ai reconstitué l'histoire de l'invasion de 247 espèces de plantes vasculaires envahissant l'Amérique du Nord dans le climat et l'espace géographique. J'ai ensuite testé dans quelle mesure trois traits fonctionnels (masse sèche des graines, hauteur des plantes, et surface foliaire spécifique) pouvaient être utilisés pour prédire diverses mesures du taux de propagation dans ces espaces. Parmi les traits testés, seule la hauteur de la plante explique statistiquement la variation de la vitesse de propagation. Cependant, la taille de l'aire de répartition indigène et l'étendue de la niche indigène, covariables de mes modèles, ont montré une certaine valeur prédictive. Mes résultats suggèrent que, lorsque les données sont agrégées à l'échelle continentale, les traits fonctionnels sont des estimateurs limités de la vitesse de propagation des plantes envahissantes.

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1. Introduction

A key question within the field of plant invasion ecology is what factors allow introduced species to successfully spread across new landscapes (Williamson & Fitter, 1996; Kolar & Lodge, 2001; Novoa et al., 2020). Predicting the rate at which a plant will spread across novel ranges has practical applications for invasive species management. When predictions can be made about how a species will move across a landscape, habitats that are vulnerable to invasion can be identified (Srivastava et al., 2019). For example, conservation experts will be able to more accurately single out the most threatening invaders and prioritize conservation efforts that will have the highest impact.

Functional traits (i.e., the physiological, morphological, and life history characteristics of a plant that influence its ability to grow, reproduce, and survive) of invading species are often postulated to determine spread rate (Baker, 1965, 1974; Pyšek & Richardson, 2007; Mathakutha et al., 2019). Functional traits are influenced by genetics (Anderson et al., 2011), abiotic factors (e.g., temperature) (Barrett et al., 2015), and biotic interactions (e.g., competition) (Gross et al., 2009), and are thought to reflect the life-history strategy of an organism (Adler et al., 2014). Consequently, it is often suggested that these traits will also influence the rate at which invasives spread (Moravcová et al., 2015). For instance, before an invasive plant can go on to disperse widely across a novel landscape, it first must be able to survive the initial conditions associated with that new habitat (i.e., colonize) and have the means necessary to establish and maintain an initial population there (Theoharides & Dukes, 2007). Hence, any trait that facilitates this colonization and establishment process (e.g., having a heavy seed mass to enhance survival in a highly stressful initial habitat (Gross & Smith, 1991)) may impact the overall rate at which a species spreads across a landscape. Traits alone have done a relatively poor job thus far of explaining variability in invasion ability among plant species (Davis, 2009; Fristoe et al., 2021). However, this research has largely focused on the impact of traits inclusively on multiple processes related to invasion success (i.e., establishment, relative abundance, and impact) rather than spread rate as a discrete process.

In this context, I define spread rate as the length of time it takes for a species to occupy a certain amount of climate space (i.e., the specific set of climatic conditions that, when combined, characterize the overall environmental suitability of a particular habitat) or reach a given range size in geographic space. Spread rate is typically measured as the speed at which a species travels from one point in geographic space to another (e.g., Drenovsky et al., 2012; Gassó et al., 2012; Palma et al., 2021). However, the capacity of species to establish in new locations in geographic space is constrained, in part, by the environmental conditions present at and between those locations. At small spatial scales, where environmental conditions remain similar among locations, spatial processes should dominate spread (Frappier et al., 2003). At larger spatial scales however, there is greater variation in climatic conditions among locations and rates of spread are likely to be increasingly influenced by environment (Huang et al., 2024). Analyzing spread separately in climate and geographic space at large scales allows us to more clearly assess the extent to which spatial and environmental processes are related, and is an approach that has provided novel insights into plant invasions in the past (Foster et al., 2022).

Of the many functional traits studied thus far, there are three that are most likely to capture aspects critical to spread rate: seed dry mass, plant height, and specific leaf area. These three traits form the basis of the leaf-height-seed plant ecology scheme, a widely employed framework used to represent the means by which a plant species sustains their population (Westoby, 1998). These traits have been shown to represent distinct and major axes of variation in plant life history strategy (Hamilton et al., 2005). Consequently, they should serve as relatively robust representatives of the relationships between spread rate and functional traits at large.

Seed dry mass has been shown to be critical to two spread-related processes: dispersal and colonization (Skarpaas et al., 2011). Lighter seeds have been shown to spread farther and faster (i.e., have greater dispersal ability) (Melo et al., 2006; Muller-Landau et al., 2008). However, this comes at a cost of less maternal provisioning (Thomson et al., 2011) and thus less resistance to harsh conditions in new locations (i.e., lighter seeds have lower colonization success than heavier seeds (Hewitt, 1998; Muller-Landau, 2010)). Meanwhile, evidence linking seed size and dispersal ability so far has been limited and mixed. For example, in a comprehensive review of studies examining seed size and dispersal ability, Thomson et al. (2011) found that heavier seeded species actually dispersed farther than lighter ones, and that it was only after accounting for plant height that seed mass was found to have a negative relationship with dispersal distance. In both cases the amount that seed mass contributed to explaining variation in the observed pattern was low (16% and 2% respectively). In another example, evidence from a large scale study of over 300 invasive species in northern Japan revealed a negative relationship between seed size and maximal geographic extent (Akasaka et al., 2012). However, this relationship was only present at the finest spatial resolution ($2km^2$ grid cell grain size) and, when data was aggregated at larger grain sizes ($10km^2$ and $80km^2$), seed size was not related. Given these studies, it is apparent that the relationship between seed size and dispersal ability is one that likely will not further emerge until ample consideration is given to the contextual ecological and environmental factors that are potentially playing a role.

Plant height has also been linked to spread rate, with taller plants tending to disperse their seeds farther distances (Thomson et al., 2011) and consequently having faster rates of spread over geographic space (Travis et al., 2010; Palma et al., 2021). The most thorough spread rate focused study to date found that, for 251 species invasive to Victoria, Australia, taller plants tended to have faster rates of spread across geographic space (Palma et al., 2021). While this evidence is compelling, there is research to suggest that the relationship between height and spread rate is not simple. For example, work on sub-Antarctic plants has shown that dispersal ability and spread rate are not always correlated (Mazibuko et al., 2024). Instead, it was highlighted by the authors how, in their particular environmental context, factors related to demography, competition, and thermal tolerance were more important predictors of species spread. Hence, clarifying the relationship between height and rate of spread requires further study in different contexts and at different scales.

Specific leaf area has been shown to be positively associated with relative growth rate and negatively associated with generation time (Grotkopp et al., 2002; Hamilton et al., 2005; Leishman & Thomson, 2005). Given that these factors have been linked to species having faster rates of spread (Hemrová et al., 2017), it follows that species with higher specific leaf areas should similarly spread faster. Helsen et al. (2021) found empirical evidence of this relationship when they showed that the major driving factor behind the invasion success of *Rosa rugosa* in northern Europe was its large specific leaf area. However, it should be noted that they were assessing 'invasiveness' (a general term that encompasses many differing factors associated with invasion success) rather than spread rate and as such, this work can only characterize the relationship between spread and specific leaf area indirectly. In contrast, Palma et al., (2021) did not find a relationship between specific leaf area and plant spread rate in geographic space when they directly tested the pattern in their multispecies study of plants invasive to Victoria, Australia. This discrepancy illustrates that the pattern between specific leaf area and spread rate is complex and may require further investigation across different ecological contexts to better understand.

Explicitly studying spread rate through climate space has the potential to provide novel insights that may not emerge through the study of solely geographic space. In this thesis I use a global trait database to test hypotheses related to whether key functional traits (seed dry mass, plant height, and specific leaf area) influence spread rate in geographic and climate space for 247 plant species invasive to North America. I evaluate whether these traits can explain variation in: a) the time since introduction required for a species to reach stability in climate space in North America; b) a species maximum 30-year rate of spread (henceforth referred to as MRS) in climate space in North America; and c) a species log-transformed MRS in geographic space in North America. I account for factors that could also influence spread rate (native range size, native niche breadth, growth form). I further investigate the potential explanatory power of these factors in influencing spread rate. I predict that if species have one of the following traits, they will reach climate space stability sooner and have higher MRS's in climate and geographic space: species with lighter seeds, taller species, or species that have higher specific leaf area. To my knowledge, this study is the first to examine patterns between plant functional traits and the spread rate in climate space of introduced species in North America.

2. Methods

2.1) Overview

Using the invasion histories of 247 plant species invasive to North America, I tested nine statistical hypotheses. To do this, I used publicly available records from the TRY global plant trait database (Kattge et al., 2020), climate data from WorldClim, and occurrence data from the global biodiversity information facility (GBIF). I characterized the spread of these species in three different ways and in both the geographic and climatic space of North America since their initial introduction. I then used linear models to assess correlations between the rates at which these species spread in these two spaces and their functional traits. Finally, I tested the strength of these correlations after accounting for relevant covariates: native niche breadth, native range size, and growth form (see Table 7 for model structure). All data manipulation and analyses were conducted in R v4.3.1 (R Core Team, 2023).

2.2) Species Selection

To build my database of trait data, I gathered information on an initial list of 258 plant species classified as invasive according to the Centre for Agriculture and Bioscience International Invasive Species Compendium (CABI, 2022). This is a subset of a list of 815 invasive species analyzed by (Atwater et al., 2018), filtered to include only taxa invasive in North America, and limited to forbs and woody plants (i.e., excluding graminoids, vines, and aquatic plants) (Krajewski et al., 2023). There was no corresponding TRY species ID for 11 of the species in this dataset; thus, they were removed from the study bringing the total number of species down to 247. These species spanned five native ranges (Table 1) and six growth forms (Table 2).

2.3) Defining Climate Space

To define climate space, I used the Ecospat procedure of Cola et al. (2017) as modified by Krajewski et al. (2023). I used global climate data from WorldClim version 2.1 for 1970-2000 (Fick & Hijmans, 2017) at a resolution of 100 km^2. This included 19 bioclimatic variables derived from monthly temperature and rainfall values (https://worldclim.org/data/bioclim.html). I used these variables to construct a principal component analysis of the environmental conditions present in all six of the (invasive and native) ranges considered in my analysis: North America, Eurasia, Europe, Asia, South Africa, and the Mediterranean. This global scale was chosen (as opposed to characterizing climate space in each native range individually) to standardize native niche breadth measurements (see 2.6.3) across all native ranges. I defined climate space as the first two axes of the principal components analysis. The first principal component axis accounted for 53.63% of the variation in climatic data while the second axis represented 21.13%. I quantified the climate space occupied by each species separately in its native range and in its invaded range (i.e., North America). To do this, I extracted WorldClim variables for all GBIF records within each range (native or invasive) and used those data to project the species' occurrences into climate space.

2.4) Invasion Curves in Geographic and Climate Space

I used occurrence records from GBIF to establish how the geographic distribution and occupied climate space of the species changed throughout the course of their invasions in North America (i.e., their invasion curves) (Krajewski et al., 2023). This was done by plotting the time since a species' first recorded occurrence in North America against the cumulative amount of geographic area occupied by this species in this range. The amount of geographic area occupied by a species in North America was estimated at five-year intervals by uniformly dividing the range into a grid of 100 km^2 cells and counting the number of cells containing at least one occurrence of the species at that time.

Invasion curves in climate space were produced in the same way as geographic space. After projecting records into the climate space ordination as described above, I recorded the cumulative amount of climate space occupied (calculated as the proportion of the native niche that is successfully filled in the invasive range) by a species in North America (obtained in 2.3) over the course of their invasion.

2.5) Response Variables

2.5.1) Time to Stability in Climate Space

Time to stability in climate space was defined as the time taken since a species earliest recorded occurrence for it to reach stability in climate space in North America. Following Krajewski et al. (2023), I identified species that had reached climate stability by assessing which had occupied an unchanging amount of climate space for at least 30 years (i.e., slope = 0; excluding the initial lag phase of an invasion). A period of 30 years was chosen to correspond with the calculation of climatic normals (https://climate.weather.gc.ca/climate_ normals/). Of the 247 species included in my study, there were 105 that reached a point of stability in climate space in North America by 2020.

2.5.2) Maximum 30-Year Rate of Spread (MRS) in Climate Space

I took each species' North American climate space invasion curve (produced in 2.4), determined the 30-year period over which the rate of change in climate space occupied was the steepest, and recorded this rate as their MRS in climate space. The amount of climate space occupied by an invasive species in North America was estimated at 5-year intervals from the year of first recorded occurrence. Four species were not considered in any analyses of MRS's in climate space as they had MRS's that were less than zero. Maximum rate of spread over a specified period, rather than overall rate of spread from introduction to 2020, was chosen to account for the variation in year of introduction across species (and thus differing residence times in North America).

2.5.3) Maximum 30-Year Rate of Spread (MRS) in Geographic Space

Using the same procedure as defined above, I took each species' invasion curve in North American geographic space (produced in 2.4), determined the 30-year period over which the rate of change in geographic space occupied was the steepest, and used this rate as their MRS in geographic space. A species' geographic distribution in North America was estimated at 5-year intervals from the year of first recorded occurrence.

2.6) Data Collection

2.6.1) Trait Data

For the 247 species selected, I extracted and cleaned all available data for three chosen traits (seed dry mass: n = 236 species; vegetative plant height: n = 237 species; and specific leaf area: n = 205 species) from the open-source TRY plant trait database (Kattge et al., 2020).

To classify the growth form of each species, I referred to a published dataset that had already cleaned and supplemented categorical growth form data from TRY with further data from high-level taxonomic classifications and a variety of other categorical traits (Díaz et al., 2016, 2022). In the TRY database, records can be reported as a variety of measurement types (i.e., averages, individual measurements, best estimates). In keeping with previously cited work that has used TRY data (Díaz et al., 2016, 2022), I considered each row of data in the database to represent a single measurement for the purpose of calculating averages, regardless of whether it was initially reported as such. I then calculated average trait values for species when multiple trait values were available.

2.6.2) Estimates of Geographic Range Sizes in Native Range

Using the occurrence data, I calculated the geographic size of each species' distribution in its native range (henceforth referred to as native range size). Each native range was uniformly divided up into a grid of 100 km^2 cells. For each species, the number of cells in its native range that it was recorded to have at least one occurrence in by 2020 was tabulated. This number was used as an estimate of its native range size.

2.6.3) Estimates of Niche Breadth in Native Range

For each species I estimated its niche breadth in its native range using Levin's (1968) niche breadth index and the relative density of occurrence points for that species in the climate space. These calculations were performed in R, as implemented in ENMTools package (Warren et al., 2021). In this measure, higher values indicate that a species has a broader niche while lower values indicate a narrower niche.

2.7) Statistical Analysis

There were two parts to the analysis. In the first part of my analysis, I investigated the association between traits (seed dry mass, plant height, and specific leaf area) and each response variable (time to stability in climate space, MRS in climate space, log-transformed MRS in geographic space) using bivariate relationships (n = 9 models; Table 3). I then investigated the effects of each trait on each response variable after taking into account the influence of relevant covariates (growth form and native niche breadth or native range size) (9 extended models; Table 7). In the second part of the analysis, I investigated the power of the covariates to explain variation in the response variables.

2.7.1) Statistical Assumptions, Practices, and Corrections

I visually assessed the normality assumption of the models. I log transformed all three traits and the maximum rate of change in geographic space prior to analysis to ensure there was a linear relationship between independent and dependent variables. To assess homoscedasticity of residuals, I plotted residual values against fitted values for each model and visually checked that the residuals were scattered randomly around zero with no pattern. No issues with homoscedasticity were observed.

I analyzed multicollinearity between traits and covariates before performing analyses. This was done by obtaining variation inflation factors (VIF) or generalized variation inflation factor values (GVIF) for each predictor variable. All VIF and GVIF values were less than two in this analysis, more than surpassing the common threshold for identifying issues with multicollinearity (i.e., being less than five (Neter et al., 1989; Menard, 2002)).

I compared models using multi-model inference. I used the Akaike Information Criterion (AIC) to determine the model of best fit (i.e., model with lowest AIC). To discriminate among competing models, I used a ΔAIC of more than 2 units as a threshold to differentiate between the best model and the model with the next smallest AIC (Burnham & Anderson, 2004).

Because I performed multiple comparisons over the course of this study, I adjusted p-values to account for an increased risk of encountering type I error. I made these adjustments according to the Bonferroni method (Napierala, 2012).

2.7.2) Association between Traits and Spread Rate

To test whether a trait (seed dry mass, plant height, or specific leaf area) explained significantly more variation in response variables than expected at random, I first compared an intercept-only model to a model with a trait. I then tested whether a trait explained significant additional variation after accounting for the combined effect of relevant covariates (i.e., the 'expanded' models). All expanded models included one or two covariates alongside a trait term (Table 7). Either native niche breadth or native range size was included as a covariate in every model. Models using response variables dependant upon climate space (i.e., time to stability in climate space and MRS in climate space) included native niche breadth as a covariate. Those dependant upon geographic space (i.e., log-transformed MRS in geographic space) used native range size. Growth form was also used as a covariate in this analysis. It was included in all expanded models except those that used plant height because the two terms were seen to be significantly related. This was determined by running a type II ANOVA and observing that mean plant height significantly differed by growth form.

2.7.3) Association between Covariates and Spread Rate

To test the extent to which the covariates predicted variation in MRS across climate and geographic space, I used the expanded models (Table 7). To assess the explanatory power that a covariate had on a model's overall ability to explain variation in a response variable against that of a trait, I compared model AICs before and after the variable was removed.

3. Results

3.1) Relationships between Response Variables and Traits

No trait explained variability in time to climate space stability in bivariate models (Table 3; Figure 1) or after accounting for relevant covariates (Table 4; Models 1, 2, and 3 in Table 7). Less than 6% variation was explained in time to climate space stability based on adjusted R^2 (Table 4).

Similarly, no trait explained variability in MRS across climate space in either bivariate (Table 3; Figure 2) or expanded models (Table 5; Models 4, 5, and 6 in Table 7). No more than 13% variation was explained in MRS across space in expanded models (Table 5).

Plant height explained variation in log-transformed MRS across geographic space (Coefficient =-0.21*,* $p < 0.001$, Table 3; Figure 3) even after accounting for covariates (Coefficient =-0.17, $p < 0.01$, model adjusted $R^2 = 0.184$, Table 6; Model 8 in Table 7). Log-transformed MRS in geographic space decreased with plant height (Figure 3). Seed dry mass explained variation in log-transformed MRS in geographic space in bivariate models (Coefficient =-0.11, $p < 0.001$, Table 3; Figure 3), but not after accounting for covariates (Table 6; Model 7 in Table 7). Specific leaf area did not explain variation in log-transformed MRS across geographic space in either bivariate (Table 3) or extended models (Table 6; Model 9 in Table 7).

3.2) Relationships between covariates and response variables

Native niche breadth explained variation in MRS in climate space when either a subset of species having seed dry mass data (n = 233 species), or plant height data (n = 233 species) were used (Coefficient = -0.03 for both, $p < 0.01$ for both, Table 5; Models 4 and 5 in Table 7). MRS in climate space decreased with native niche breadth (Figure 4). Native niche breadth did not explain variation in MRS in climate space on the subset of species with data on specific leaf area (n = 203 species, Table 5; Model 6 in Table 7). There was no relationship between native niche breadth and time to climate space stability in any of the three models I ran using this response variable (Table 4; Models 1, 2, and 3 in Table 7).

Native range size explained variation in log-transformed MRS in geographic space regardless of which subset of species was used (seed dry mass subset: n = 236 species; plant height subset: n = 236 species; specific leaf area subset: n = 205 species) (Table 6; Models 7, 8, and 9 in Table 7). Log-transformed MRS in geographic space increased with native range size (Coefficient = 2.9e-4, 3.1e-4, 2.8e-4 respectively, $p < 0.001$ for all, Table 6; Figure 4).

Growth form explained variation in MRS in climate space only when the subset of species with seed dry mass data was used (n = 233 species) (Coefficient = 0.02, $p < 0.01$, Table 5; Model 4 in Table 7; Figure 5). This was interpreted as MRS in climate space significantly differing between species of different growth forms. Growth form further explained variation in log-transformed MRS in geographic space when the subset of species with specific leaf area data was used (n = 205 species) (Coefficient = 0.63, $p = 0.02$, Table 6; Model 9 in Table 7; Figure 5). Growth form did not explain variation in the time to climate space stability (Table 4; Models 1, 2, and 3 in Table 7; Figure 5).

4. Discussion

Currently there is a dearth of research regarding the direct relationship between functional traits and the rates at which invasive plant species spread across geographic and climate space in invaded ranges. Despite insights having been drawn about how traits influence processes integral to invasion (i.e., competition, dispersal, and tolerance to extreme conditions), there exists little empirical evidence demonstrating the extent to which these trait-facilitated benefits contribute to enabling faster spread. In this study, I assessed how well traits can explain the spread of invasive plants in climate and geographic space. I found that i) plant height could explain a low amount of variation in log-transformed MRS in geographic space; ii) estimates of native niche breadth and native range size explain low amounts of variability in species MRS in climate and geographic space respectively; and iii) log-transformed MRS in geographic space was better explained by traits than MRS in climate space. Conversely, I did not find any relationships between my three response variables and either seed dry mass or specific leaf area.

4.1) Plant Height and MRS in Geographic Space

While I did not find any pattern between plant height and time to stability in climate space or MRS in climate space, taller plants did have a lower log-transformed MRS in geographic space than shorter plants, contrary to my prediction. Past work has shown that taller plants tend to spread faster across geographic space (Palma et al., 2021), and have larger geographic ranges (Ruokolainen & Vormisto, 2000; Mashau et al., 2021; Sporbert et al., 2021). Taller plants are hypothesized to have greater spread rates because they can disperse their seeds greater distances (Thomson et al., 2011). The discrepancy between the literature and my result is likely attributed to the complex relationship between height and spread rate. For instance, while being shorter may decrease local dispersal distances, shorter plants mature earlier and have increased fecundity

(Aarssen et al., 2006). This may explain why, although tall plants generally spread faster (Crawley et al. 1997), in some ecological contexts smaller, faster growing species have greater dispersal rates (Hodkinson & Thompson, 1997).

Ecological context may also influence the relationship between plant height and spread rate. For example, disturbed sites have been found to be among the most susceptible habitats to invasion (Lonsdale, 1999), with past work showing that invasive species are more abundant in locations subject to frequent disturbances (Calinger et al., 2015; Meyer et al., 2021). Successful colonizers of these habitats are often those who are shorter as they can reach maturity faster (i.e., before the next disturbance occurs) (Lake & Leishman, 2004). Thus, the dispersal benefits associated with being taller may not be realized if species cannot complete their lifecycle in the disturbed habitats most available to invaders.

4.2) Native Niche Breadth as a Predictor of MRS in Climate Space

I found a negative relationship between native niche breadth and MRS's in climate space. The results found here are surprising given that the broad environmental tolerance of generalist species should enable them to spread readily through landscapes with relatively diverse climate conditions, establishing large geographic distributions (Wisheu, 1998; Boulangeat et al., 2012). In contrast, specialists will find much of the landscape inhospitable and as such, will encounter more barriers to expansion. Given this, one would expect spread across climate space in invaded ranges to be faster among generalist species.

Native niche breadth may have been found to negatively correlate with MRS in climate space due to the existence of an underlying trade-off between dispersal rate and specialization (Büchi & Vuilleumier, 2016). Through evolutionary processes generalists have adapted to compete in a wide range of conditions (i.e., tolerance to wide ranges of temperature and precipitation) (Kirsch

& Kaproth, 2022). However, this increased ecological breadth may come at the cost of reduced dispersal and colonization ability (Kneitel & Chase, 2004). Meanwhile, the reverse is true for specialists; individuals can persist under narrower environmental conditions but may have instead adapted to excel otherwise (i.e. in dispersal ability or in extreme climates (Thompson et al., 1998; Fridley et al., 2007)). Given this, it is possible that, while species with narrower native niche breadths may have less suitable climate space in North America, they were able to invade this space at a high rate. Conversely, species with broader native niche breadths may have had more suitable climate space in the range overall but may not have been adapted to spread through it as quickly.

Alternatively, the observation of a negative correlation between native niche breadth and MRS in climate space where I expected a positive one may stem from the failure of a species to conserve its niche over the course of an invasion. There is a growing body of work to suggest that when species colonize new ranges, the environmental conditions they are eventually found in differ from those that they occupied in their native ranges (Early & Sax, 2014; Atwater et al., 2018). In the case of species who were initially specialists, niche shifts have been shown to typically result in an expansion of niche breadth, while generalists tend to retain their niche breadth (Early & Sax, 2014). Hence, species with smaller native niche breadths may stand to benefit more from undergoing niche shifts in their introduced range.

4.3) Native Range Size as a Predictor of Log-Transformed MRS in Geographic Space

I found that species with larger native range sizes had higher log-transformed MRS's in geographic space. As mentioned above, species with larger geographic ranges are typically assumed to have broader environmental tolerances (Brown, 1984; Slatyer et al., 2013) and increased dispersal ability (Lloyd et al., 2003; Lowry & Lester, 2006). While I was unable to find any work that directly tested the relationship between a species' native range size and its maximal rate of spread across geographic space in a novel range, my findings align with more general studies that have identified positive relationships between native range size and measures of invasiveness or naturalization success (Bucharova & Van Kleunen, 2009; Shah et al., 2012). These patterns suggest that any spread related relationship associated with having a large geographic distribution in one's native range is carried over when species invade. Hence, it is to be expected that species who were able to spread far in their native range should similarly be able to spread far in invaded ones.

4.4) Comparing the Predictive Ability of Traits and Covariates in Different Spaces

Overall, my traits and covariates were able to better explain variation in my geographic space-based response variable (log-transformed MRS in geographic space) than they were my climate space-based ones (time to stability in climate space and MRS in climate space). Variation in log-transformed MRS in geographic space could have been more robustly explained due to spread through this space being simpler to measure and thus easier to accurately model. Climate space is composed of a collection of interacting factors that vary non-linearly and change over geographic space and time. Moreover, while the variables used to define the climate space present in a region (i.e., temperature, precipitation) are directly measured at a relatively small number of locations (i.e., weather stations), they are interpolated for the majority of the range. The concept of climate space is further complicated by the fact that adjacent niches (i.e., areas of similar yet distinct climatic conditions) are not necessarily geographically adjacent. As such, a species expansion across climate space is additionally dependant on both the geographic distribution of niches and a species ability to spread across geographic space (Smith &

Lundholm, 2012). Hence, estimations of climate space are inherently less accurate than those of geographic space which singularly rely on geographic coordinates.

Native range size was a stronger predictor of log-transformed MRS in geographic space than native niche breadth was of MRS in climate space. The weakness of native niche breadth in relation to native range size as a predictor variable could again point to the possibility of niche shifts occurring in species after they enter novel ranges. Alternatively, it may be a consequence of the complexity of a species' response to climatic conditions. Species often display unimodal distributions along environmental gradients (Whittaker, 1967; Legendre & Legendre, 2012). Their response to one variable (e.g., temperature) may be depend on another (e.g., moisture), and may change over time as a consequence of local adaptation (Leimu & Fischer, 2008).

Finally, alongside my two metrics of MRS, I also examined how well the total amount of time it takes for species to reach climate space stability could be predicted. For this metric I measured how long it took for a species to reach a period of stability in its climate space distribution following its first recorded occurrence. Consequently, the importance of a trait during all stages of invasion (i.e., colonization, establishment, and spread (Theoharides & Dukes, 2007)) is inclusively assessed here. Meanwhile, for my MRS in geographic or climate space response variables, we are primarily looking at the impact a trait has during the landscape spread stage. Given my results, it is possible that plant height is more relevant during the landscape spread stage of an invasion and less significant when we consider all stages together.

4.5) Seed Dry Mass

Among my bivariate models, seed dry mass was shown to negatively correlate with log-transformed MRS in geographic space (Table 3). However, after accounting for relevant covariates, this trait did not significantly explain either the time it took for a species to reach stability in climate space or the MRS of a species in either climate or geographic space. This is inconsistent with a recent large-scale analysis that found that species with lighter seeds had quicker geographic spread rates (Palma et al., 2021). However, in addition to finding this overall general trend, they also showed that different patterns emerged when different seed types were isolated for. Hooked or fleshy seeds that are usually dispersed by animals showed a positive correlation between spread rate and size while smooth, wind-dispersed seeds showed a negative one. Hence, it is possible that the failure to account for the contrasting effects of different dispersal syndromes prevented the emergence of a general relationship in my analysis.

Another reason relationships may not have emerged in my study could be due to the presence of multiple trade-offs in seed mass strategies. I predicted that lighter seed mass would be associated with high MRS's. Generally lighter seeds disperse further and have higher fecundity, thus spreading more quickly across geographic space (Moles & Westoby, 2006; Muller-Landau et al., 2008). However, studies have found a negative relationship between seed mass and latitude (Moles et al., 2007; Gallagher & Leishman, 2012). This is likely due to the changes in climatic conditions associated with moving towards the poles (i.e., colder temperatures, shorter growing seasons) making the benefits of having a small seed (i.e., increased dispersal ability (Muller-Landau et al., 2008)) outweigh those of having a large one (i.e., maternal provisioning (Thomson et al., 2011)). Not accounting for this context driven trade-off may have obscured the relationship between seed dry mass and spread rate in my analysis.

4.6) Specific Leaf Area

Despite predicting the presence of one, there were no significant relationships found between specific leaf area and my three response variables in either my bivariate or expanded models. This finding is consistent with a recent analysis that also did not find a relationship between geographic spread rate and specific leaf area (Palma et al., 2021). To my knowledge, no other work directly testing the relationship between specific leaf area and spread rate in geographic or climate space exists. However, in studies analyzing the links between specific leaf area and adjacent metrics like naturalization success, positive relationships have been identified (Junaedi et al., 2021). Hence, there is reason to believe that specific leaf area and spread rate are connected, even if said connection has failed to emerge in the limited work that has been done.

A lack of pattern between specific leaf area and log-transformed MRS in geographic space could stem from a failure to account for the strong dependence of this trait on environmental context. For example, when *Brachypodium genuense*, a tall grass in the Italian peninsula, grows in productive conditions (deeper soil, medium to high pH values, and northward-facing slopes), it has higher specific leaf areas (Tardella et al., 2017). These larger, thinner, more productive leaves have fast relative growth rates and larger surface areas that more efficiently capture solar radiation (Wilson et al., 1999). Meanwhile when conditions were less favourable, plants shifted their ecological strategy to favour lower specific leaf areas, a response that has been echoed in previous work (Butterfield & Callaway, 2013). This leads plants towards having thicker, smaller leaves that are more tolerant to resource shortages (Fonseca et al., 2000) and more efficient at dealing with high levels of solar irradiance (Gratani et al., 2014). Hence, a trade-off ensues: when conditions are favourable and plants can respond by increasing their specific leaf area, benefitting from the increased rate of spread this provides (indirectly through increased growth rate). Given the coarse resolution of my study, and the absence of intraspecific variation in the TRY data, I was unable to account for such relationships (see 4.8).

4.7) Limitations

One reason for the low explanatory power of functional traits on metrics of spread rate in my study (and likely many others in the field of macroecology) is that of the spatial resolution at which I assessed patterns. Take for example the relationship between spread rate and seed dry mass. This functional trait plays a large role during the colonization stage of an invasion, influencing the likelihood with which a species will spread and persist when initially introduced. However, during this initial period, spread is occurring at a much smaller spatial scale than it does during later stages of invasion. Hence, if too coarse a resolution is used for analysis, this relationship may be missed despite its importance for facilitating species establishment and enabling landscape spread down the line (Suárez-Castro et al., 2018). Others have found that the impact of seed mass during this colonization process is heavily dependent on local environmental conditions that would not emerge at a large geographic scale (i.e., how deeply shaded a habitat is) (Gross & Smith, 1991). Therefore, I may have failed to find patterns between traits and spread rate because I was limited to analyzing spread at too coarse a grain size.

Another potential limiting factor behind the weakness of my observed relationships between traits and spread rate could be seen in the failure to better account for environmental context in my analyses. As discussed above with seed dry mass, certain traits have been shown to correlate either positively or negatively with spread rate according to the environmental conditions in which they find themselves. In this study I attempted to account for environmental context by analyzing how traits influence spread rate in climate space directly. I anticipated this would allow me to evaluate how a trait influenced a species' expansion in climate space separately from its role in geographic dispersion. However, key environmental processes may occur at the local scale, particularly habitat conditions including disturbance (as discussed above), and thus be unaccounted for at the coarse resolution of this study.

4.8) The Caveats of Using Open-Source Data

I relied upon public databases and assumed that the data coming from these sources was by and large of the highest quality (i.e., coordinates given for species occurrence records were precise, specimens were being correctly and consistently identified, and trait values were being appropriately measured, recorded, and curated). I made these assumptions under the notion that, of the vast number of records drawn from (i.e., 1.1 million GBIF records and decades of climate data from WorldClim), enough were accurate to ensure that any erroneous data included would have minimal impact. However, when calculating average trait values, the number of records used to generate these averages was often low. For example, 79 of the 236 species that I had seed dry mass data for had just 10 or fewer records available. Due to the limited availability of records for certain species, I was unable to accurately assess the extent to which traits varied intraspecifically. Moreover, if this limited data was of poor quality, the trait averages I calculated could represent a significant deviation from what they were truly like in nature.

Beyond the issue of record availability, I identified several structural issues with TRY that could have impacted data quality. For example, when researchers contribute to TRY it is possible that they misreport their trait data, confusing one trait variable for another (i.e., reporting a plants average vegetative height as its maximum vegetative height). This can occur because TRY collects data on an extremely wide breadth of traits, many of which can justifiably be confused with each other. TRY curators have tried to account for this by grouping similar traits (i.e., plant height observed, plant height maximum, plant height at 20 years) and providing them with a unifying identifier (i.e., vegetative plant height). While this is the most feasible solution for this quantity of data, it is imperfect in that some of the metrics grouped together are more so adjacent than they are different names for the same metric. This could have served to introduce variability into my results in that, when I used these consolidated values to calculate averages, it is possible that not all the individually used measurements measured precisely the same thing.

Data presented in TRY was also initially confusing to work with because the trait data consolidated within it was not always reported the same way. Depending upon the study from which they originated, trait values presented in TRY for each species were either individual measurements of a single plant or already computed averages taken from a group of unreported individual measurements. This methodology is cause for some concern given that researchers in the past have found that locally taken individual measurements can differ widely from those reported in TRY (Tuthill et al., 2023). Because I treated all measurements in TRY as equal in this analysis, these two types of data held equal weight when calculating my trait averages across species. While this was the most feasible way to organize this data, treating it as such could lead to a decrease in the level of precision of trait averages computed. Take for example a species that had 10 reports of seed dry mass available in TRY for me to calculate a trait average from. Of these reports, nine are individual measurements (i.e., the weight of one seed) while one is an average taken from 32 unreported seed masses. In this scenario, there are effectively 41 seeds being used to calculate an average but 90% of the weight of that average is being lent towards 9 seeds. For species that are highly variable this can decrease precision as, even if measures are accurate, I may be disproportionately representing a minority of the true total observations in my calculated averages.

A further limitation of using TRY data is that the trait measurements contained within originated from a wide range of locations. In TRY, it is not possible to identify the geographic location of measurement for a recorded trait value for most entries. Therefore, reported trait values may originate from a species' native or invaded range. Given this, I assumed there was no adaptation in the trait in the invaded range. However, evidence suggests this may not be the case. For example, invasive plants have been shown to grow larger in their invaded ranges (e.g. Willis & Blossey, 1999) and some report that even growth strategies can change (Leishman et al., 2014). Furthermore, this assumption is less likely to hold as the invasion progresses. Invaders can also adapt to their new environments, further differentiating themselves from their counterparts that remain in their native range (Clements et al., 2004; Montesinos, 2022). Given this, it is possible that trait data taken from a species' native range or from the early stages of their invasion could be a poor representation of the species current state in North America, especially if it has been invading for a longer duration. This in turn may have skewed the relationships that I drew between traits and metrics of spread rate in climate and geographic space.

4.8) Low Explanatory Power in Ecological Studies

Even though I managed to find some significant relationships between metrics of invasive plant spread in North America and a group of functional traits and covariates, most of my results were non-significant. In fact, of the 24 terms used across my 9 expanded models, just 8 were shown to significantly impact their models' ability to explain variation in its respective response variable (Table 4,5,6). The correlations I did find were weak (Model adjusted R^2 value < 0.25 across all 9 expanded models). However, macroecological studies often reveal results of a similar or even weaker strength to mine (Møller & Jennions, 2002; Anderegg, 2023). For example, Thomson et al. (2011) showed that seed mass could explain 16% of variation in dispersal distance while Moles et al. (2009) found that precipitation of wettest month could explain 25.6% of variation in global plant height.

The problem of low coefficients of determination is one that has increasingly plagued the field of ecology as it has become more focused on quantitative results (Lin & Wiegand, 2023). This issue stems from the challenge of designing scientific studies that account for the inherent complexity of ecological systems. These are not static systems but rather ones that are constantly responding to changing ecological interactions and evolutionary pressures among species. For these reasons, and many more (Møller & Jennions, 2002), large amounts of variance often goes unexplained in ecological studies and it can become extremely difficult for large coefficients of determination to emerge.

Given this context, the results presented in this thesis should highlight the challenges associated with identifying ecological relationships at large scales. While weak statistically, these were the patterns that were strong enough to emerge despite all the inherent variability of an ecological system. However, regardless of their value relative to other studies in the field, these coefficients of determination remain objectively low. Therefore, while these findings should not be discounted for the purposes of better understanding the invasion process in climate and geographic space, they at their foremost reassert the limited potential these traits/covariates alone have for explaining variability in rates of spread.

5. Conclusion

None of the traits I analyzed significantly explained variation in either time to stability in climate space or MRS in climate space. Plant height did significantly explain variation in the log-transformed MRS in geographic space of species but seed dry mass and specific leaf area could not. Despite the general absence of patterns between traits and my various metrics of spread in climate and geographic space, I did find that native niche breadth and native range size often had significant relationships with their respective response variable(s). Moreover, these covariates accounted for most of the overall predictive power of my expanded models. When confronted with these results, I considered why stronger overarching general trends between key traits and spread rates did not emerge in either climate or geographic space. I hypothesize that the importance of a trait to overall invasion rate in climate space was more dependent upon environmental context (i.e., certain traits being beneficial to spread rate in some habitats while the same traits are detrimental in others) than first thought. Moreover, it is likely that the influence of a trait varies greatly over the stages of invasion. As such, metrics like time to climate space stability that assess the role of a trait over all invasion stages were inherently more complex than ones like MRS that apply primarily to one stage (i.e., landscape spread).

Overall, my findings suggest that trait-response models supplemented by a few covariates have limited explanatory power with respect to spread rate in either climate or geographic space at the continental scale. While these simple models offer some insight towards understanding how invasive plants spread, they mostly reinforce the notion that the relationships between traits and spread rate is complex. Future work might produce more fruitful results with a more focused scope, either geographically, taxonomically, as accounting for environmental context and interactions among traits at the continental scale for a large number of species presents serious challenges.

Tables

Table 1. Breakdown of the native geographic ranges and number of species (n=247) from each range included in this study.

Native Range	Number of Species
Eurasia	95 (38.5%)
Mediterranean	70 (28.3%)
Europe	43 (17.4%)
Asia	28 (11.3%)
South Africa	11 (4.5%)

Table 2. Breakdown of growth forms and number of species (n=247) from each growth form included in this study.

Growth Form	**Number of Species**
Herbaceous	193 (78.1%)
Tree	18 (7.3%)
Shrub	18 (7.3%)
Tree/Shrub	10 (4.0%)
Climber	7 (2.8%)
Fern	1 (0.4%)

Table 3. Coefficients and standard errors (SE) for trait terms in simple bivariate models. The change in AIC presented is the difference between an intercept-only model and a model with the trait. Models can be interpreted as improved if AIC decreases by more than 2 units when a term is removed, and vice versa. Sample sizes (n), F-values and their corresponding p-values are also presented. P-values that have been adjusted for multiple comparisons according to the Bonferroni method (n=9) are presented. Bolded results indicate statistically significant terms (α=0.05).

Response Variable	n	Trait	Coefficient	SE	ΔAIC	F-value	Adj. p
Time to climate space stability	101	Log Seed Dry Mass	-3.68	2.78	-0.22	1.76	1
	103	Log Plant Height	-10.29	4.63	2.92	4.93	0.27
	91	Log Specific Leaf Area	8.12	10.61	-1.4	0.59	1
Maximum rate of spread in climate space	233	Log Seed Dry Mass	-5.7e-4	4.3e-4	-0.25	1.75	1
	233	Log Plant Height	-8.4e-4	7.5e-4	-0.73	1.26	1
	203	Log Specific Leaf Area	-3.7e-4	2.0e-3	-1.97	0.03	1
Log-transformed maximum rate of spread in geographic space	**236**	**Log Seed Dry Mass**	**-0.11**	**0.03**	**15.36**	**17.87**	**3.1e-4**
	236	**Log Plant Height**	**-0.21**	**0.05**	**19.47**	**22.29**	**3.6e-5**
	205	Log Specific Leaf Area	0.32	0.13	3.97	6.00	0.18

Table 4. The relative importance of species' traits and other covariates in predicting time to climate space stability. The resulting change in expanded model AIC and degrees of freedom after removal of a given term is given for each model. Models can be interpreted as improved if AIC decreases by more than 2 units when a term is removed, and vice versa. Sample sizes (n), coefficients, standard errors (SE), F-values and their corresponding p-values are also presented. P values that have been adjusted for multiple comparisons according to the Bonferroni method (n=9) are presented. Expanded model adjusted R^2 values and partial R^2 values are also presented. Bolded results indicate statistically significant terms (α=0.05).

Focal Trait	**n**	**Term**	**Coefficient**	**SE**	**Δdf**	**ΔAIC**	**F-value**	**Adj. p**	**Model Adjusted / Partial R^2**
Seed Dry Mass	101	Expanded Model	-	-	-	0	-	-	0.03
		Log Seed Dry Mass	-5.8	3.43	1	1.02	2.85	0.81	0.03
		Native Niche Breadth	100.74	54.45	1	1.62	3.42	0.54	0.04
		Growth Form	82.81	12.92	4	-4.69	0.78	1	0.03
Plant Height	103	Expanded Model	-	-	-	0	-	-	0.06
		Log Plant Height	-10.34	4.57	1	3.13	5.11	0.27	0.05
		Native Niche Breadth	95.48	51.23	1	1.51	3.47	0.63	0.03
Specific Leaf Area	91	Expanded Model	-	-	-	0	-	-	0.001
		Log Specific Leaf Area	3.35	11.37	1	-1.91	0.09	1	0.001
		Native Niche Breadth	84.90	55.27	1	0.52	0.13	1	0.03
		Growth Form	79.87	12.60	4	-4.97	0.59	1	0.03

Table 5. The relative importance of species' traits and other covariates in predicting maximum 30-year rate of spread in climate space. The resulting change in expanded model AIC and degrees of freedom after removal of a given term is given for each model. Models can be interpreted as improved if AIC decreases by more than 2 units when a term is removed, and vice versa. Sample sizes (n), coefficients, standard errors (SE), F-values and their corresponding p-values are also presented. P values that have been adjusted for multiple comparisons according to the Bonferroni method (n=9) are presented. Expanded model adjusted R^2 values and partial R^2 values are also presented. Bolded results indicate statistically significant terms (α=0.05).

Focal Trait	n	Term	Coefficient	SE	Δdf	ΔAIC	F-value	Adj. p	Model Adjusted / Partial R^2
Seed Dry Mass	233	Expanded Model	-	-	-	0	-	-	0.13
		Log Seed Dry Mass	-4.2e-4	4.6e-4	1	-1.16	0.81	1	0.004
		Native Niche Breadth	**-0.03**	**7.5e-3**	**1**	**12.14**	**14.13**	**2.0e-3**	**0.06**
		Growth Form	**0.02**	**2.1e-3**	**4**	**15.84**	**6.08**	**1.1e-3**	**0.10**
Plant Height	233	Expanded Model	-	-	-	0	-	-	0.05
		Log Plant Height	-5.4e-4	7.0e-4	1	-1.45	0.59	1	0.003
		Native Niche Breadth	**-0.03**	**7.8e-3**	**1**	**9.45**	**11.59**	**7.0e-3**	**0.05**
Specific Leaf Area	203	Expanded Model	-	-	-	0	-	-	0.09
		Log Specific Leaf Area	-1.8e-3	2.0e-3	1	-1.16	0.82	0.37	0.004
		Native Niche Breadth	-0.02	8.7e-3	1	5.14	7.03	0.08	0.03
		Growth Form	0.02	2.4e-3	5	6.24	3.26	0.07	0.08

Table 6. The relative importance of species' traits and other covariates in predicting log-transformed maximum 30-year rate of spread in geographic space. The resulting change in expanded model AIC and degrees of freedom after removal of a given term is given for each model. Models can be interpreted as improved if AIC decreases by more than 2 units when a term is removed, and vice versa. Sample sizes (n), coefficients, standard errors (SE), F-values and their corresponding p-values are also presented. P values that have been adjusted for multiple comparisons according to the Bonferroni method (n=9) are presented. Expanded model adjusted R^2 values and partial R^2 values are also presented. Bolded results indicate statistically significant terms (α=0.05).

Focal Trait	n	Term	Coefficient	SE	Δdf	ΔAIC	F-value	Adj. p	Model Adjusted / Partial R^2
Seed Dry Mass	236	Expanded Model	-	-	-	0	-	-	0.21
		Log Seed Dry Mass	-0.05	0.03	1	0.7	2.63	0.99	0.01
		Native Range Size	**2.9e-4**	**5.8e-5**	**1**	**23.29**	**25.90**	**6.8e-6**	**0.10**
		Growth Form	0.63	0.13	4	5.49	3.37	0.09	0.05
Plant Height	236	Expanded Model	-	-	-	0	-	-	0.18
		Log Plant Height	**-0.17**	**0.04**	**1**	**12.7**	**14.97**	**1.3e-3**	**0.06**
		Native Range Size	**3.1e-4**	**5.7e-5**	**1**	**26.74**	**30.17**	**9.0e-7**	**0.11**
Specific Leaf Area	205	Expanded Model	-	-	-	0	-	-	0.20
		Log Specific Leaf Area	0.02	0.13	1	-1.96	0.03	1	0.0001
		Native Range Size	**2.8e-4**	**6.1e-5**	**1**	**19.59**	**21.88**	**4.9e-5**	**0.10**
		Growth Form	**0.63**	**0.16**	**5**	**9.92**	**4.02**	**0.02**	**0.09**

Table 7. Summary of expanded models and expanded model structure.

Model #	Response Variable		Trait		Covariate 1		Covariate 2
1	Time to climate space stability	~	Seed dry mass	+	Native niche breadth	+	Growth form
2	Time to climate space stability	~	Plant height	+	Native niche breadth	+	NA
3	Time to climate space stability	~	Specific leaf area	+	Native niche breadth	+	Growth form
4	Maximum 30-year rate of spread in climate space	~	Seed dry mass	+	Native niche breadth	+	Growth form
5	Maximum 30-year rate of spread in climate space	~	Plant height	+	Native niche breadth	+	NA
6	Maximum 30-year rate of spread in climate space	~	Specific leaf area	+	Native niche breadth	+	Growth form
7	Log-transformed maximum 30-year rate of spread in geographic space	~	Seed dry mass	+	Native range size	+	Growth form
8	Log-transformed maximum 30-year rate of spread in geographic space	~	Plant height	+	Native range size	+	NA
9	Log-transformed maximum 30-year rate of spread in geographic space	~	Specific leaf area	+	Native range size	+	Growth form

Figures

Figure 1. Relationships between time to climate space stability and (a) log seed dry mass (mg) (n=101), (b) log plant height (m) (n=103), and (c) log specific leaf area (mm^2/mg) (n=91).

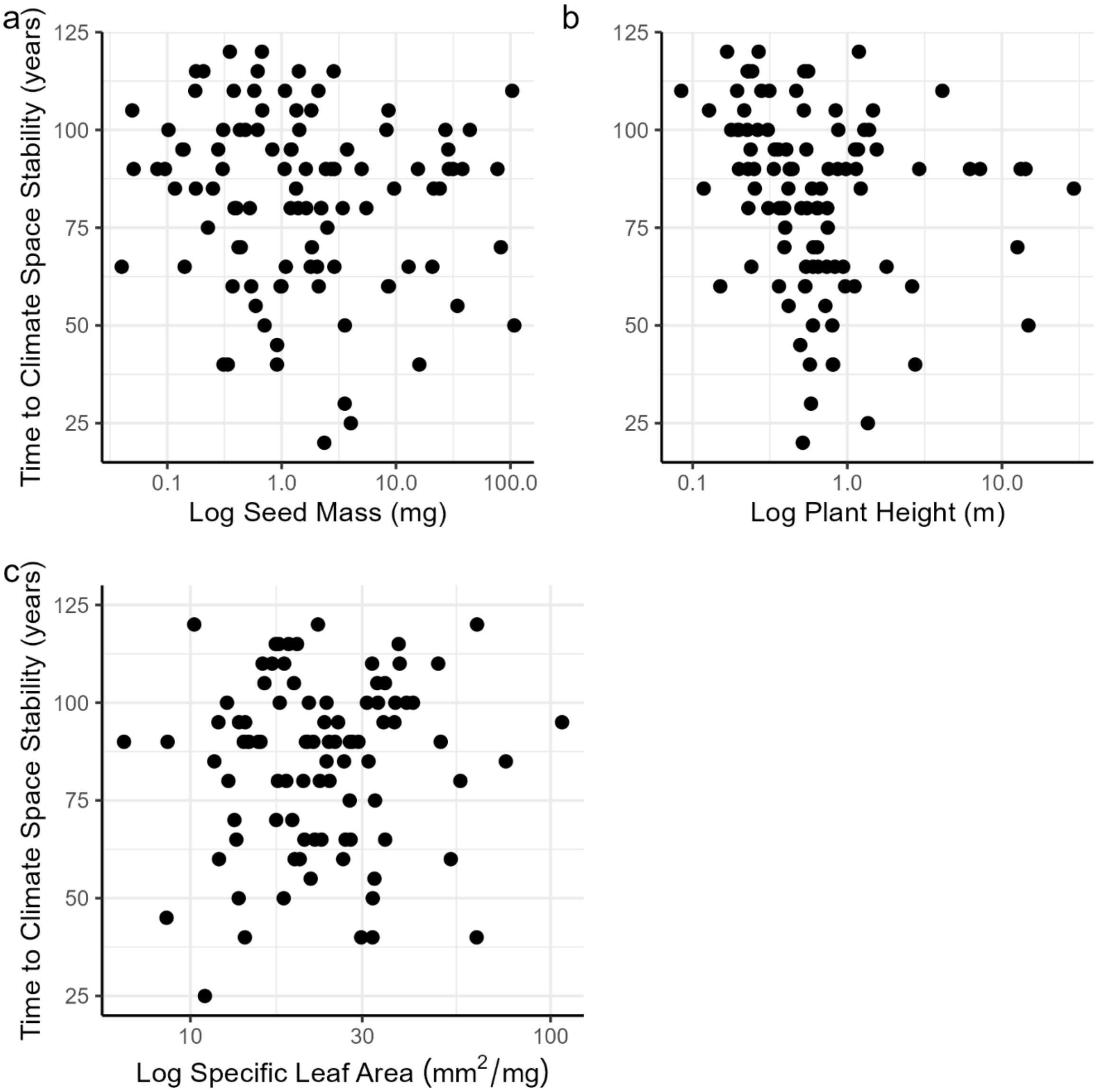


Figure 2. Relationships between maximum 30-year rate of spread in climate space and (a) log seed dry mass (mg) (n=233), (b) log plant height (m) (n=233), and (c) log specific leaf area (mm^2/mg) (n=203).

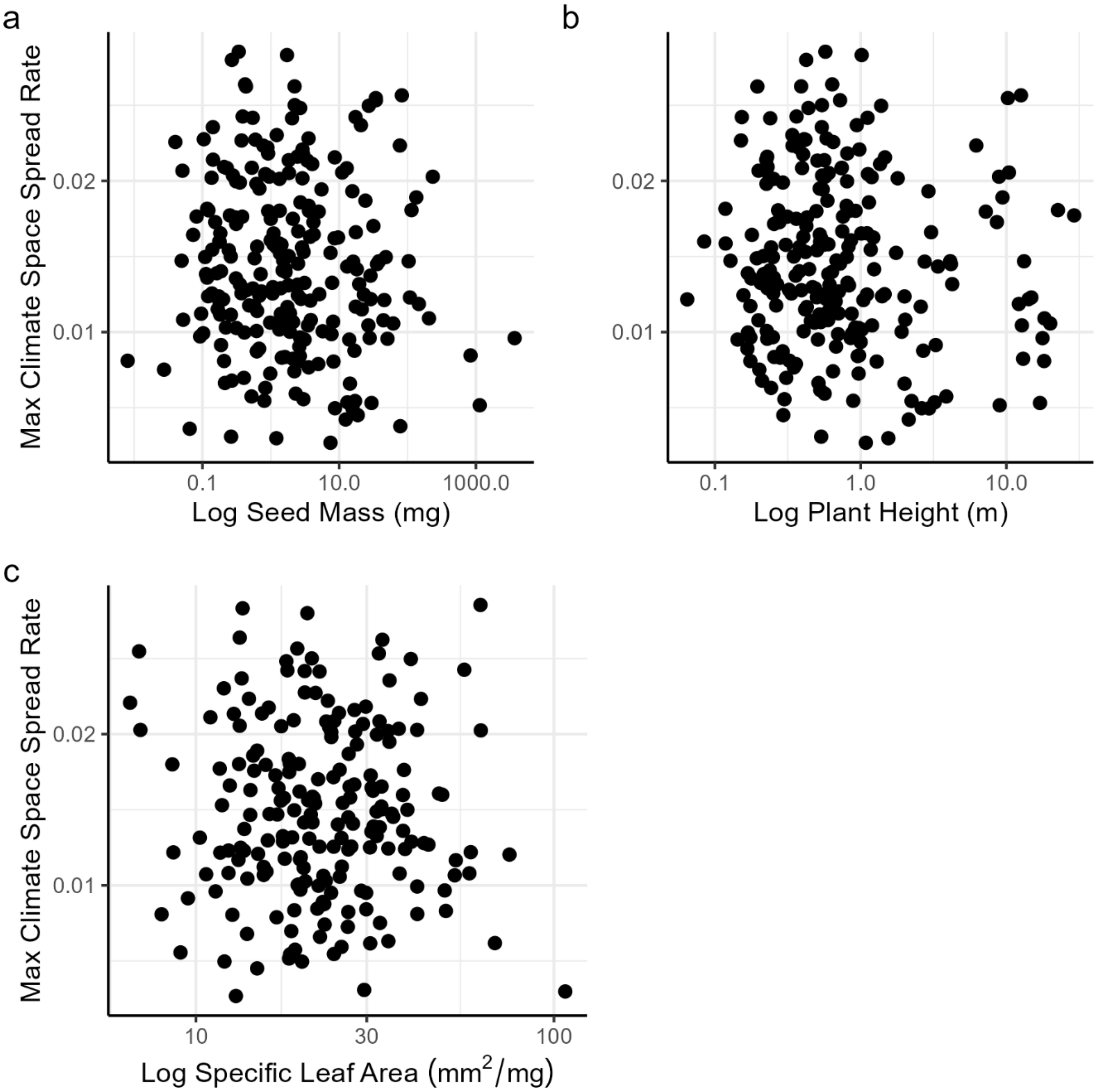


Figure 3. Relationships between log-transformed maximum 30-year rate of spread in geographic space and (a) log seed dry mass (mg) (n=236), (b) log plant height (m) (n=236), and (c) log specific leaf area (mm^2/mg) (n=205). A line of best fit and shaded regions representing the bounds of 95% confidence intervals are shown for log plant height as it was found to significantly explain variation in the extended model for this response variable (α=0.05).

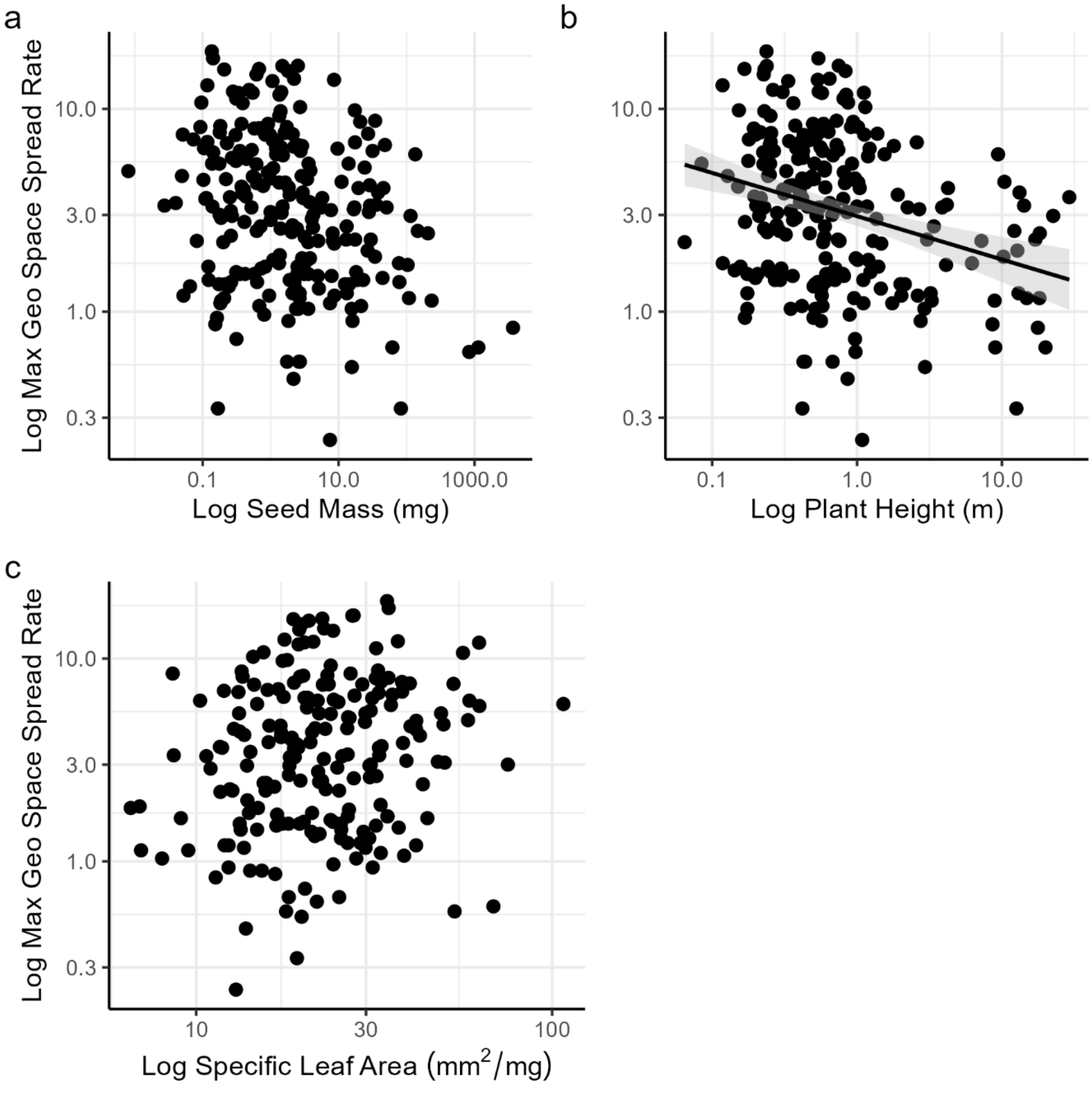


Figure 4. Relationships between (a) time to climate space stability (years) and native niche breadth (n= 105), (b) maximum 30-year rate of spread in climate space and native niche breadth (n=243), and (c) log-transformed maximum 30-year rate of spread in geographic space and native range size (n=247).

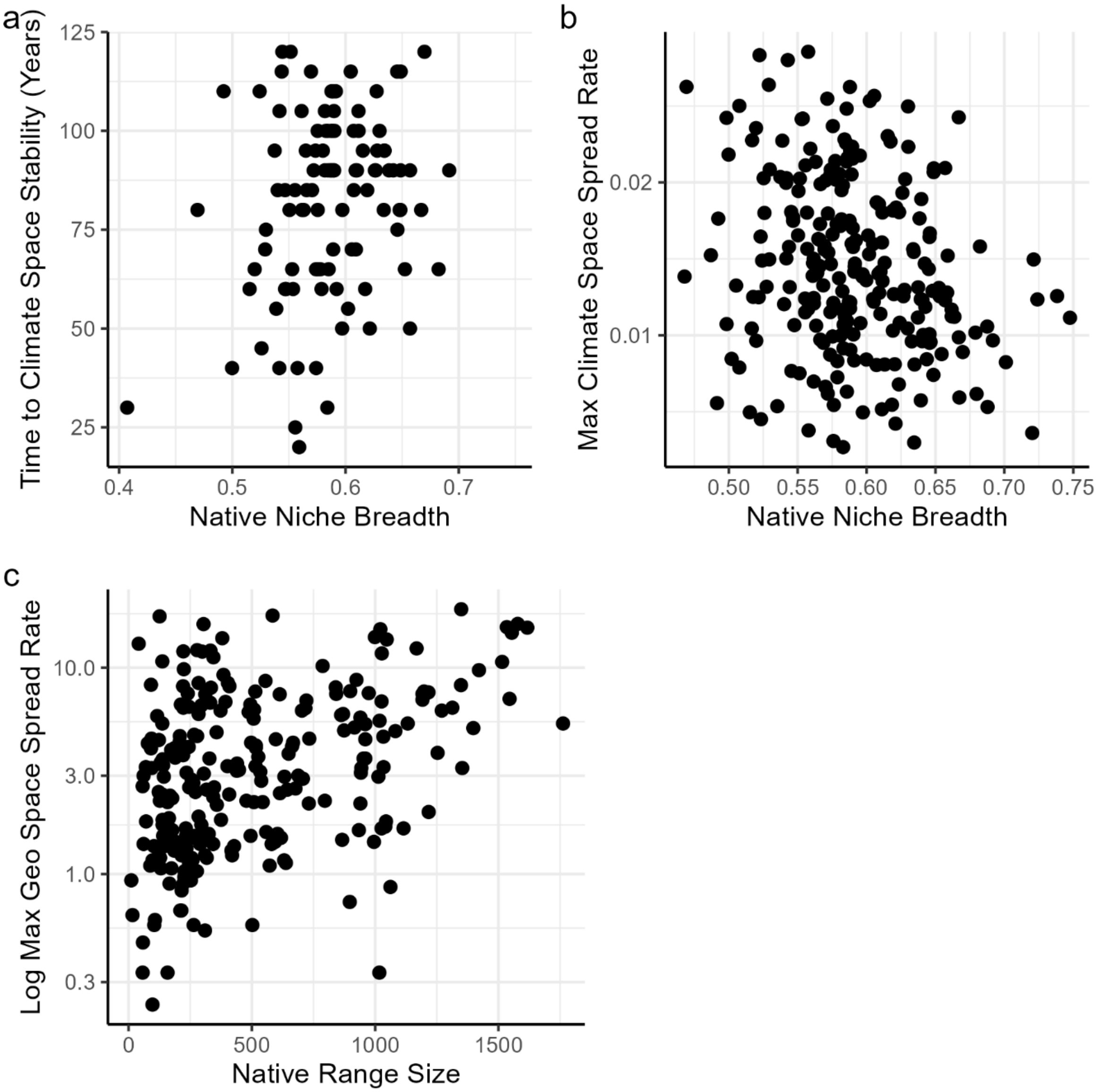
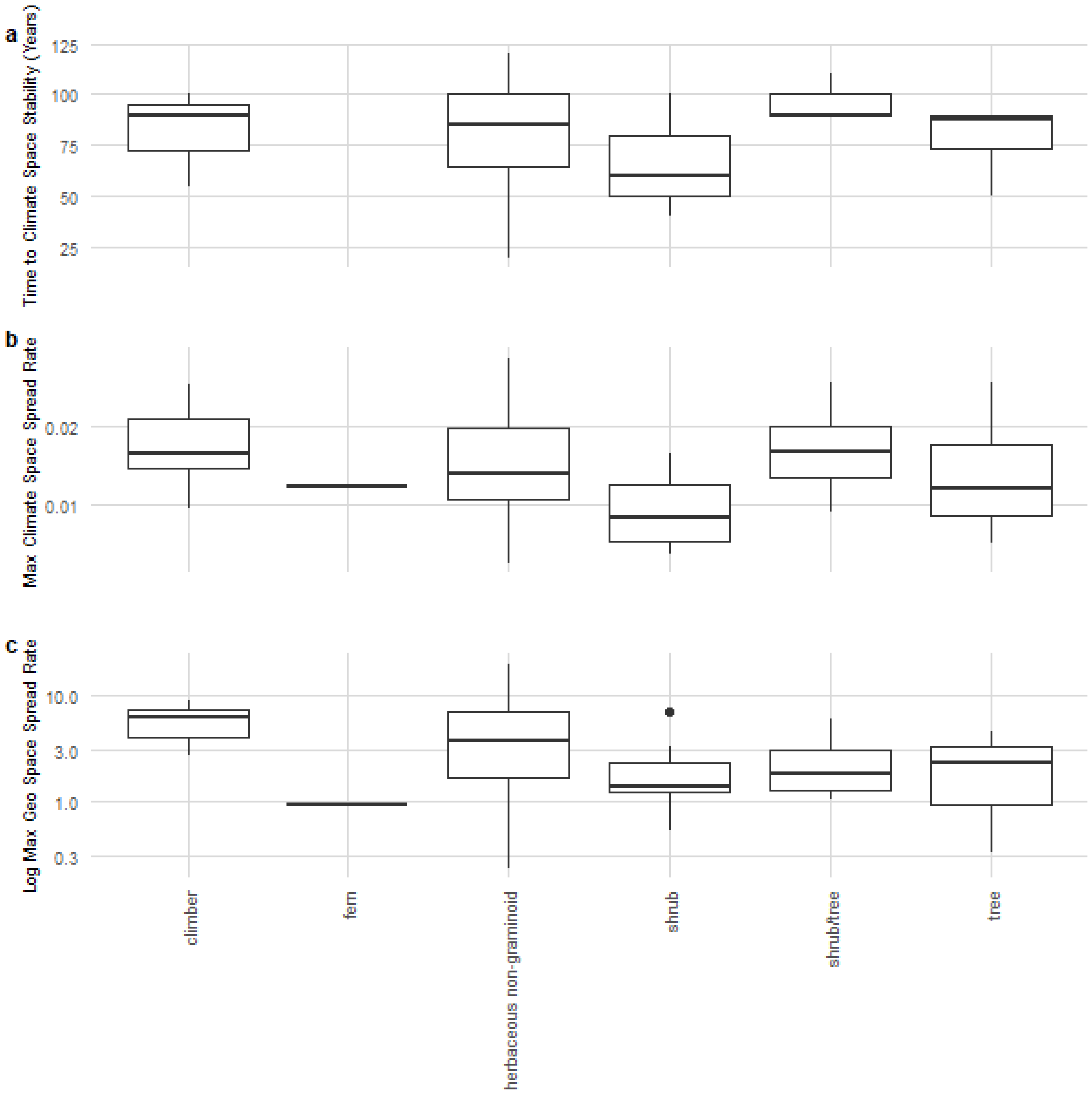


Figure 5. Boxplots showing the association between growth forms and (a) time to climate space stability (years) (n=105), (b) maximum 30-year rate of spread in climate space in (n=243), and (c) log-transformed maximum 30-year rate of spread in geographic space (n=247). Shown for each growth form are bolded horizontal lines representing the median value and vertical lines extending to respective minimum and maximum values. Points falling 1.5 times outside either end of the inter-quartile range are also shown.



Appendix

Table S1. Term p-values before and after being adjusted according to the Bonferroni adjustment for multiple comparisons for bivariate models. P-values were multiplied by nine as nine hypotheses were tested. Bolded rows indicate that a previously significant result (α=0.05) is no longer significant following an adjustment.

Response Variable	Trait	Initial p	Bonferroni- adjusted p	Significance Boundary Crossed?
Time to climate space stability	Log Seed Dry Mass	0.19	1	No
	Log Plant Height	**0.03**	**0.27**	**Yes**
	Log Specific Leaf Area	0.45	1	No
Maximum rate of spread in climate space over a 30-year period	Log Seed Dry Mass	0.19	1	No
	Log Plant Height	0.26	1	No
	Log Specific Leaf Area	0.86	1	No
Logged maximum rate of spread in geographic space over a 30-year period	Log Seed Dry Mass	3.4e-5	3.1e-4	No
	Log Plant Height	4.0e-6	3.6e-5	No
	Log Specific Leaf Area	**0.02**	**0.18**	**Yes**

Table S2. Term p-values before and after being adjusted according to the Bonferroni adjustment for multiple comparisons for expanded models using time to climate space stability as a response variable. P-values were multiplied by nine as nine hypotheses were tested. Bolded rows indicate that a previously significant result (α=0.05) is no longer significant following an adjustment.

Focal Trait	Term	Initial p	Bonferroni-adjusted p	Significance Boundary Crossed?
Seed Dry Mass	Log Seed Dry Mass	0.09	0.81	No
	Native Niche Breadth	0.06	0.54	No
	Growth Form	0.54	1	No
Plant Height	**Log Plant Height**	**0.03**	**0.27**	**Yes**
	Native Niche Breadth	0.07	0.63	No
Specific Leaf Area	Log Specific Leaf Area	0.77	1	No
	Native Niche Breadth	0.13	1	No
	Growth Form	0.59	1	No

Table S3. Term p-values before and after being adjusted according to the Bonferroni adjustment for multiple comparisons for expanded models using maximum 30-year rate of spread in climate space as a response variable. P-values were multiplied by nine as nine hypotheses were tested. Bolded rows indicate that a previously significant result (α=0.05) is no longer significant following an adjustment.

Focal Trait	Term	Initial p	Bonferroni-adjusted p	Significance Boundary Crossed?
Seed Dry Mass	Log Seed Dry Mass	0.37	1	No
	Native Niche Breadth	2.2e-4	2.0e-3	No
	Growth Form	1.2e-4	1.1e-3	No
Plant Height	Log Plant Height	0.44	1	No
	Native Niche Breadth	7.8e-4	7.0e-3	No
Specific Leaf Area	Log Specific Leaf Area	0.37	1	No
	Native Niche Breadth	**8.7e-3**	**0.08**	**Yes**
	Growth Form	**7.5e-3**	**0.07**	**Yes**

Table S4. Term p-values before and after being adjusted according to the Bonferroni adjustment for multiple comparisons for expanded models using log-transformed maximum 30-year rate of spread in geographic space as a response variable. P-values were multiplied by nine as nine hypotheses were tested. Bolded rows indicate that a previously significant result (α=0.05) is no longer significant following an adjustment.

Focal Trait	Term	Initial p	Bonferroni-adjusted p	Significance Boundary Crossed?
Seed Dry Mass	Log Seed Dry Mass	0.11	0.99	No
	Native Range Size	7.5e-7	6.8e-6	No
	Growth Form	**0.01**	**0.09**	**Yes**
Plant Height	Log Plant Height	1.4e-4	1.3e-3	No
	Native Range Size	1.0e-7	9.0e-7	No
Specific Leaf Area	Log Specific Leaf Area	0.86	1	No
	Native Range Size	5.4e-6	4.9e-5	No
	Growth Form	1.7e-3	0.02	No

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