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Environmental matching mediates the naturalization success of cultivated alien plants in Southern Africa

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Abstract

The rapid growth of global trade, tourism, and human mobility has facilitated the widespread introduction of alien plant species. A substantial proportion of these species managed to naturalize outside of their native ranges. However, it remains unclear whether certain plant characteristics contribute to a higher likelihood of naturalizing, due to conferring a higher ability to pass environmental filters. This study aims to elucidate the interplay of plant characteristics and environmental conditions on naturalization success of alien species. By analyzing a dataset of 1,407 cultivated alien plants in Southern Africa, the study distinguishes between the direct effects of the plant characteristics, including phylogenetic distance to native flora, seed mass, plant height, native origins, native range size and growth forms on naturalization success and the indirect effects mediated by climatic suitability (assessed using species distribution modeling). My findings show the importance of climatic suitability in determining naturalization success, with naturalized cultivated plants demonstrating greater climatic suitability compared to non-naturalized species. I found positive direct associations between naturalization success and the plant characteristics: seed mass, plant height, species native to Southern America, Africa and Tropical Asia, short-lived herbaceous species and native range size. Whereas, the associations of naturalization success with phylogenetic distance to the native flora and species native to Europe were negative. Most of these associations were mediated through climatic suitability, highlighting the crucial role of climate matching in the naturalization of alien plants. Accordingly there is a need for future research to consider the mediating role of climatic suitability.

Keywords

Biological traits, Drivers of invasion, Invasion, Non-native plants, Ornamental plants, Southern Africa, Species distribution modeling

Zusammenfassung

Das rapide Wachstum des globalen Handels, Tourismus und Mobilität haben zu einem massiven weltweiten Anstieg gebietsfremder Pflanzenarten geführt. Ein großer Teil dieser Arten hat es geschafft in neuen Lebensräumen, außerhalb ihrer natürlichen Verbreitung, einzubürgern. Es ist jedoch unklar, ob bestimmte Pflanzeneigenschaften die Einbürgerungswahrscheinlichkeit begünstigen, indem sie Arten die Fähigkeit verleihen Umweltfilter zu passieren. Ziel dieser Arbeit ist es, Aufschluss über die Pflanzeneigenschaften und Umwelteinflüsse zu geben, welche den Einbürgerungserfolg von gebietsfremden Arten bestimmen. Durch die Analyse von 1,407 kultivierten gebietsfremden Arten im südlichen Afrika, unterscheidet diese Arbeit zwischen den direkten Effekten der Pflanzeneigenschaften: phylogenetische Distanz zur einheimischen Flora, Samenmasse, Wuchshöhe, Herkunft, Größe der natürlichen Verbreitung, sowie Wuchsformen und indirekten Effekten, welche durch die klimatische Eignung (ermittelt durch Artverbreitungsmodelle) mediiert sind. Meine Ergebnisse zeigen die Bedeutung der klimatischen Eignung hinsichtlich des Einbürgerungserfolges, da sie postulieren, dass eingebürgerte kultivierte gebietsfremde Pflanzenarten eine höhere klimatische Eignung zeigen als nicht-eingebürgerte Arten. Des Weiteren habe ich positive direkte Verbindungen zwischen dem Einbürgerungserfolg und den Pflanzeneigenschaften Wuchshöhe, Herkunft aus Südamerika, Afrika und tropischem Asien, krautigen kurzlebigen Wuchsformen und der Verbreitung im Ursprungsgebiet gefunden. Wohingegen die Verbindungen zwischen Einbürgerungserfolg und der phylogenetischen Distanz zur einheimischen Flora, sowie der Herkunft Europa negativ waren. Die meisten dieser Zusammenhänge wurden jedoch durch die klimatische Eignung vermittelt, was die Wichtigkeit der Übereinstimmung des Klimas in der ursprünglichen und neuen Verbreitung von gebietsfremden Arten im Einbürgerungsprozess betont. Folglich, hebt diese Arbeit die Dringlichkeit hervor, die vermittelnde Rolle der klimatischen Eignung in zukünftiger Forschung zu berücksichtigen.

Introduction

The accelerating pace of global trade, tourism and human mobility has led to a substantial increase in the exchange of biota among historically isolated regions (Meyerson et al. 2007; Hall 2015). This has resulted in a ubiquitous man-made introduction of new alien plant species (Banks et al. 2015; Hulme et al. 2021; Perrings et al. 2005). Over 13,000 of these introduced species managed to establish self-sustaining populations outside their native ranges (i.e. naturalize; van Kleunen et al. 2015). A subset of these naturalized species has become invasive and therefore poses a great threat to global biodiversity as well as ecosystem functioning in their new environments (Secretariat of the Convention on Biological Diversity 2006). In 2019, the UN finally recognized invasive alien plant species (IAPS) as major drivers of biodiversity loss moving this persisting topic more into the public eye (Díaz et. al 2019). Facilitation of pathogen spread, predation and competition are only a few examples of the manifold impacts that IAPS might have on native species (Settele et al. 2010). Therefore, investigating the drivers of plant naturalization success has become a major task in ecology.

Several studies have investigated plant characteristics and functional traits that are associated with successful alien plants. Invasion success, for instance, has been shown to be positively correlated with phylogenetic distance to the native flora as such plants are able to occupy empty niches (Divisek et al. 2018; Omer A. et al. 2022). Plant characteristics like fast growth and self-compatibility have also been found to be important in the success of alien plants (van Kleunen et al. 2015). Functional traits such as seed mass, plant height and specific leaf area were also associated with plants' invasion success (Mayer et al. 2017). Moreover, Geographical characteristics such as native origins and native range size are also associated with alien plants' success (Fristoe et al. 2021; Omer et al. 2021). Other researches address the environmental variables which influence the establishment of alien plant species. Climatic suitability for, example, is positively associated with the establishment of Chinese woody species in multiple countries (Feng et al. 2016). Moreover, climatic suitability will allow several of the currently cultivated alien plants in Europe to escape cultivation in the future, which might increase their naturalization risk (Dullinger et al. 2016). Environmental similarity between native and target alien ranges is thus a vital driver of the naturalization and spread of alien plants (Richardson et al. 2012). It reflects the pre-adaptation of non-native plants to the new environmental conditions. This is indeed depicted in the climatic similarity between the native and non-native ranges of most naturalized alien plants (Lambdon et al. 2008; Wiens et al. 2005; Richardson et al. 2012).

Thus, species characteristics and climatic suitability are both associated with alien plant naturalization success. Particular species characteristics and functional traits are indicative of their adaptation to their environment (Reich 2014). The latter relationship could conceal the relationship between functional traits and characteristics of alien plants and naturalization success. In other words, it is not clear if species with specific characteristics are more likely to naturalize due to their increased likelihood of passing the environmental filter. For example, species introduced from the continent of Australasia have a higher naturalization success rate in Southern Africa (Omer et al. 2021). This could be, solely because they found a high climatic suitability in the environmentally similar region of Southern Africa. Climbers plants, another example, showed a high naturalization success in Southern Africa, but a lower rate of naturalization in Great Britain (Kinlock et al. 2022). These contradictory results indicate that the higher climatic suitability of the warmer Southern Africa indeed promotes climbers' establishment more than the temperate climate of Great Britain. Plant characteristics and climatic suitability index could be used to disentangle the direct effects of plant characteristics on naturalization success from the indirect effects mediated by climatic suitability.

The introduction of living organisms to non-native regions has occurred through various means and for different purposes, as noted by Hulme et al. (2008). As a result, it can be challenging to identify all the species that have been introduced to a specific area. However, intentional introduction for cultivation is the primary means for vascular plant species, according to Lambdon et al (2008) and Faulkner et al. (2020). Many of these species are grown in home gardens and have economic value, as highlighted by van Kleunen et al (2018) and van Kleunen et al. (2020). Consequently, regional cultivated plant checklists, such as the currently used checklist of cultivated flora of Southern Africa, are critical for evaluating naturalization risks.

The main aim of this study is to gain a better understanding of the role of plant characteristics and environmental conditions on the naturalization success of alien plant species. As naturalization is the stage just before invasion along the invasion process gradient (Richardson et al. 2000), further knowledge on this topic may enable decision makers to take actions sufficiently early to prevent species from becoming invasive in the first place. The direct effects of plant characteristics on naturalization success will be disentangled from the indirect effects which are mediated by the climatic suitability using the list of South African cultivated alien flora. A statistical analysis containing a series of Generalized Linear Models as well as a complex association analysis will enable us to analyze the hidden drivers of naturalization success and their interactions. To specify the direct and indirect drivers of naturalization, I

hypothesize that naturalization success is associated with plant characteristics, mainly geographical origin (i.e. native origin, native range size), functional traits (i.e. growth form, seed mass, height and specific leaf area), phylogenetic relatedness to the native flora and climatic suitability. Furthermore, I hypothesize that the climatic suitability variable and other species characteristics are interrelated with one another.

Methods

Study area

This study focuses on the region of Southern Africa with approximately 4,000,000 km^2. This includes ten countries: Angola, Botswana, Eswatini, Lesotho, Malawi, Mozambique, Namibia, South Africa, Zambia and Zimbabwe. As data on species occurrence in nine provinces of South Africa were available, I divided our study area into 18 subregions (Figure 1). Southern Africa has a long history of plant introductions with the first ones dating back to the arrival of the Dutch in 1652 (Henderson 2006). The region of Southern Africa is considered one of the hotspots of environmental change, considering its irregular predicted change in temperature and precipitation regimes, as well as the expected considerable increase in water availability (Hoegh-Guldberg et al. 2019). The temperature increase in Southern Africa is predicted to have a range of 3,2-4,4°C towards the end of this century, while the region is expected to become drier in the future (Almazroui et al. 2020).

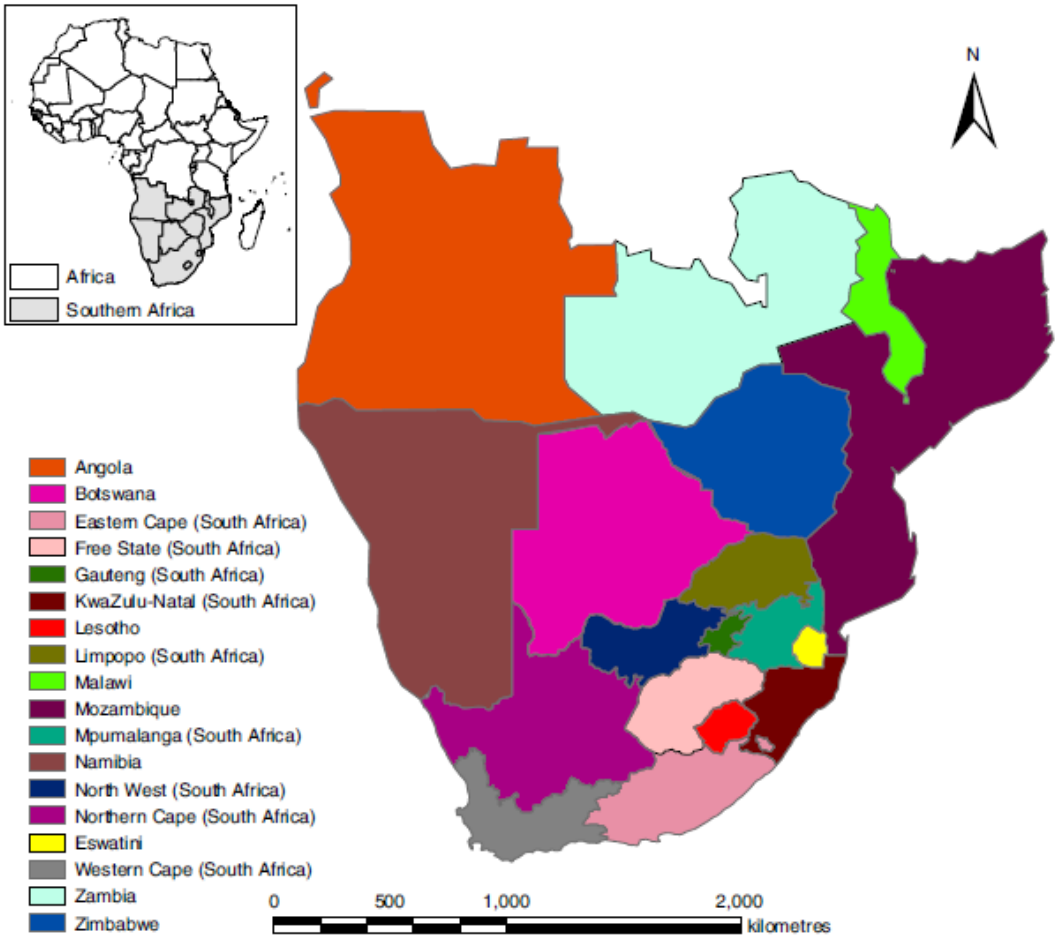


Figure 1: Map of Africa and the study regions showing the ten South African countries. Included in this map are Angola, Botswana, Eswatini, Lesotho, Malawi, Mozambique, Namibia, South Africa, Zambia and Zimbabwe. Due to differences in native species occurrence data for the nine provinces of South Africa, a total of 18 different regions for South Africa was used. This map was produced by Omer A. et al. (2022).

Cultivated alien flora of Southern Africa

This study is mainly based on a list of species and intraspecific taxa which have been reported to be cultivated in at least one region of Southern Africa according to the book Cultivated Plants of Southern Africa (Glen 2002). It originally contains about 8,000 species. To ensure the comparability of the data with other sources, the taxonomic names in this list were aligned and validated using The Plant List (v.1.1 <http://www.theplantlist.org/>) and the R package "Taxonstand" (Cayuela et al. 2019). Species native to Southern Africa were removed in synchronization with The Global Inventory of Floras and Traits database (GIFT) (Weigelt et al. 2020). For simplicity, the intraspecific taxa were rounded to the species level. Ferns and

Gymnosperms were removed because of their phylogenetical differentness from Angiosperms. This resulted in a list of 5,214 cultivated alien plants of Southern Africa.

Furthermore, it was identified which species, among the cultivated alien species of Southern Africa, successfully managed to naturalize using the Global Naturalized Alien Flora Database (GLoNAF). The database contains information about over 13,000 naturalized vascular plant taxa in more than 1000 regions globally (van Kleunen et al. 2019).

Species characteristics data

Species characteristics data (that is geographical origins, growth forms, functional traits and phylogenetic relatedness to the native flora) were collected for all species in the list. For geographical origins (i.e. native origins and native range size) I compiled data from multiple sources including the Plants of the World Online database (POWO 2019); <www.plantsoftheworldonline.org/>), the Germplasm Resources Information Network (GRIN; <https://ars-grin.gov>) and the World Checklist of Selected Plant Families (WCSP; <http://apps.kew.org/wcsp>).

The nine level-1 regions of the World Geographical Scheme for Recording Plant Distributions of the Taxonomic Databases Working Group (TDWG) have been used as continents of origin. As an estimate for the native range size of the cultivated species the TDWG level-3 regions were used (n=369) (Brummitt 2001).

Growth form data was also gathered from multiple sources (Omer et al. 2021). I then assigned each species to one or more of the following seven standardized categories: short-lived (annual or biennial) free-standing herb, long-lived free-standing herb, free-standing woody, aquatic, climber, epiphyte and parasite.

For functional traits, the specific leaf area, height and seed mass were chosen as they represent crucial variations in plant strategies (Diaz et al. 2016). The data on this was collected from the TRY database and compiled with other sources (Kattge et al. 2020).

To describe the phylogenetic relatedness between alien and native plant species, I first constructed a phylogenetic tree of all native and alien angiosperms in Southern Africa with accepted names according to The Plant List. As a basis for this phylogeny, I used the currently most comprehensive and time-calibrated phylogeny of seed plants (Smith et al. 2018). Then, for each alien cultivated species, I calculated the three most commonly used phylogenetic

distance indices. They provide information on the phylogenetic composition at the tips, as well as the deeper branches of the tree (Thuiller et al. 2010).

To sufficiently show the structures at the deeper branches of the phylogenetic tree PD_{mean} was calculated. It estimates an equal contribution of the whole native flora to the success or failure of the alien species in spite of the abundance of the natives. The second measure included is PD_{wmean}. Here it is assumed that the occurrence frequency of the native species plays a role, as more prevalent native species are more likely to interact with alien species. The phylogenetic distance is therefore weighted by the occurrence frequency of the native species. For this measure, the number of occurrences in African subregions (total n = 18), according to GIFT, was used as an estimate. Finally, PD_{min} was calculated to show the phylogenetic composition at the tree tips. According to this measure, alien species success is determined by the distance to its closest relative as they are most likely to share similar resources, mutualists and enemies (Thuiller et al. 2010; Divisek et al. 2018).

Climatic suitability assessment

To assess the climatic suitability of Southern Africa for the cultivated flora of Southern Africa, I used Omar's (unpublished) species distribution models (SDM) to combine the bioclimatic variables with presence records and randomly generated pseudo-absences. First, I retrieved current global climate data, the average from 1970 until 2000, in a 10' resolution from WorldClim version 2.1 (Fick et al. 2017). I selected the following five variables from all the available bioclimatic variables: (1) Temperature Seasonality, (2) Maximum Temperature of Warmest Month, (3) Precipitation of the Wettest Month, (4) Precipitation of the Driest Month, (5) Precipitation Seasonality. These variables were chosen based on their recognized influence on plant distributions, as documented by Root et al (2003). In addition, I used population density as a proxy of propagule pressure which is available in the NASA Socioeconomic Data and Applications Center (Gao 2020). These explanatory variables have pairwise Pearson's r values below 0.75, and thus a negligible effect of multicollinearity. I then used the species list of the cultivated flora of Southern Africa to collect data on global distribution (presence data) from the Global Biodiversity Information Facility (GBIF.org 2021), using the 'rgbif' library in R (Chamberlain 2017). To not violate the assumption of niche conservatism and niche adaptation (Pearman et al. 2010; Sax,Early et al. 2013), I considered native and introduced occurrences globally. Erroneous records (e.g. those that occur on ocean surfaces and capitals), were automatically removed using the 'CoordinateCleaner' library in R (Zizka et al. 2019).

Additionally, to avoid pseudoreplication, duplicated data points (multiple presence data points within the 10′ × 10′ grid cells) were removed. The resulting species list hence consists of 1,407 species, of which 492 are fully naturalized in at least one region of Southern Africa. Therefore, I used the final list with 1,407 species in further analysis.

Finally, to define the current suitability of Southern Africa for the cultivated alien species, I combined the bioclimatic variables with presence records and randomly generated pseudo-absences using the BIOMOD2 platform that is implemented in the 'biomod2' R package version 3.4-6 (Thuiller et al. 2009). I used four modelling algorithms. The two regression techniques generalized linear model (GLM) and general additive model (GAM) as well as the two classification techniques random forest (RF) and boosted regression trees (BRT). To use the GBIF presence-only data, I randomly generated 10,000 pseudo-absence records three times. All models were fitted using an equal weight of presences and pseudo-absence data. Finally, to evaluate our models, each model was separately run three times using a split-sampling approach in which the data was split into 80% calibration and 20% evaluation datasets for each of the three pseudo-absence datasets (resulting in nine models per modelling algorithm and a total of 36 models for each species). We used the True Skill Statistic (TSS) to assess the predictive performance of the SDMs (Allouche et al. 2006). TSS ranges from −1 to 1, where 1 indicates perfect agreement, 0 indicates a random prediction and negative values indicate that predictions perform worse than random. The calibrated models have a very good performance with an average TSS value of over 0.8. I then used the calibrated models to project the current climatic suitability in Southern Africa using a weighted mean ensemble forecast (Thuiller et al. 2009). I aggregated all the models of the repeated pseudo-absences and split-sampling into an ensemble projection to reduce uncertainties associated with each technique. The contribution of each model was weighted according to its TSS score (only models with a TSS score > 0.5 were included). The resulting variable is the probability of South Africa being a suitable habitat for the alien species ranging from 0 to 1.

Statistical analysis

All analyses were done in R, version 3.6.1 (R Core Team 2019).

First, I tested whether the naturalization success of cultivated alien plants in Southern Africa is directly associated with plant characteristics and climatic suitability, following Baron et al.'s (1986) causal step method, to establish that mediation takes place. Hence, a series of

complementary generalized linear models (GLMs) with binomial error distribution and a logit function was conducted to check if there is an indirect effect (mediation) on naturalization success through climatic suitability. Naturalization success (i.e. whether a species is recorded to be naturalized in Southern Africa or not according to the GloNAF database) was used as the response variable. The predictor variables were the following: geographical origin (TDWG level 1), native range size (TDWG level 3), plant traits (Seed mass [mg], height [m] and specific leaf area [mm^2 mg^{-1}]), growth form (epiphyte, climber, parasite, aquatic, free-standing woody, short-lived herb and long-lived herb), phylogenetic distance to the native flora (PD_{mean}, PD_{wmean}, PD_{min}) and climatic suitability (number of climatically suitable 10′ × 10′ grid cells). Each continuous variable was scaled to a mean of 0 and a standard deviation of 1 to enhance comparability among the estimates.

Then, for plant characteristics that show a significant effect on naturalization success, it was tested whether that relationship is mediated through climatic suitability. To do that, a path analysis was applied using the "lavaan" package v.0.6-14 in R (Rosseel 2012) to examine the direct and indirect effects of plant characteristics on the naturalization success. This analysis allows the distinction of direct effects, which originate from the plants' own characteristics, from the indirect effects, which are mediated through climatic suitability. The path model was constructed using the plant characteristics as independent variables, the climatic suitability index as a mediator and the naturalization success as the dependent variable. The direct effects of the plant characteristics on the naturalization success were represented by the path coefficients. The indirect effects of the plant characteristics on the naturalization success were calculated using the product of the path coefficients of the mediating variables. Since naturalization success is a binary variable, a diagonally weighted least square estimation method with robust standard errors was used. Following (Razanajatovo et al. 2016) the model fit was assessed by using the Comparative Fit Index and the root mean square error of approximation. A Comparative Fit Index >0.95 and a root mean square error of approximation <0.06 are considered good.

Results

Direct association of naturalization success with plant characteristics and climatic suitability

Of the 1,407 angiosperm alien species cultivated in Southern Africa used in this analysis, 492 (34,9%) managed to naturalize in at least one subregion of Southern Africa.

Climatic suitability showed a significant positive direct effect on naturalization success (Table 1; Est. = 1.34, $p < 0.001$). Although naturalization success appeared to be negatively associated with the three phylogenetic distance indices, this effect was only significant in the minimum pairwise distance (Table 1; Est. = -0.12, $p < 0.05$). Naturalization success was significantly higher for plants with larger seed mass (Table 1; Est. = 0.17, $p < 0.01$) and higher plant height (Table 1; Est. = 0.22, $p < 0.001$). However, no significant relationship was observed between specific leaf area and naturalization (Table S1; Est. = -0.06, $p = 0.403$). While no significant association was found between naturalization success and species introduced from Australasia (Table S1; Est. = 0.1, $p = 0.542$) and Pacific islands in Southern Africa (Table S1; Est. = 0.82, $p = 0.059$), naturalization success was positively associated with plants originating from continents (i.e., TDWG level-1 region) that are predominantly located in the tropical zone, including South America (Table 1; Est. = 1.20, $p < 0.001$), Africa (Table 1; Est. = 0.30, $p < 0.05$) and Tropical Asia (Table 1; Est. = 0.64, $p < 0.001$). In contrast, a negative association was observed between naturalization success and plants originating from temperate regions such as Europe (Table 1; Est. = -0.57, $p < 0.001$). Among the growth forms only short-lived herb species significantly influenced the naturalization success (Table 1; Est. = 0.76, $p < 0.001$). Plants with higher native range size also showed a significant positive effect on the naturalization success (Table 1; Est. = 0.82, $p < 0.001$).

Table 1: Results of the binomial generalized linear models (GLMs) testing how the probability of naturalization success relates to the climatic suitability, minimum phylogenetic distance to the native flora (PD_{min}), seed mass, plant height, growth form, geographical origins and the native range size. Numerical predictor variables were standardized to a mean of zero and a standard deviation of one. Furthermore, the pseudo-R-squared (R^2) value was calculated using Nagelkerke's method. Only significant relationships are shown here, for non-significant models see Table S1 in the appendix.

Predictors	**Estimate ± SE**	**Z**	**P**	**R^2**	**Predictors**	**Estimate ± SE**	**Z**	**P**	**R^2**
Intercept	-0.84 ± 0.07	-12.11	<0.001	0.35	Intercept	-0.75 ± 0.06	-11.79	<0.001	0.02
Climatic suitability	1.34 ± 0.08	17.35	<0.001		Tropical Asia	0.63 ± 0.14	4.55	<0.001	
AIC	1409.2				AIC	1804.9			
Intercept	-0.62 ± 0.06	-11.11	<0.001	0.004	Intercept	-0.41 ± 0.07	-5.91	<0.001	0.02
Minimum phylogenetic distance	-0.12 ± 0.05	-2.11	<0.05		Europe	-0.57 ± 0.12	-4.82	<0.001	
AIC	1820.9				AIC	1801.4			
Intercept	-0.63 ± 0.06	-10.50	<0.001	0.01	Intercept	-0.84 ± 0.06	-13.19	<0.001	0.06
Seed mass	0.17 ± 0.06	2.85	<0.01		Southern America	1.20 ± 0.15	8.16	<0.001	
AIC	1608				AIC	1757.4			
Intercept	-0.61 ± 0.06	-10.63	<0.001	0.02	Intercept	-0.78 ± 0.07	-11.73	<0.001	0.03
Height	0.22 ± 0.06	3.95	<0.001		Short-lived herb	0.76 ± 0.13	5.61	<0.001	
AIC	1750.9				AIC	1714.9			
Intercept	-0.69 ± 0.06	-10.74	<0.001	0.01	Intercept	-0.72 ± 0.06	-11.74	<0.001	0.15
Africa	0.30 ± 0.13	2.33	<0.05		Native range size	0.82 ± 0.07	11.62	<0.001	
AIC	1820				AIC	1659.5			

The indirect association of naturalization success with plant characteristics

The indirect effects of the climatic suitability on naturalization success and species characteristics differed substantially among plant characteristics (Table 2, Figure 2). Regarding the phylogenetic relatedness of the cultivated alien flora to the native flora of Southern Africa, I found that the naturalization probability decreased with phylogenetic distance to the native flora and that 85% of this relationship is mediated through climatic suitability (Figure 2; Table 2, Est. -0.06, $p < 0.001$).

The positive effects of seed mass (Figure 2; Est.: 0.1, 95% CI: 0.176/0.104) and plant height (Figure 2; Est.: 0.14, 95% CI: 0.069/0.207) on naturalization success of cultivated alien plants were also indirectly mediated through high climatic suitability in Southern Africa (seed mass: Est.: 0.1, $p < 0.001$, height: Est.: 0.07, $p < 0.001$; Table 2; Figure 2). The average indirect effect to the direct effect was 97% for seed mass and 51% for plant height (Table 2; Figure 2).

The indirect effect of finding high climatic suitability in Southern Africa for plant species native to South America (Figure 2; Table 2; Est. 0.75, 95% CI: 0.567/0.925) and Tropical Asia (Figure 2; Table 2; Est.: 0.39, 95% CI: 0.565/0.394) mediated a proportion of the positive effect of species native to South America and Tropical Asia on naturalization success in Southern Africa. The average indirect effect to the direct effect was 99.7% for species native to South America and 89% for species native to Tropical Asia, respectively. Moreover, the indirect effect of finding less climatic suitability in Southern Africa for plant species native to Europe (Figure 2; Table 2; Est.: -0.35, 95% CI: -0.491/-0.209) also mediated a proportion of the negative effect of species native to Europe on naturalization success in Southern Africa. However, climatic suitability did not indirectly mediate the naturalization success of plant species that were introduced from Africa (excluding Southern Africa) (Figure 2; Table 2; Est.: 0.02, $p=0.667$).

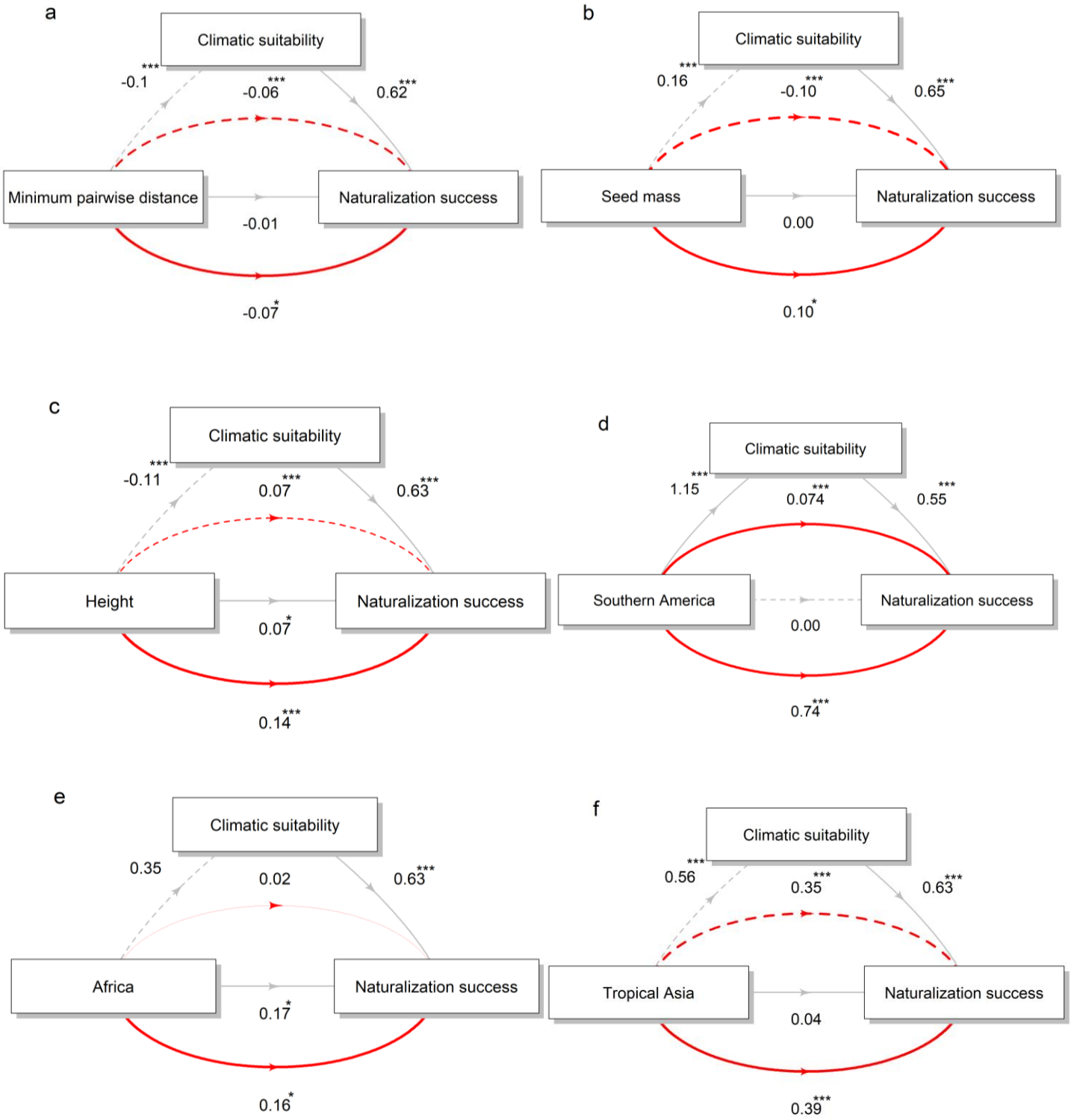
The short-lived herbs were found to have a significant positive association with naturalization success in Southern Africa (Figure 2; Table 2; Est.: 0.3, 95% CI: 0.160/0.448). This positive association was, at least partially (35% average indirect effect to the direct effect), attributed to the indirect effect of finding high climatic suitability in Southern Africa (Figure 2; Table 2; Est.: 0.16, $p < 0.001$).

Similarly, plants with wider native range sizes have a significantly higher probability to successfully naturalize in Southern Africa (Figure 2; Table 2; Est.: 0.47, 95% CI: 0.542/0.472) and that this positive association is, at least partially (30% average indirect effect to the direct

effect) mediated through the indirect effect of finding high climatic suitability in Southern Africa (Figure 2; Table 2; Est.: 0.14, $p < 0.001$).

Table 2: Results of the path analyses testing the mediating (indirect) effect of climatic suitability on the relationship between plant characteristics and naturalization success in Southern Africa. Plant characteristics included were minimum phylogenetic distance to the native flora (PD_{min}), seed mass, plant height, growth form, geographical origins and the native range size.

a) Minimum phylogenetic distance to native flora			
Predictors	**Estimate ± SE**	**P**	**Lower-/upper CI**
Indirect effect (a*b)	-0.061 ± 0.017	< 0.001	-0.094/ -0.028
Direct effect (c)	-0.011 ± 0.031	0.720	-0.072/0.050
Total effect c+(a*b)	-0.072 ± 0.34	< 0.05	-0.140/-0.005
b) Seed mass			
Indirect effect (a*b)	0.101 ± 0.017	< 0.001	0.068/0.135
Direct effect (c)	0.003 ± 0.032	0.937	-0.060/0.065
Total effect c+(a*b)	0.104 ± 0.037	< 0.05	0.176/0.104
c) Height			
Indirect effect (a*b)	0.071 ± 0.017	< 0.001	0.037/0.104
Direct effect (c)	0.067 ± 0.031	< 0.05	0.007/0.127
Total effect c+(a*b)	0.138 ± 0.035	< 0.001	0.069/0.207
d) Southern America			
Indirect effect (a*b)	0.744 ± 0.057	< 0.001	0.633/ 0.854
Direct effect (c)	0.002 ± 0.086	0.977	-0.166/0.171
Total effect c+(a*b)	0.746 ± 0.091	< 0.001	0.567/0.925
e) Africa			
Indirect effect (a*b)	0.020 ± 0.046	0.667	-0.071/0.111
Direct effect (c)	0.167 ± 0.071	< 0.05	0.028/0.306
Total effect c+(a*b)	0.187 ± 0.080	< 0.05	0.029/0.345
f) Tropical Asia			
Indirect effect (a*b)	0.352 ± 0.049	< 0.001	0.255/0.449
Direct effect (c)	0.042 ± 0.081	0.604	-0.117/0.201
Total effect c+(a*b)	0.394 ± 0.087	< 0.001	0.565/0.394
g) Europe			
Indirect effect (a*b)	-0.357 ± 0.041	< 0.001	-0.437/-0.209
Direct effect (c)	0.007 ± 0.063	0.912	-0.116/0.130
Total effect c+(a*b)	-0.350 ± 0.72	< 0.001	-0.491/-0.209
h) Short-lived herb			
Indirect effect (a*b)	0.165 ± 0.044	< 0.001	0.080/0.251
Direct effect (c)	0.304 ± 0.074	< 0.001	0.160/0.448
Total effect c+(a*b)	0.470 ± 0.084	< 0.001	0.305/0.634
i) Native range size			
Indirect effect (a*b)	0.140 ± 0.019	< 0.001	0.104/0.177
Direct effect (c)	0.331 ± 0.034	< 0.001	0.265/0.398
Total effect c+(a*b)	0.472 ± 0.036	< 0.001	0.542/0.472


a
Climatic suitability
-0.1***
-0.06***
0.62***
Minimum pairwise distance
Naturalization success
-0.01
-0.07*
b
Climatic suitability
0.16***
-0.10***
0.65***
Seed mass
Naturalization success
0.00
0.10*
c
Climatic suitability
-0.11***
0.07***
0.63***
Height
Naturalization success
0.07*
0.14***
d
Climatic suitability
1.15***
0.074***
0.55***
Southern America
Naturalization success
0.00
0.74***
e
Climatic suitability
0.35
0.02
0.63***
Africa
Naturalization success
0.17*
0.16*
f
Climatic suitability
0.56***
0.35***
0.63***
Tropical Asia
Naturalization success
0.04
0.39***

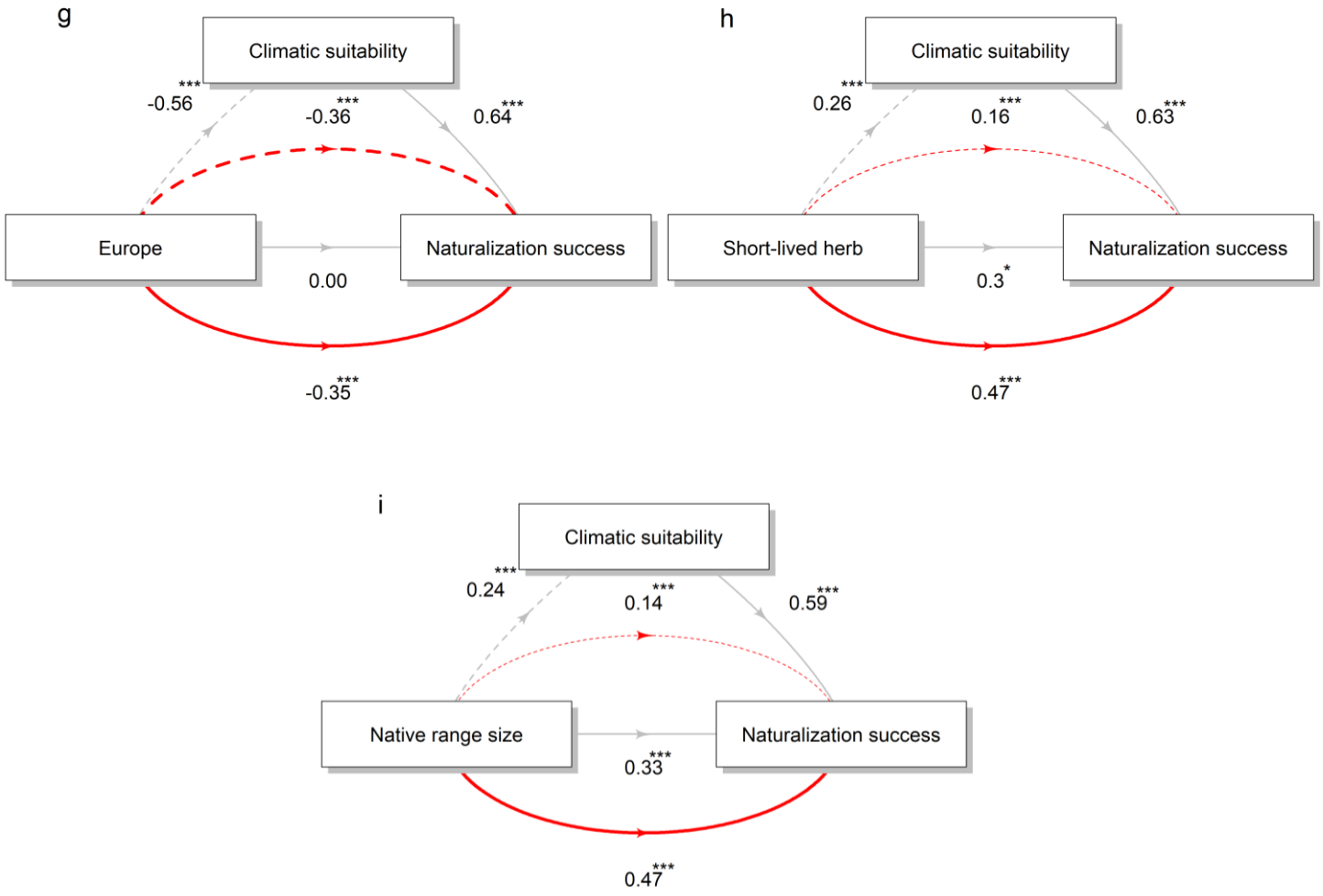


Figure 2: Direct and indirect association of plant characteristics and naturalization success with climatic suitability as mediator. (a) Effect of the minimum phylogenetic distance to the native flora and climatic suitability on naturalization success (expressed as being naturalized in Southern Africa or not); $R^2_{\text{climatic suitability}} = 0.01$, $R^2_{\text{naturalization success}} = 0.39$. (b) Effect of seed mass and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0.02$, $R^2_{\text{naturalization success}} = 0.41$. (c) Effect of plant height and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0.01$, $R^2_{\text{naturalization success}} = 0.41$. (d) Effect of the origin South America and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0.18$, $R^2_{\text{naturalization success}} = 0.39$. (e) Effect of the origin Africa and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0$, $R^2_{\text{naturalization success}} = 0.40$. (f) Effect of the origin Tropical Asia and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0.05$, $R^2_{\text{naturalization success}} = 0.39$. (g) Effect of the origin Europe and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0.08$, $R^2_{\text{naturalization success}} = 0.39$. (h) Effect of the growth form short-lived herb and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0.01$, $R^2_{\text{naturalization success}} = 0.41$. (i) Effect of the native range size and climatic suitability on naturalization success; $R^2_{\text{climatic suitability}} = 0.06$, $R^2_{\text{naturalization success}} = 0.45$. The arrowed lines indicate directed paths connecting the variables. Significant paths ($p < 0.05$) are indicated with their numbers. Stars next to the numbers indicate level of significance. Dashed lines indicate non-significant effects. The red arrows indicate the indirect effect and total effects.

Discussion

I used a list of 1,407 cultivated alien plants that were introduced to southern Africa to test the extent to which the effect of plants characteristics on the naturalization success can be attributed to finding climatically suitable habitat in the new non-native ranges. The results showed that climatic suitability has a significant positive effect on naturalization success. Moreover, I found that naturalization success is also directly associated with plants characteristics (minimum phylogenetic distance to the native flora, seed mass, height, species native to Southern America, Africa, Tropical Asia and Europe, species that have the growth form short-lived herb and native range size). However, most of the associations between naturalization success and these plant characteristics were mediated through climatic suitability.

Naturalization success association with plant characteristics and climatic suitability

The role of environmental conditions' suitability on the ability of alien plants to naturalize has long been established (Darwin 1859; Elton 1958). I show that climatical suitability was significantly higher for naturalized cultivated plants compared to not naturalized cultivated alien plants in Southern Africa. This supports previous findings which suggest a correlation between climatic suitability and naturalization success (Feng et al. 2016; Mayer et al. 2017; Haeuser et al. 2018). Thus, this result supports the widely accepted notion that climate matching between native and non-native ranges is fundamental for the naturalization success of alien plants (Richardson et al. 2012).

The negative effect of phylogenetic distance to the native flora on naturalization success I found in this study is in line with previous studies, which found that alien plant species closely related to the native flora are more likely to naturalize in Southern Africa particularly (Omer et al. 2022) and in other regions as listed in (Cadotte et al. 2018; Qian 2023). This might be because closely related species tend to share the same resources, mutualists and survival-facilitating traits (Divisek et al. 2018). Moreover, this could be explained by Darwin's preadaptation hypothesis, where he hypothesized, that plant species closely related to the native flora are more like to succeed in naturalization as they are preadapted to the new environment and are more likely to pass the environmental filter (Darwin 1859).

Seed mass and plant height exhibited a positive relationship with the naturalization success of cultivated alien plants in Southern Africa. The larger size of seeds can contribute to higher energy reserves, enabling successful germination, survival and growth during the establishment

phase (Wilson 2013; Dawson et al. 2009). Additionally, previous studies have also linked plant height to the naturalization of alien plants (Dehnen-Schmutz et al. 2007; Bucharova et al. 2009). However, these findings differ from a recent study by Omer et al (2021), which found a non-linear association between seed mass, plant height and naturalization success. They observed that intermediate values of seed mass and plant height were associated with the highest naturalization success. The contrasting results suggest the potential influence of context dependence, indicating that the relationship between height and invasion may be moderated by specific circumstances. Considering the heterogeneity of these pieces of evidences, further investigation is needed to fully understand the variation of these associations.

Alien plant species native to South America, Africa and Tropical Asia have shown significant positive correlations with naturalization success in Southern Africa. Species native to these regions are largely adapted to the tropical climate. Therefore, plant species from these native origins find high climatic suitability in Southern Africa, which enhances naturalization success (Petipierre et al. 2012). In contrast, cultivated alien plant species native to Europe, which is largely located in the temperate climate, were less likely to naturalize in Southern Africa. However, climatic similarity might not fully explain the naturalization success, as species native to other regions with similar climates to Southern Africa, such as Australasia, are not associated with naturalization success. Possibly other invasion drivers (e.g., propagule pressure and earlier introduction) better explain the higher naturalization probability of plants native to other continents (Lockwood et al. 2005).

Short-lived herbs introduced to Southern Africa showed a significantly higher naturalization success compared to other growth forms. Short-lived herbs were also found to be more likely to be introduced for cultivation and to further naturalize in Southern Africa (Omer et al. 2021). Such patterns should, however, be interpreted with caution since they largely reflect man-made introduction biases of cultivation. It has been found for example, that the differences in naturalization or invasion among growth forms can be ascribed to their representation in nursery catalogues rather than to their inherent features (Kinlock et al. 2022). Nevertheless, fast growth, a trait most Short-lived herbs have, enhances naturalization success as this trait promotes competitive ability (van Kleunen et al. 2015).

The findings showed that naturalization success in Southern Africa is positively correlated with the species' native range size. This provides further evidence that alien species with larger native range sizes have a higher probability of becoming naturalized (Banerjee et al. 2021; Omer et al. 2021; Razanajatovo et al. 2016). Furthermore, this result suggests that species with extensive

native ranges possess greater ecological and genetic adaptability, along with specific traits that facilitate their successful naturalization (Pysek et al. 2009).

The naturalization success and indirect effects of climatic suitability

The finding that the effect of phylogenetic distance to the native flora on naturalization success is indirectly mediated by climatic suitability (Figure 2) could be because cultivated alien plants with close relatives in the native flora share several traits that allow them to adapt to the new environment (Divisek et al. 2018). This finding provides great empirical support to Darwin's preadaptation hypothesis (Darwin 1859) as he proposed that alien species that are closely related to native species should be more successful, because their similarity to the native species would indicate pre-adaptation to local environmental conditions.

Seed masses' significant effect on naturalization success was to a large extent mediated through climatic suitability. A small seed mass has been found to facilitate a better spread of alien plants (Westoby et al. 1992). However, a large seed mass might indicate sufficient resources to warrant seedling survival and adaptation in the stressful environments of Southern Africa. The mediation effect of climatic suitability on the association between seed mass and naturalization could only hold true under such resource-limited environments. The significant positive effect of plant height on naturalization success, however, is almost equally achieved directly and indirectly through climatic suitability. Ecologically, plant height enhances the plants' competitive ability and seed dispersal distance (Moles et al. 2008; Thomson et al. 2011). However, plant height also allows for better adaptation in hot conditions as long as precipitation levels are high enough to offset its negative effects (Lingfeng et al. 2020).

The high naturalization success of South American and Tropical Asian plant species is mainly mediated by the high climatic suitability of Southern Africa to species native to these regions. Cultivated plants that were introduced from the African continent were also more likely to naturalize in Southern Africa. Interestingly, the high naturalization probability of species native to Africa was not mediated by climatic suitability. In other words, other ecological factors than climatic suitability determine the naturalization success of cultivated alien plants native to Africa. Similar, but in a different direction to Southern American and Tropical Asian species, the low naturalization success of plants native to Europe was also mediated by the low climatic suitability of Southern Africa to species native to this region. This result can be explained by the very different climate of temperate Europe from the (sub)tropical-dry Southern Africa. This

confirms the important role of climatic similarity between the native and non-native regions for the naturalization success of alien plants (Theoharides et al. 2007; Yang et al. 2021).

From all the growth forms included in the analysis, only short-lived herbs showed a positive association with naturalization success in Southern Africa. The probability to be selected for cultivation was found to drive the naturalization success of Short-lived herbs in Southern Africa (Omer et al. 2021) and Great Britain (Kinlock et al. 2022). In addition, this study showed that their naturalization success is partially mediated by climatic suitability in Southern Africa (Figure 2). Short-lived plant species, such as annuals and biennials, have the remarkable ability to complete their life cycles within a single year or two, respectively. This unique characteristic allows them to take advantage of transient favorable conditions, particularly out of their native ranges (Milton 2004). This further increases short-lived plants' abilities to adapt to the climatic conditions once introduced (Compagnoni et al. 2021).

A larger native range size showed positive indirect and direct associations with naturalization success. The literature consistently reports a correlation between the native range size of a species and its likelihood of naturalization (Omer et al. 2021; Kinlock et al. 2022; Razanajatovo et al. 2016). A broader native range is often associated with a larger ecological niche, which in turn implies a higher degree of abiotic and biotic exposure (Gaston et al. 2001; Kalusova et al. 2017). This implies that species with a wider native range size would be more likely to overcome biotic- (Sax et al. 2000) and abiotic- or environmental filters (Forsyth et al. 2004) and thus naturalize.

Conclusion

This thesis examined the relationship between plant characteristics, climatic suitability and the naturalization success of cultivated alien plants in Southern Africa. The findings highlight the importance of climatic suitability in determining naturalization success, with naturalized cultivated plants demonstrating higher climatic suitability compared to non-naturalized cultivated alien plants. These results align with previous research emphasizing the correlation between climatic suitability and naturalization success. The study also revealed direct associations between naturalization success and plant characteristics such as phylogenetic distance to the native flora, seed mass, plant height, species native to specific regions (Southern America, Africa, Tropical Asia and Europe), species with short-lived growth forms and native range size. However, most of these associations were found to be mediated through climatic

suitability, indicating the pivotal role of climate matching between native and non-native ranges for the naturalization of alien plants. Thus, this thesis underlines the importance of considering the indirect role of climatic suitability in plant invasions in further research.

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Appendix

Table S1: Non-significant results of the binomial generalized linear models (GLMs) testing how the probability of naturalization success relates to the mean phylogenetic distance to the native flora, mean weighted phylogenetic distance to the native flora, specific leaf area, geographical origins and growth form. Numerical predictor variables were standardized to a mean of zero and standard deviation of one. Furthermore, the pseudo-R-squared (R^2) value was calculated using Nagelkerke's method.

	Predictor variables -> Naturalization success					Predictor variables -> Naturalization success			
Predictors	Estimate ± SE	Z	P	R^2	Predictors	Estimate ± SE	Z	P	R^2
Intercept	-0.62 ± 0.05	-11.1	<0.001	0.00022	Intercept	-0.62 ± 0.05	-11.1	<0.001	0.00052
Mean phylogenetic distance	-0.03 ± 0.05	-0.48	0.633		Mean weighted phylogenetic distance	-0.04 ± 0.05	-0.73	0.468	
AIC	1825.1				AIC	1824.8			
Intercept	-0.64 ± 0.07	-8.9	<0.001	0.00114	Intercept	-0.55 ± 0.07	-7.4	<0.001	0.00197
Specific leaf area	-0.06 ± 0.07	-0.83	0.403		Temperate Asia	-0.16 ± 0.11	-1.42	0.157	
AIC	1091.5				AIC	1823.3			
Intercept	-0.63 ± 0.06	-10.6	<0.001	0.00036	Intercept	-0.60 ± 0.06	-9.2	<0.001	0.00018
Australasia	0.10 ± 0.17	0.61	0.542		Northern America	-0.05 ± 0.12	-0.43	0.666	
AIC	1825				AIC	1825.2			
Intercept	-0.63 ± 0.06	-11.23	<0.001	0.00349	Intercept	-0.64 ± 0.06	-10.6	<0.001	0.00372
Pacific Islands	0.82 ± 0.43	1.89	0.0587		Climber	0.35 ± 0.18	1.92	0.0547	
AIC	1821.8				AIC	1743.4			
Intercept	-0.60 ± 0.06	-10.37	<0.001	0.00094	Intercept	-0.60 ± 0.06	-10.55	<0.001	0.00089

Epiphyte	-0.44 ± 0.48	-0.93	0.353		Parasite	-11.96 ± 324.74	-0.04	0.971	
AIC	1745.2				AIC	1745.3			
Intercept	-0.60 ± 0.06	-10.53	<0.001	5.12430 6e-06	Intercept	-0.73 ± 0.09	-8.19	<0.001	0.0038 4
Aquatic	0.04 ± 0.63	0.071	0.944		Free-standing woody	0.22 ± 0.12	1.93	0.0534	
AIC	1746.1				AIC	1742.4			
Intercept	-0.51 ± 0.07	-6.73	<0.001	0.0035					
Long-lived herb	-0.21 ± 0.11	-1.85	0.0649						
AIC	1742.7								