Invasion risk of the currently cultivated alien flora in Southern Africa is predicted to decline under climate change

Ali Omer[1], Franz Essl[1], Stefan Dullinger[1], Bernd Lenzner[2], Adrián García-Rodríguez[1], Dietmar Moser[1], Trevor Fristoe[3], Wayne Dawson[4], Patrick Weigelt[5], Holger Kreft[6], Jan Pergl[7], Petr Pysek[8], Mark van Kleunen[3], and Johannes Wessely[1]

[1]University of Vienna
[2]Universitat Wien Fakultat fur Lebenswissenschaften
[3]University of Konstanz
[4]Durham University
[5]University of Goettingen
[6]Georg-August-Universitat Gottingen
[7]Institute of Botany Czech Academy of Sciences
[8]Academy of Sciences of the Czech Republic

July 8, 2023

Abstract

Alien species can have massive impacts on native biodiversity and ecosystem functioning. Assessing which species from currently cultivated alien floras may escape into the wild and naturalize is hence essential for ecosystem management and biodiversity conservation. Climate change has promoted the naturalization of many alien plants in temperate regions, but whether outcomes are similar in (sub)tropical areas is insufficiently known. In this study, we used species distribution models to evaluate the current naturalization risk of 1,527 cultivated alien plants in 10 countries of Southern Africa and how their invasion risk might change due to climate change. We assessed changes in climatic suitability across the different biomes of Southern Africa. Moreover, we assessed whether climatic suitability for cultivated alien plants varied with their naturalization status and native origin. The results of our study indicate that a significant proportion (53.9%) of the species are projected to lack suitable climatic conditions in Southern Africa, both currently and in the future. Based on the current climate conditions, 10.0% of Southern Africa is identified as an invasion hotspot (here defined as the top 10% of grid cells that provide suitable climatic conditions to the highest numbers of species). This percentage is expected to decrease slightly to 7.1% under moderate future climate change and shrink considerably to 2.0% under the worst-case scenario. This decline in climatic suitability is observed across most native origins, particularly under the worst-case climate change scenario. Our findings indicate that climate change is likely to have an opposing effect on the naturalization of currently cultivated average plants in (sub)tropical Southern Africa compared to colder regions. Specifically, the risk of these plants' naturalizing is expected to decrease due to the region's increasingly hot and dry climate, which will be challenging for the persistence of both native and alien plant species.

Introduction

The number of species that are naturalizing outside of their native ranges continues to increase (Seebens, et al. 2020). The associated ecological and economic costs make alien species management an urgent task (Pyšek, et al. 2020). Estimations and projections of current and future distributions are important for alien species management, especially as their spread will certainly be affected by other drivers of global changes, such as climate change (Bellard, et al. 2015, Liu, et al. 2023, Northrup, et al. 2019, Vilà and Hulme 2017). These changes alter both biotic and abiotic ecosystem properties known to be critical for biological invasions (Bellard, et al. 2016, Dullinger, et al. 2017, Rodríguez-Labajos, et al. 2009).

Predicting the species that could successfully escape into the wild and naturalize from a larger pool of deliberately introduced species (e.g., those cultivated in a region) is one of the biggest challenges in invasion ecology. Apart from specific functional traits and evolutionary history (e.g., seed mass, geographical origins and phylogenetic composition; Divíšek, et al. 2018, Lenzner, et al. 2021, Maurel, et al. 2016, Omer, et al. 2021, Omer, et al. 2022), climate matching between native and alien ranges has been demonstrated to be fundamental for the naturalization success of alien plants (Feng, et al. 2016, Mayer, et al. 2017, Richardson and Pyšek 2012). Climate-suitability analyses have thus emerged as promising tools for predicting the naturalization risk of alien plants (Dullinger, et al. 2017, Haeuser, et al. 2018, Oduor, et al. 2023, Robin Pouteau, et al. 2021, Thuiller, et al. 2005, Mark van Kleunen, et al. 2018). However, as climate change alters the abiotic and biotic conditions that mediate biological invasions, projections based on future climate scenarios are increasingly important for predicting the potential distributions of alien species. In temperate regions such as those in Europe and Northern America, climate warming is predicted to generally increase the likelihood of biological invasions (Bellard, et al. 2013, Dullinger, et al. 2017, Haeuser, et al. 2018, Oduor, et al. 2023). However, biological invasion studies, including those that use climate-suitability analyses, are geographically biased towards regions in the northern hemisphere (Pyšek, et al. 2008). Most of such studies have been conducted in intensively researched regions (e.g., Europe; Dullinger, et al. 2017, Haeuser, et al. 2018, Robin Pouteau, et al. 2021) or for a specific set of species (e.g., the 100 world's worst invasive species; Bellard, et al. 2013). These biases in research might hinder a general understanding of how a changing climate will affect biological invasions across the globe. Indeed, some studies suggest that in non-temperate regions, and especially in areas with extreme climates (e.g., hot desert), the risk of alien plant naturalization will decrease rather than increase under climate change (Bellard, et al. 2013, Fulgêncio-Lima, et al. 2021).

The link between environmental suitability and the ability of alien plants to naturalize has long been established (Darwin 1859, Elton 1958). However, with continuing climate change, invasion dynamics have become more complex to predict. For example, while the current climate might have favored the naturalization of species that have already been established in a region, it is not clear whether the climate of the future will promote those that have been introduced but have not managed to naturalize yet. A warming climate might hence constrain the spread of some established alien species but simultaneously foster expansions or new naturalizations of others. More generally, a changing climate might also alter the characteristics (e.g., geographical origins) that are associated with successful naturalization in alien plants (Madani, et al. 2018, Soudzilovskaia, et al. 2013). For example, climate change might change the currently observed patterns that the majority of naturalized alien plants are native to continents of the Northern Hemisphere (van Kleunen, et al. 2015).

The introduction of organisms outside their native range has occurred through various pathways and for different purposes (Hulme, et al. 2008). However, intentional introduction for cultivation represents the primary pathway for vascular plant species (Faulkner, et al. 2020, Lambdon, et al. 2008). The majority of these species are grown in domestic gardens or have other economic uses (M. van Kleunen, et al. 2018, van Kleunen, et al. 2020). The high prevalence of cultivated species among naturalized alien vascular plants implies that future naturalizations will likely also emerge mainly from cultivated plant populations. Therefore, regional cultivated floras further increase our understanding of assessing current and future naturalization risks under a warming climate.

Southern Africa has a tropical to subtropical climate and large (semi-)arid regions (Engelbrecht and Engelbrecht 2015). Therefore, it is not immediately clear whether climate change will result in an increase or decrease in the area suitable for a species from the large alien flora that is currently cultivated in the region. In the Republic of South Africa, for instance, alien woody trees and shrubs are projected to experience a reduction in habitat and shift their ranges towards higher elevations with lower temperatures in response to future climate scenarios (Bezeng, et al. 2017).

Here, we used species distribution modeling to evaluate the potential current and future naturalization risk of 1,527 alien species currently cultivated in the ten countries of Southern Africa, of which 371 have already naturalized in at least one part of the region. Our specific objectives were (1) to predict the potential current distribution of cultivated alien plants of Southern Africa; (2) to assess how these potential distributions could change under a changing climate in the future by using two climate change scenarios; (3) to identify hotspot areas with the highest suitability for cultivated alien plants under current and future climatic conditions in Southern Africa; (4) to compare the biomes within southern Africa with respect to changes in climatic suitability for introduced cultivated plants; and (5) to assess whether and to which degree naturalization status and geographical origins explain current and future potential range size of cultivated alien plants of Southern Africa.

Methods

Study area

Our study focused on the Southern Africa region, comprising ten countries: Angola, Botswana, Eswatini, Lesotho, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe, with a land area of around 4,000,000 km^2 (Bezeng, et al. 2015). The history of plant modern introductions in Southern Africa dates back to the late 18th century when European settlers arrived in the region (Wells, et al. 1986). The lattest global IPCC report (IPCC 2023) shows that southern Africa is likely to become substantially hoter, while precipitation is likely to decrease in most regions. With the predicted changes in temperature, precipitation regimes, and water availability, Southern Africa is expected to become one of the global climate-change hotspots (Hoegh-Guldberg, et al. 2019).

Species selection and occurrence records

For our study, we used a list of cultivated alien plants of Southern Africa extracted from (Cultivated Plants of Southern Africa; Glen 2002). The initial list included more than 5,316 taxa that are described to be cultivated in at least one region in Southern Africa. To harmonize the list of cultivated alien plants of Southern Africa with other datasets used in this study (see below), we standardized the names of the species following The Plant List (version 1.1; http://www.theplantlist.org) using the R package 'Taxonstand' (Cayuela, et al. 2019). Intraspecific taxa (varieties and subspecies) were merged at the species level to reduce complexity. The resulting list, therefore, consisted of 5,212 cultivated alien plants with accepted names.

We collected occurrence data on the global distribution of these species from the Global Biodiversity Information Facility (GBIF.org 2021; https://doi.org/10.15468/dl.9jsscb) using the 'rgbif' library in R (Chamberlain, et al. 2021). To account for the full realized niche of the species, we considered native and introduced occurrences globally (Early and Sax 2014, Fernández and Hamilton 2015, Pearman, et al. 2008). Erroneous records (e.g., those that occur on ocean surfaces due to possible georeferencing errors and those in capitals, where they might have been planted) were automatically removed using the 'CoordinateCleaner' library in R (Zizka, et al. 2019). Additionally, we removed duplicate data points (that is, multiple occurrence records within each 10' × 10' grid cell, ~ 20 x 20 km) for bias correction. The resulting species list, therefore, consisted of 1,527 species with at least 50 occurrences per species from their native and alien ranges.

Climatic data

We retrieved global climate data from WorldClim version 2.1(10' resolution for the period 1970-2000) (Fick and Hijmans 2017). From all the available bioclimatic variables, we selected the following five: (1) Temperature Seasonality (standard deviation ×100), (2) Max Temperature of Warmest Month (°C), (3) Precipitation of Wettest Month (°C), (4) Precipitation of Driest Month (mm), (5) Precipitation Seasonality (coefficient of variation). We selected these variables because they are known to strongly affect plant distributions (Root, et al. 2003). In addition, we used human population density (person / 10' × 10' grid cell), available from the NASA Socioeconomic Data and Applications Center, as an interaction term with nativeness as an indicator of propagule pressure (Gao 2020). Moreover, all explanatory variables have pairwise Pearson's r values $<$ 0.7 (Supporting Information Fig. S1), limiting the risk of biased model estimates due to multicollinearity (Dormann, et al. 2013).

To represent possible future climatic conditions, we used projected climate data for the period 2081–2100 (means of the above-listed climatic variables), again retrieved from WorldClim version 2.1 (Fick and Hijmans 2017). We also used human population density projection for the year 2100, retrieved from NASA Socioeconomic Data and Applications Center. We used two Shared Socioeconomic Pathways (SSPs) to characterize future climate conditions, specifically SSP1 and SSP5 – to represent a best-case scenario (the sustainability/taking the green road scenario) and a worst-case scenario (fossil-fueled development/taking the highway scenario), respectively (O'Neill, et al. 2017, Riahi, et al. 2017). Because different global circulation models (GCMs) significantly affect species range projections, we selected three GCMs for each SSP scenario, namely CanESM5, CNRM-ESM2-1, and MIROC6. According to The Inter-Sectoral Impact Model Intercomparison Project (Lange 2019), these GCMs represent relatively low, moderate, and high global projected mean precipitation and temperature.

Data on naturalization status, native origins and biomes

To analyze whether the potential current and future climatic suitability differ according to plants' naturalization status, biogeographical origin and biome within Sothern Africa, we first extracted the naturalization status of each species (that is, cultivated but not yet naturalized or cultivated and naturalized) using the latest version of the Global Naturalized Alien Flora (GloNAF) database (van Kleunen, et al. 2019). Second, we used the nine level-1 regions of the World Geographical Scheme for Recording Plant Distributions of the Taxonomic Databases Working Group (TDWG; Brummitt 2001) to identify the native geographical origin of each species. This data was extracted from the Germplasm Resources Information Network (GRIN; https://ars-grin.gov), the World Checklist of Selected Plant Families (WCSP; http://apps.kew.org/wcsp), and the Plants of the World Online database (POWO 2019); http://www.plantsoftheworldonline.org/). Finally, we assigned each 10' × 10' grid cell in Southern Africa to one of the biomes defined by Dinerstein, et al. (2017) (Supporting Information Fig. S4).

Species distribution modeling

To define the current and future potential climatic suitability for the cultivated alien plants in Southern Africa, we combined the bioclimatic variables with presence records and randomly generated pseudo-absence data using the BIOMOD2 platform as implemented in the 'biomod2' R package version 3.4-6 (Thuiller, et al. 2020). We used four modeling algorithms: i) two regression techniques (that is, i) generalized linear model (GLM) and ii) general additive model (GAM)) and two classification techniques: iii) random forest (RF) and iv) boosted regression trees (BRT). We kept the default argument settings of these four modeling algorithms in biomod2. For all the models, we randomly generated three sets of 10,000 pseudo-absence records from the GBIF presence-only data. All models were fitted using an equal weight of presences and pseudoabsences. Finally, to evaluate our models, each model was separately run three times using a random split-sampling approach in which data was split into 80% calibration and 20% evaluation datasets for each of the three pseudo-absence datasets (resulting in nine models per modeling algorithm and a total of 36 models for each species). We used the True Skill Statistic (TSS) of Allouche, et al. (2006) to assess the predictive performance of the SDMs. TSS values range from -1 to 1, where 0 indicates a random prediction, negative values indicate that predictions perform worse than random, and 1 indicates perfect agreement.

We then used the calibrated models to project the current and future climatic suitability in Southern Africa using a weighted mean ensemble forecast (Thuiller, et al. 2009). To do that, we first 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 (we only included models with a TSS score > 0.5). Then, the mean weighted ensemble was transformed into binary maps using a threshold that maximized the TSS to predict presences and absences for the 'current' climate and each of the two climate change scenarios. Three binary projections were produced for each SSP scenario, one for each GCM. We then combined these three projections into one consensus map where each cell was identified as suitable when the majority of GCMs (that is, two of three) predicted it as suitable; otherwise, the cell was identified as unsuitable.

This subset of modeled species (n = 1,527) effectively represents the cultivated flora of Southern Africa. This conclusion is supported by the similar distribution of native origins between the modeled and unmodeled species (n = 3,685) (Supporting Information Fig. S2). With the exception of species native to Europe and Southern America, the proportion of species from each native origin was quantitatively consistent in the modeled species subset when compared to the entire pool of the cultivated flora.

We explored the potential impact of each bioclimatic variable on the future distribution of the cultivated alien species. To do so, we made predictions for future climatic conditions fixing one of the five predictors at its value of the reference period 1970–2000 in turn. We then compared these predictions to those of the fully adapted model (= all predictors set to future conditions) by computing the difference in the number of suitable cells. The rationale is that a predictor variable has more impact the more the two projected future distributions differ (Supporting Information Fig.S3).

Hotspot analysis

To identify potential invasion hotspots for cultivated alien plants in Southern Africa for each climatic scenario, we stacked the binary consensus maps of all 1,527 modeled species. We then calculated a per grid cell (10' x 10') sum of number of species that find suitable climatic conditions there. We defined invasion hotspots as the top 10% of grid cells that provide suitable climatic conditions to the highest numbers of species. To depict the potential contraction or expansion of invasion hotspots, we also identified the high-risk region under future climatic scenarios by applying the top 10% cut-off value (128 species) determined under current conditions to the future climatic scenarios.

Climatic suitability and biomes

We assessed the difference between biomes within Southern Africa with respect to changes in climatic suitability under climate change. To do this, we calculated for each grid cell in the different biomes of Southern Africa (see above) the number of alien species that encounter suitable climatic conditions under current and future scenarios. Then, we calculated the difference in number of alien species between current and future climate scenarios and divided it by the number of alien species under current climatic scenario (proportion of change). To test whether the potential number of alien species in each biome will, on average, increase, decrease, or remain constant under future climate change scenarios, we calculated the mean proportion of change for each group and then calculated the 95 % confidence intervals around these means with 1,000 bootstrap replications using the boot.ci function in the "boot" R package version 1.3-28 (Canty and Ripley 2021). We considered the mean proportion of change of each group to deviate from zero if the confidence intervals did not overlap with zero. We also tested if there are differences in the numbers of potential alien species among biomes. To account for the fact that each species can potentially occur in multiple biomes, we applied simple randomizations to determine whether the mean potential number of alien species in each biome deviated from those expected by chance ($p < 0.05$, two-tailed test; see Divišek, et al. 2018, Omer, et al. 2021). Therefore, from the pool of all proportions of changes, we randomly drew 999 times as many species as are in each biome. We defined the observed mean proportions of change to differ from random expectations if it was in or beyond the lower 2.5% or upper 2.5% of the distributions of random draws.

Climatic suitability and naturalization status

Under both current and future climatic scenarios, 824 (which accounts for 53.9% of all modeled species) were predicted to lack suitable climatic conditions in Southern Africa. Therefore, we will not include these species in our subsequent analysis. Speices with modeled unsuitable climatic suitability may still be successfully cultivated in gardens and public spaces as under cultivation, weeding, irrigation and tendering may allow them to persist and flourish.

We tested whether the naturalization status of cultivated alien plants in Southern Africa is correlated with the size of the current potential range (= number of suitable 10' × 10' cells) and whether cultivated alien and naturalized plants differ in their response to climate change (change in the future range size compared to the current range size). We first calculated the difference in potential range sizes between current and future climate scenarios. Then we divided that difference by the potential range size under current climatic conditions (proportion of change). Negative and positive values indicate a net reduction or expansion in the climatically suitable area under climate change, respectively. Then, we fitted three generalized linear models (GLMs) with a binomial error distribution and a logit link function. For each GLM model, we set naturalization status as the binary response variable and the number of climatically suitable cells under the three climatic scenarios (that is, current and change in SSP1 and SSP5 to the current climate) as explanatory variables. To facilitate comparisons of the estimates within and between the models, we also scaled each explanatory variable to a mean of zero standard deviation of one (Schielzeth 2010).

Climatic suitability and geographical origins

We assessed whether current potential range sizes would, on average, increase, decrease, or remain constant under future climate change scenarios for species of different geographical origins. First, we calculated the mean proportion of change for each group and then calculated 95 % confidence intervals around these means with 1,000 bootstrap replications using the boot.ci function in the "boot" R package version 1.3-28 (Canty and Ripley 2021). We considered the mean proportion of change to deviate from zero if the confidence intervals did not overlap with zero. We also tested if there are differences in the projected range-size change among geographical origins. Again to account for the fact that each species can be native to multiple continents, we applied simple randomizations to determine whether the mean projected range size change of each geographical origin deviated from those expected by chance ($p < 0.05$, two-tailed test; see Divišek, et al. 2018, Omer, et al. 2021). Therefore, from the pool of all proportions of changes, we randomly drew 999 times as many species as are in each geographical origin. We defined the observed mean proportions of change to differ from random expectations if it was in or beyond the lower 2.5% or upper 2.5% of the distributions of random draws.

Unmodeled species climatic suitability imputation

Due to the limited availability of the species' geographical distribution data, we could only predict the current and future species distribution for 1,527, which represents just 29.2% of our entire pool of 5,212 cultivated species. Although we showed that this subset of modeled species is representative of the entire pool of cultivated flora (Supporting Information Fig. S2), we conducted further analysis to evaluate the impact of the unmodeled species on our conclusions. To address this, we used the result of the 1,527 modeled species to impute the climatic suitability for the unmodeled species in our pool of cultivated flora of Southern Africa. To do so, we fitted three separate linear models using the number of climatically suitable cells under the three climatic scenarios (that is, current and change in SSP1 and SSP5 to the current climate) as response variables. Naturalization status and geographical origins were used as explanatory variables. We then used the fitted values to predict the number of climatically suitable cells under the three climatic scenarios for species that were not included in the SDMs. Finally, we redid the analysis of how the change in climatic suitability is related to naturalization status and native origins using the pool of all species (including imputed species). The results using the entire pool of cultivated species show a more or less similar trend for the effects of naturalization status (Supporting Information Figure S6) and native origins (Supporting Information Figure S7).

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

Results

All calibrated models performed well with an average TSS value above 0.8 (Supporting Information Fig.S2). The results reported below were consistent across all GCMs explored (Supporting Information Fig. S5). The number of grid cells projected suitable for the 1,527 cultivated alien species in Southern Africa under current conditions varied from 0 to 9,244, or approximately 51% of Southern Africa's area. The number of species projected to encounter climatically suitable conditions in at least one grid cell under the current conditions also varied greatly, ranging from 0 to 313 species per grid cell, or approximately 20% of the modeled cultivated alien flora of Southern Africa (Fig. 1a). Under climate warming scenarios (SPP1 and SSP5), these numbers were projected to decrease (Fig. 1b-e). Projected changes in Maximum Temperature of the Warmest Month resulted in the highest future contraction of potential ranges of alien cultivated plants in Southern Africa (Supporting Information Fig. S3).

Of Southern Africa, 10.0% were defined as invasion hotspots that were considered climatically suitable under current climatic conditions for at least 128 from the pool of 1,527 modeled cultivated alien species (Fig. 2a). Until the end of the century, the size of the invasion hotspot is predicted to decrease slightly under SSP1 climatic scenario (to 7.1%; Fig. 2b), but substantially under the worst-case climatic scenario SSP5 (to 2.0%; Fig. 2c).

We compared the number of alien species predicted to find suitable conditions in the various biomes in Southern Africa under current and future climatic conditions and found slight differences among them (Fig. 3a, b). Based on both future scenarios, tropical biomes are likely to experience less of a reduction in species richness, while other biomes may either not differ significantly from random expectations or even lose more species richness than anticipated by chance. Furthermore, under the worst-case scenario SSP5, the average potential species richness was significantly less than zero in all biomes (indicating a significant decrease in cultivated alien species richness) (Fig. 3a, b).

Under current climatic conditions, naturalized plants were predicted to have a larger potential range than non-naturalized cultivated plants in Southern Africa (GLM: Z = 9.64, P [?] 0.001; Fig. 3a, Supporting information Table S1). However, as climate becomes warmer, the size of potential ranges is projected to decline for all species (Fig. 3b&c). While contraction is projected to be more significant for non-naturalized species than for naturalized ones under the moderate future climatic scenario SSP1 (GLM: Z = 2.15, P = 0.031; Fig. 3b, Supporting information Table S1), under the worst-case scenario SSP5, there will be no significant difference between the two groups (GLM: Z = 1.87, P = 0.060; Fig. 3c, Supporting information Table S1). While the average cultivated plant in Southern Africa will experience a reduction of its potential range, an increase is projected for ~13% and 9% of species under the scenarios SSP1 and SSP5, respectively.

Our results indicated that under the SSP1 climate-change scenario, species native to TDWG continents mainly located in the Southern Hemisphere (i.e., Pacific Islands, Australasia, Tropical Asia, and Southern America) would likely lose less climatically suitable areas than the average cultivated species. Species native to Pacific Islands and Australasia have an average change in range size significantly greater than zero, indicating a significant increase in areas with suitable climates. In contrast, species native to continents mainly located in the Northern Hemisphere (i.e., Europe, other parts of Africa, and Asia Temperate) will likely lose climatically suitable range in Southern Africa at an above-average rate (Fig. 4a). However, for SSP5 climate-change scenario all species are predicted to have an average change in range size significantly less than zero, indicating a significant contraction in areas with suitable climates (Fig. 4b).

Discussion

Numerous regional studies have indicated that alien plants are projected to experience increased range sizes due to climate change, particularly in the Northern Hemisphere (Adhikari, et al. 2022, Bellard, et al. 2013, Dullinger, et al. 2017, Thapa, et al. 2018). Here, we used species distribution models to predict the potential distribution of the cultivated flora of Southern Africa under current climatic conditions and assessed how it would change under a warmer future climate. The results of our study indicate that, under current conditions, many cultivated alien plants could thrive in many regions within the area. Moreover, Southern Africa shows a higher prevalence of climatically suitable areas for naturalized cultivated plants than non-naturalized ones. However, our analysis indicates that the potential distribution of most cultivated alien plants in Southern Africa will decline under a warmer future climate.

The projected shrinkage of suitable climatic space for alien species under climate warming contradicts previous studies for other regions. Climate warming, which may allow cultivated species to escape and naturalize outside their native ranges in cooler and humid (arctic to temperate) regions (Adhikari, et al. 2022, Dullinger, et al. 2017, Haeuser, et al. 2018), is unlikely to have this effect in Southern Africa and other hot and semi-arid subtropical parts of the world (Beaumont, et al. 2011). This result parallels findings by Broennimann, et al. (2006), who have shown that also the native flora of Southern Africa will experience range losses under climate change. Particularly, endemic plant species in Southern Africa are predicted to lose approximately 50% of their suitable ranges by 2050, even under the most optimistic climate change scenario (Broennimann, et al. 2006). In line with our findings, Bellard, et al. (2013) projected that the potential distribution of the 100 world's worst invasive species will decrease under climate change in some regions, especially in regions like the western part of Southern Africa. Similarly, (Bezeng, et al. 2017) projected that climatically suitable areas for the majority of alien trees and shrubs in South Africa would contract under climate change.

The southeastern region of Southern Africa appears to remain the invasion hotspot for the cultivated alien flora (Fig. 2a-c) into the future. This pattern might be explained by the predicted higher increase in temperature and the higher aridity in the western part of Southern Africa, which already experiences extreme climatic conditions (such as the Namib desert) (Almazroui, et al. 2020). Our findings further support this pattern, as we identified the Maximum Temperature of the Warmest Month as the most influential bioclimatic variable in determining the future distribution of climatically suitable areas of alien cultivated plants in Southern Africa (Supporting Information Fig.S3). Temperature was also found to be the most essential macroecological factor reducing the species richness and diversity of native savanna flora at the plant community scale in Kruger National Park, Republic of South Africa (Hejda, et al. 2022). We also observed regional variation in the specific biomes in Southern Africa; for example, the tropical biomes are expected to experience fewer losses of alien species due to future climate changes. In contrast, other biomes, such as semi-deserts, are expected to undergo significant contractions in the potentially suitable area for a large number of cultivated alien plants. The regional variation in future climatic suitability might be again attributed to the fact that regions that suffer more losses are subject to increasingly hot and arid climatic conditions under climate change that will affect the survival of most native and cultivated alien plants (Almazroui, et al. 2020).

Naturalized plants have significantly larger climatically suitable areas than non-naturalized cultivated alien plants under current climatic conditions. This supports previous findings that suggest a correlation between climatic suitability and naturalization success (Feng, et al. 2016, Haeuser, et al. 2018, Mayer, et al. 2017). However, under warmer climatic conditions in the future, differences between naturalized and non-naturalized species are predicted to decrease. For example, the will be no significant difference in mean climatic suitability between naturalized and non-naturalized (Fig. 3c, Supporting information Table S1). This implies that as climate change progresses, some non-naturalized cultivated alien plants may still have a high potential to become naturalized. Moreover, it may indicate that invasion dynamics will become more complex to predict with continuing climate change.

Despite the overall decrease in the future potential distribution of cultivated alien species in Southern Africa, our analysis also revealed variations among species with different native origins. Species native to continents mainly located in the Northern Hemisphere (i.e., Europe, other parts of Africa, and Asia Temperate) were less likely to find suitable climatic conditions in Southern Africa than species native to the Southern Hemisphere. In line with our findings, a recent study showed that the potential alien ranges of European endemic plants would shrink under climate change (R. Pouteau, et al. 2021). Our result showed that plants of tropical origins are more likely to encounter suitable climatic conditions in Southern Africa than those from temperate regions. This could be both because tropical biomes in Southern Africa are less likely to lose climatic suitability under climate change (Fig. 6) and because these species were introduced from areas with a climate similar to Southern Africa. For example, the majority of alien trees and shrubs in Southern Africa were introduced from regions with similar climates, such as Australia and Southern America (Rejmánek and Richardson 2013).

The reduction in climatic suitability for cultivated alien plants in Southern Africa can be attributed to the future climatic conditions that will be unfavorable to their growth. However, it is essential to note that by the end of this century, the region is projected to experience novel combinations of climatic factors, which could affect species distributions (Williams, et al. 2007). It is possible that current species distribution models (SDMs) do not appropriately account for how these cultivated plants will respond to such novel conditions, potentially leading to an overestimation of the effect of future climate on species distribution (Early and Sax 2014, Fitzpatrick and Hargrove 2009).

Conclusion

This study indicates that naturalized species have higher levels of climatic suitability than cultivated plants that have not naturalized. However, under a warmer climate, naturalized species are predicted to lose mostly equal areas with suitable climates as cultivated plants that did not naturalize yet. Therefore, as climate change progresses, we might see a turnover in the composition of the naturalized species pool. The study also reveals that plants with different native origins and biomes in southern Africa are affected differently. These findings can assist in identifying cultivated alien plants that pose invasion risks early and in developing effective management strategies to mitigate their impacts. Our study highlights that the potential distribution of the cultivated alien flora in Southern Africa is unlikely to be amplified by future climate changes. On the contrary, climatically suitable ranges are projected to shrink, particularly under severe climate change. The main reason for this finding is that climate change will likely result in increasingly hot, semi-arid climates in the region, which will impose strong constraints on the survival of many plant species; accordingly, many native species are projected to experience shrinking in climatically suitable space in the region. Thus, our study highlights that increased climatic suitability for alien species under climate change, which seems to be the norm in cold and temperate climates, does not necessarily translate to similar results in regions of the subtropics.

References

Adhikari, P., et al. 2022. Climate change-induced invasion risk of ecosystem disturbing alien plant species: An evaluation using species distribution modeling. - Frontiers in Ecology and Evolution 10.

Allouche, O., et al. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). - Journal of Applied Ecology 43: 1223-1232.

Almazroui, M., et al. 2020. Projected change in temperature and precipitation over Africa from CMIP6. - Earth Systems and Environment 4: 455-475.

Beaumont, L. J., et al. 2011. Impacts of climate change on the world's most exceptional ecoregions. - Proceedings of the National Academy of Sciences 108: 2306-2311.

Bellard, C., et al. 2013. Will climate change promote future invasions? - Global Change Biology 19: 3740-3748.

Bellard, C., et al. 2015. Combined impacts of global changes on biodiversity across the USA. - Scientific Reports 5: 11828.

Bellard, C., et al. 2016. Major drivers of invasion risks throughout the world. - Ecosphere 7: e01241.

Bezeng, B. S., et al. 2017. Climate change may reduce the spread of non-native species. - Ecosphere 8: e01694.

Bezeng, S. B., et al. 2015. Revisiting Darwin's naturalization conundrum: explaining invasion success of non-native trees and shrubs in southern Africa. - J Ecol 103: 871-879.

Broennimann, O., et al. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? - Global Change Biology 12: 1079-1093.

Brummitt, R. K. 2001. World Geographical Scheme for Recording Plant Distributions. - Hunt Institute for Botanical Documentation.

Canty, A. and Ripley, B. 2021. boot: Bootstrap R (S-Plus) Functions. R package, 1.3-28.1.

Cayuela, L., et al. 2019. Taxonstand: Taxonomic Standardization of Plant Species Names R package 2.2.

Chamberlain, S., et al. 2021. rgbif: Interface to the Global Biodiversity Information Facility API. R package 3.5.2.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection Or the Preservation of Favoured Races in the Struggle for Life. - John Murray.

Dinerstein, E., et al. 2017. An ecoregion-based approach to protecting half the terrestrial realm. - Bioscience 67: 534-545.

Divíšek, J., et al. 2018. Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. - Nature Communications 9: 4631.

Dormann, C. F., et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. - Ecography 36: 27-46.

Dullinger, I., et al. 2017. Climate change will increase the naturalization risk from garden plants in Europe. - Global Ecology and Biogeography 26: 43-53.

Early, R. and Sax, D. F. 2014. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. - Global Ecology and Biogeography 23: 1356-1365.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. - The University of Chicago Press, Chicago, United States.

Engelbrecht, C. J. and Engelbrecht, F. 2015. Shifts in Köppen-Geiger climate zones over southern Africa in relation to key global temperature goals. - Theoretical and Applied Climatology 123: 247-261.

Faulkner, K. T., et al. 2020. South Africa's pathways of introduction and dispersal and Hhow they have changed over time. B. W. van Wilgen, et al. (eds), Biological Invasions in South Africa. Springer International Publishing, pp. 313-354.

Feng, Y., et al. 2016. Introduction history, climatic suitability, native range size, species traits and their interactions explain establishment of Chinese woody species in Europe. - Global Ecology and Biogeography 25: 1356-1366.

Fernández, M. and Hamilton, H. 2015. Ecological niche transferability using invasive species as a case study. - PLOS ONE 10: e0119891.

Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. - International Journal of Climatology 37: 4302-4315.

Fitzpatrick, M. C. and Hargrove, W. W. 2009. The projection of species distribution models and the problem of non-analog climate. - Biodiversity and Conservation 18: 2255-2261.

Fulgêncio-Lima, L. G., et al. 2021. Invasive plants in Brazil: climate change effects and detection of suitable areas within conservation units. - Biological Invasions 23: 1577-1594.

Gao, J. 2020. Global 1-km Downscaled Population Base Year and Projection Grids Based on the Shared Socioeconomic Pathways, Revision 01. - In: NASA Socioeconomic Data and Applications Center (SEDAC).

GBIF.org 2021. GBIF Occurrence Download https://doi.org/10.15468/dl.9jsscb. June 2021. https://www.gbif.org/occurrence/download/0293436-200613084148143

Glen, H. F. 2002. Cultivated Plants of Southern Africa: Botanical Names, Common Names, Origins, Literature. - Jacana: National Botanical Institute, 2002.

Haeuser, E., et al. 2018. European ornamental garden flora as an invasion debt under climate change. - Journal of Applied Ecology 55: 2386-2395.

Hejda, M., et al. 2022. Water availability, bedrock, disturbance by herbivores, and climate determine plant diversity in South-African savanna. - Scientific Reports 12: 338.

Hoegh-Guldberg, O., et al. 2019. The human imperative of stabilizing global climate change at 1.5°C. - Science 365: eaaw6974.

Hulme, P. E., et al. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. - Journal of Applied Ecology 45: 403-414.

IPCC 2023. Climate Change 2023: Synthesis Report. A Report of the Intergovernmental Panel on Climate Change. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. H. L. Team and J. Romero (eds), Geneva, Switzerland.

Lambdon, P.-W., et al. 2008. Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. - Preslia -Praha 80: 101-149.

Lange, S. 2019. Trend-preserving bias adjustment and statistical downscaling with ISIMIP3BASD (v1.0). - Geosci. Model Dev. 12: 3055-3070.

Lenzner, B., et al. 2021. Role of diversification rates and evolutionary history as a driver of plant naturalization success. - New Phytologist 229: 2998-3008.

Liu, D., et al. 2023. The impact of land use on non-native species incidence and number in local assemblages worldwide. - Nature Communications 14: 2090.

Madani, N., et al. 2018. Future global productivity will be affected by plant trait response to climate. - Scientific Reports 8: 2870.

Maurel, N., et al. 2016. Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. - Global Ecology and Biogeography 25: 1500-1509.

Mayer, K., et al. 2017. Naturalization of ornamental plant species in public green spaces and private gardens. - Biological Invasions 19: 3613-3627.

Northrup, J. M., et al. 2019. Synergistic effects of climate and land-use change influence broad-scale avian population declines. - Global Change Biology 25: 1561-1575.

O'Neill, B. C., et al. 2017. The roads ahead: Narratives for shared socioeconomic pathways describing world futures in the 21st century. - Global Environmental Change 42: 169-180.

Oduor, A. M. O., et al. 2023. Alien ornamental plant species cultivated in Taizhou, southeastern China, may experience greater range expansions than native species under future climates. - Global Ecology and Conservation 41: e02371.

Omer, A., et al. 2021. Characteristics of the naturalized flora of Southern Africa largely reflect the non-random introduction of alien species for cultivation. - Ecography 14: 1812-1825.

Omer, A., et al. 2022. The role of phylogenetic relatedness on alien plant success depends on the stage of invasion. - Nature Plants 8: 906-914.

Pearman, P. B., et al. 2008. Niche dynamics in space and time. - Trends in Ecology & Evolution 23: 149-158.

Pouteau, R., et al. 2021. Potential alien ranges of European plants will shrink in the future, but less so for already naturalized than for not yet naturalized species. - Diversity and Distributions 27: 2063-2076.

Pouteau, R., et al. 2021. Potential alien ranges of European plants will shrink in the future, but less so for already naturalized than for not yet naturalized species. - Diversity and Distributions 27: 2063-2076.

POWO 2019. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/ Retrieved 10-26 August 2020.

Pyšek, P., et al. 2008. Geographical and taxonomic biases in invasion ecology. - Trends Ecol Evol 23: 237-44.

Pyšek, P., et al. 2020. Scientists' warning on invasive alien species. - Biological Reviews 95: 1511-1534.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. 3.6.1.

Rejmánek, M. and Richardson, D. M. 2013. Trees and shrubs as invasive alien species – 2013 update of the global database. - Diversity and Distributions 19: 1093-1094.

Riahi, K., et al. 2017. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. - Global Environmental Change 42: 153-168.

Richardson, D. M. and Pyšek, P. 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. - New Phytologist 196: 383-396.

Rodríguez-Labajos, B., et al. 2009. Multi-level driving forces of biological invasions. - Ecological Economics 69: 63-75.

Root, T. L., et al. 2003. Fingerprints of global warming on wild animals and plants. - Nature 421: 57-60.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. - Methods in Ecology and Evolution 1: 103-113.

Seebens, H., et al. 2020. Projecting the continental accumulation of alien species through to 2050. - Global Change Biology n/a:

Soudzilovskaia, N. A., et al. 2013. Functional traits predict relationship between plant abundance dynamic and long-term climate warming. - Proceedings of the National Academy of Sciences 110: 18180-18184.

Thapa, S., et al. 2018. Understanding the dynamics in distribution of invasive alien plant species under predicted climate change in Western Himalaya. - PLOS ONE 13: e0195752.

Thuiller, W., et al. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. - Global Change Biology 11: 2234-2250.

Thuiller, W., et al. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. - Ecography 32: 369-373.

Thuiller, W., et al. 2020. biomod2: Ensemble Platform for Species Distribution Modeling. R package, 3.4.6.

van Kleunen, M., et al. 2015. Global exchange and accumulation of non-native plants. - Nature 525: 100-103.

van Kleunen, M., et al. 2018. The ecology and evolution of alien plants. - Annual Review of Ecology, Evolution, and Systematics 49: 25-47.

van Kleunen, M., et al. 2018. The changing role of ornamental horticulture in alien plant invasions. - Biol Rev 93: 1421-1437.

van Kleunen, M., et al. 2019. The Global Naturalized Alien Flora (GloNAF) database. - Ecology 100: e02542.

van Kleunen, M., et al. 2020. Economic use of plants is key to their naturalization success. - Nat Commun 11: 3201.

Vilà, M. and Hulme, P. E. 2017. Non-native species, ecosystem services, and human well-being. M. Vilà and P. E. Hulme (eds), Impact of Biological Invasions on Ecosystem Services. Springer, pp. 1-14.

Wells, M. J., et al. 1986. History of introduction of invasive alien plants to southern Africa. I. A. W. Macdonald and A. A. Kruger (eds), Ecology and Management of Biological Invasions in Southern Africa : Proceedings of the National Synthesis Symposium on the Ecology of Biological Invasions. Oxford University Press.

Williams, J. W., et al. 2007. Projected distributions of novel and disappearing climates by 2100 AD. - Proceedings of the National Academy of Sciences 104: 5738-5742.

Zizka, A., et al. 2019. CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. - Methods in Ecology and Evolution 10: 744-751.

Figures

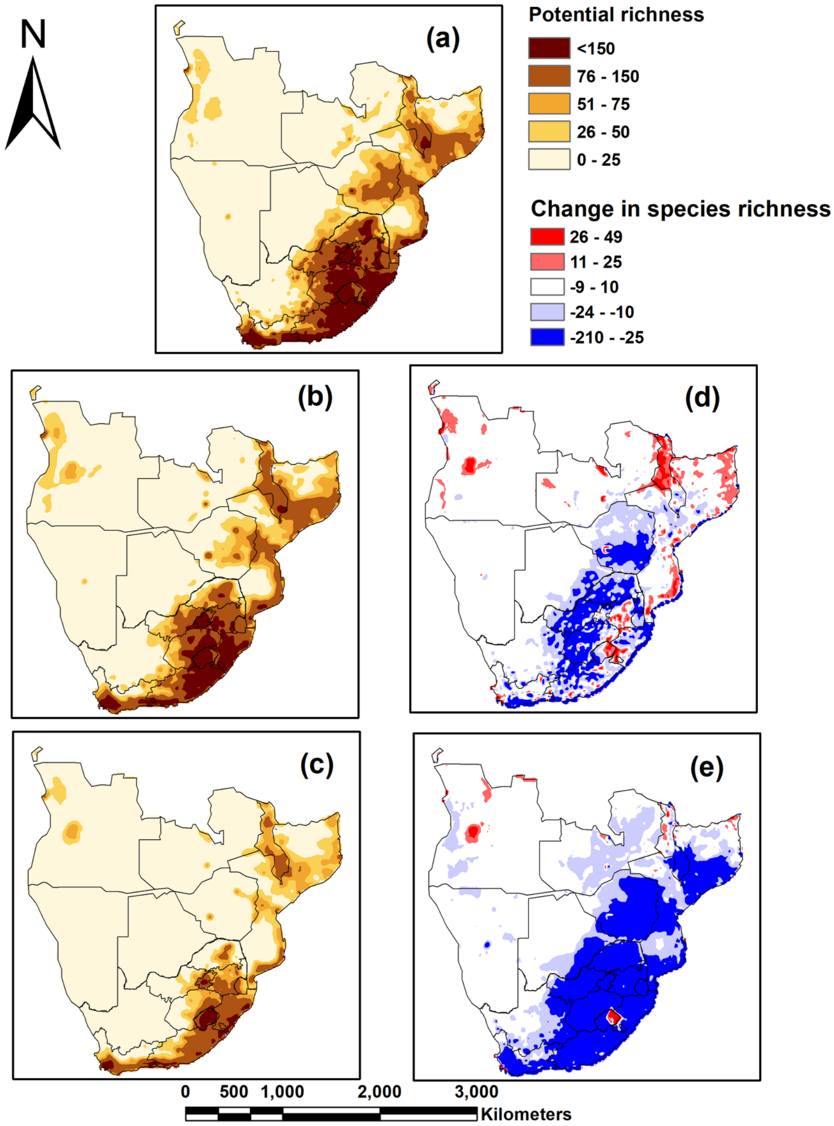

Figure 1: Current and future potential richness of cultivated alien plants of Southern Africa. The maps show the predicted number of species that are expected to encounter suitable climatic conditions per 10' grid cell under current climatic conditions (a), moderate future climate change (SSP1) (b) and severe climate change (SSP5) by the end of the 21st century (2081-2100). (c) and the expected change to current species richness under future climate change scenarios; SSP1 (d) and SSP5 (e).

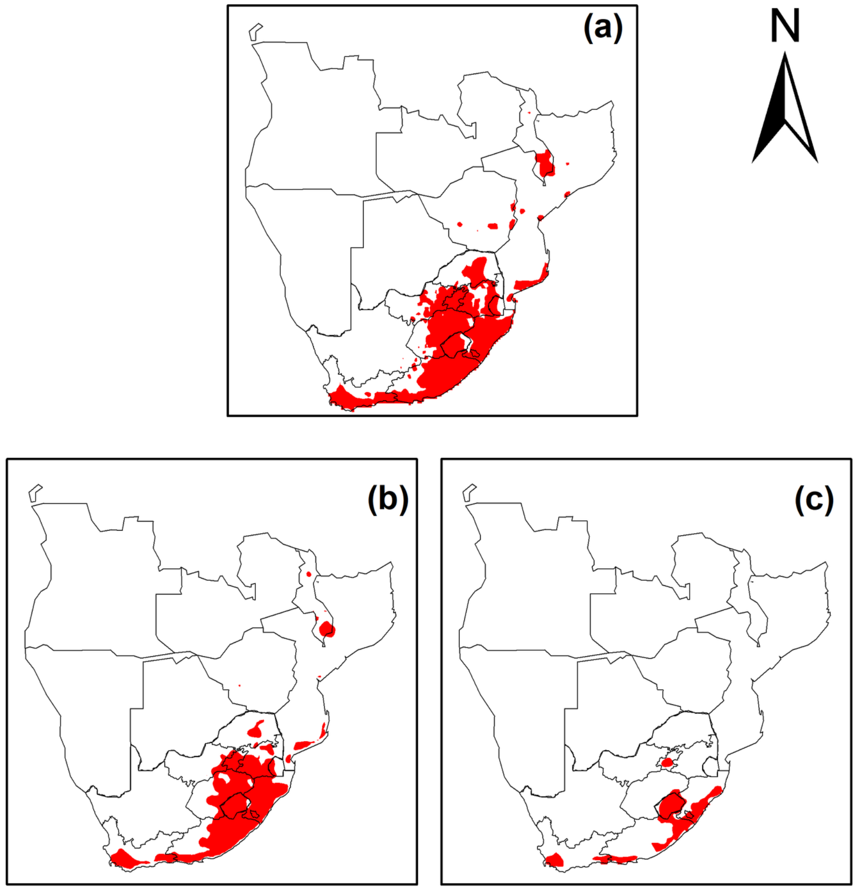

Figure 2: Current and future potential invasion hotspots of cultivated alien plants in Southern Africa . The maps represent current climatic conditions (a), moderate future climate change (SSP1) (b), and severe climate change (SSP5) by the end of the 21stcentury (2081-2100). We stacked the binary distribution maps of the 1,527 species and then identified high-risk regions defined as the top 10% of cells that were predicted to be suitable under current climatic conditions for the highest number of species (depicted in red); the same cut off value was then used for climate change scenarios.

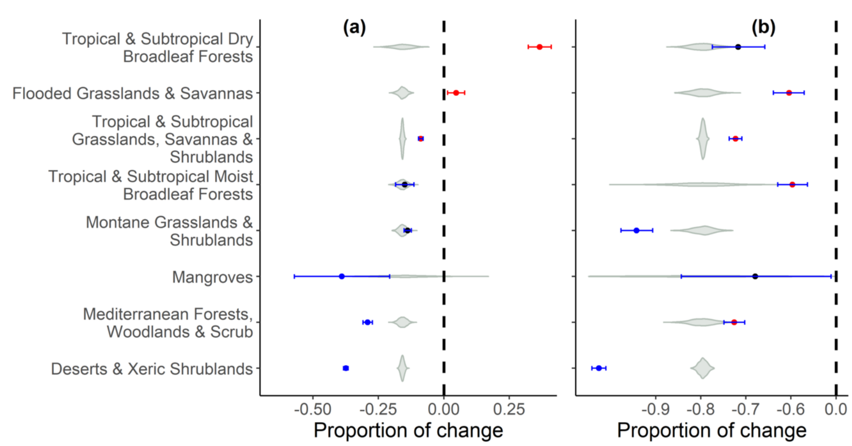

Figure 3: Predicted change in current climatic suitability under moderate future climate change (SSP1) (a) and severe climate change (SSP5) (b) of cultivated alien plants of Southern Africa by 2081-2100 separated by their biomes. The dots represent the observed mean of the predicted change of a certain group. The lines are the 95% bootstrapped confidence intervals of the means of 1000 resamples from the population of species of a certain group. Red, blue and black lines indicate whether the mean of the group is significantly larger, small or not different from zero. The violin plots show the distribution of the means of predicted changes sampled by bootstrapping from the population of all species. Red, blue, and black dots indicate whether the observed means are significantly higher, lower, or not different from the random expectations, respectively.

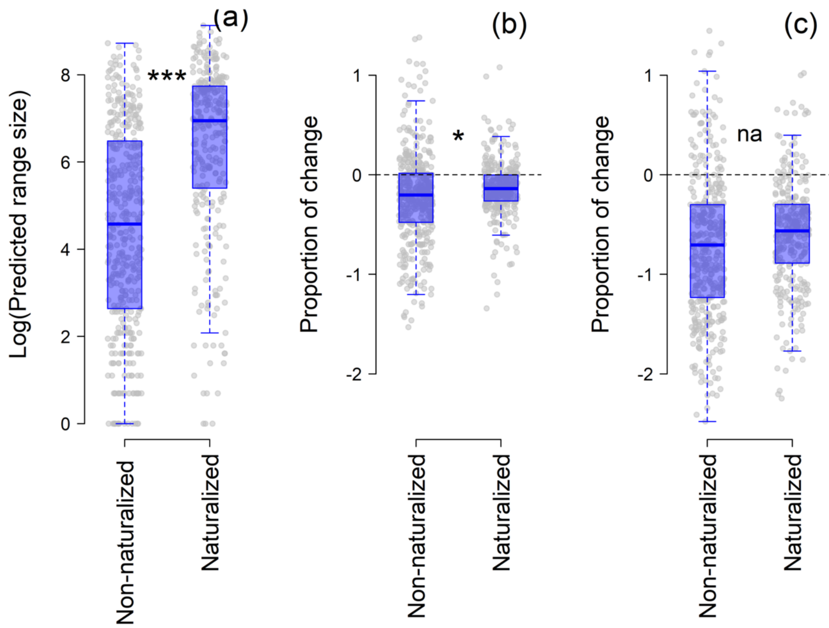

Figure 4: Current climatic suitability (number of grid cells; a) and predicted change to current climatic suitability under moderate (SPP1) (b) and severe (SSP5) (c) climate change by 2081-2100 of cultivated non-naturalized and naturalized plants of Southern Africa. The grey dots represent the number of grid cells predicted to be suitable for each species under current conditions (a) and are predicted to be lost or gained in the future (b, c). The thick horizontal line in each box indicates the median number of cells predicted to be suitable under the current climate (a) and changed to suitable or not suitable under future climate scenarios. The boxes indicate the interquartile range, and the whiskers extend outside the box to 1.5 times the interquartile range. Asterisks indicate significant differences between the compared means according to the GLMs models, with *** indicating $p < 0.001$ and * indicating $p < 0.05$, and na indicating non-significant.

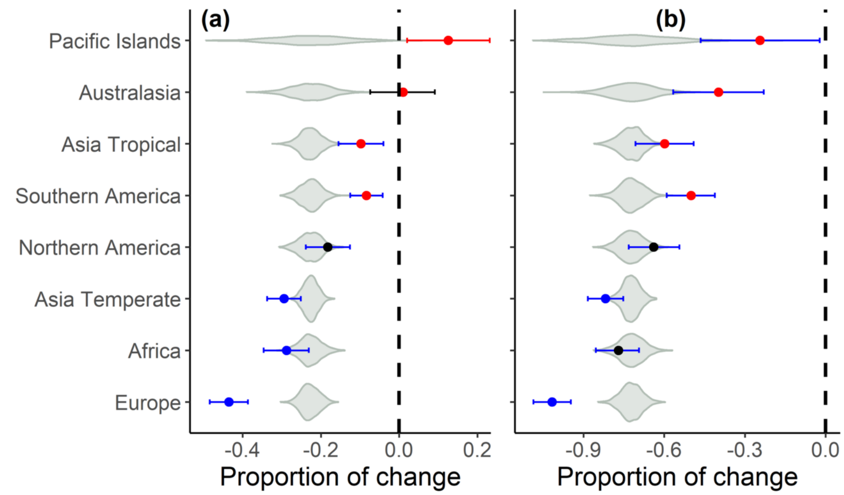

Figure 5: Predicted change in current climatic suitability under moderate (SSP1) (a) and severe climate change (SSP5) (b) by 2081-2100 of cultivated alien plants of Southern Africa separated by their native origins. The dots represent the observed mean of the predicted change of a certain group. The lines are the 95% bootstrapped confidence intervals of the means of 1000 resamples from the population of species of a certain group. Red, blue and black lines indicate whether the mean of the group is significantly larger, small or not different from zero. The violin plots show the distribution of the means of predicted changes sampled by bootstrapping from the population of all species. Red, blue, and black dots indicate whether the observed means are significantly higher, lower, or not different from the random expectations, respectively.