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

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Abstract:	Alien species can have massive impacts on native biodiversity, ecosystem functioning, and human livelihoods. Assessing which species from currently cultivated alien floras may escape into the wild and naturalize is essential for efficient and proactive ecosystem management and biodiversity conservation. Climate change has already promoted the naturalization of many alien plants in temperate regions, but whether it is similar in (sub)tropical areas is insufficiently known. In this study, we used species distribution models for 1,527 cultivated alien plants to evaluate current and future invasion risks across different biomes and 10 countries in southern Africa. Our results confirm that the area of suitable climate is a strong predictor of naturalization success among the cultivated alien flora. In contrast to previous findings from temperate regions, however, climatic suitability is generally predicted to decrease for potential aliens across our (sub)tropical study region. While increasingly hotter and drier conditions are likely to drive declines in suitability for potential aliens across most biomes of southern Africa, in some the number of potential invaders is predicted to increase under moderate climate change scenarios (e.g., in dry broadleaf forests and flooded grasslands). We found that climatic suitability is expected to decline less for aliens originating from continents with the tropical biome or from the Southern Hemisphere. In addition, we found that the climatically suitable area will decline less for aliens that have already naturalized in the region. While the number of potential invaders may decrease across southern Africa under future climate change, our results suggest that already naturalized aliens will continue to threaten native species and ecosystems.

Abstract

Alien species can have massive impacts on native biodiversity, ecosystem functioning, and human livelihoods. Assessing which species from currently cultivated alien floras may escape into the wild and naturalize is essential for efficient and proactive ecosystem management and biodiversity conservation. Climate change has already promoted the naturalization of many alien plants in temperate regions, but whether it is similar in (sub)tropical areas is insufficiently known. In this study, we used species distribution models for 1,527 cultivated alien plants to evaluate current and future invasion risks across different biomes and 10 countries in southern Africa. Our results confirm that the area of suitable climate is a strong predictor of naturalization success among the cultivated alien flora. In contrast to previous findings from temperate regions, however, climatic suitability is generally predicted to decrease for potential aliens across our (sub)tropical study region. While increasingly hotter and drier conditions are likely to drive declines in suitability for potential aliens across most biomes of southern Africa, in some the number of potential invaders is predicted to increase under moderate climate change scenarios (e.g., in dry broadleaf forests and flooded grasslands). We found that climatic suitability is expected to decline less for aliens originating from continents with the tropical biome or from the Southern Hemisphere. In addition, we found that the climatically suitable area will decline less for aliens that have already naturalized in the region. While the number of potential invaders may decrease across southern Africa under future climate change, our results suggest that already naturalized aliens will continue to threaten native species and ecosystems.

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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 change, such as climate and land-use 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, Fristoe, et al. 2023, Mayer, et al. 2017, Richardson and Pyšek 2012). 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 current climate might be favorable for alien species that have already naturalized in a region, future climates may promote the establishment of alien species that have been introduced already but have not yet naturalized. A warming climate might hence constrain the spread of some naturalized alien species but simultaneously might foster expansions or new naturalizations of others.

Climate-suitability analyses have emerged as promising tools for predicting the naturalization risk of alien plants (Dullinger, et al. 2017, Haeuser, et al. 2018, Oduor, et al. 2023, Pouteau, et al. 2021, Thuiller, et al. 2005, Mark van Kleunen, et al. 2018); with projections based on future climate scenarios becoming increasingly important for predicting the potential distributions of alien species. In temperate regions as found 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, 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 outside of 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).

Southern Africa has a tropical and subtropical climate, including large areas of (semi-)arid habitats (Engelbrecht and Engelbrecht 2015). It is not immediately clear how climate change will affect the potential future distribution of alien species across this diverse region. Here, we evaluate current and future invasion risks across biomes of southern Africa using species distribution modelling to investigate the climate suitability for 1,527 alien species currently cultivated in the 10 countries comprising the region. Cultivation in domestic gardens for economic use represents the primary pathway for vascular plant introductions (Faulkner, et al. 2020, Lambdon, et al. 2008, van Kleunen, et al. 2020), and the high prevalence of cultivated species among naturalized floras (M. van Kleunen, et al. 2018) implies that future naturalizations will likely also emerge mainly from cultivated plant populations. Our specific objectives were (1) to predict the current potential distributions 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 assess whether naturalization status explains current and future potential range size of cultivated alien plants of southern Africa; (4) to compare the biomes within southern Africa and native origins of the species with respect to changes in climatic suitability for introduced cultivated plants; and (5) to identify hotspot areas with the highest suitability for cultivated alien plants under current and future climatic conditions in southern Africa.

Methods

Study area

Our study focused on the southern Africa region, comprising ten countries: Angola, Botswana, Eswatini, Lesotho, Malawi, Mozambique, Namibia, Republic of South Africa, Zambia, and Zimbabwe, with a land area of around 4,000,000 km^2 (Bezeng, et al. 2015). The history of modern plant introductions in southern Africa dates back to the late 18th century when European settlers arrived in the region (Wells, et al. 1986). The latest global IPCC report (IPCC 2023) shows that southern Africa is likely to become substantially hotter, 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 combined 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 $SSP_{1\text{-}2.6}$ and $SSP_{5\text{-}8.5}$ – 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, life forms and biomes

To analyze whether the potential current and future climatic suitability differ according to plants' naturalization status, biogeographical origin and biome within southern 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/). Moreover, we assigned each species to one or more major life forms using data on species life forms that we compiled from different data sources (see Omer, et al. 2021). 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. S2).

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. Since all models require presences and pseudo-absences (or background), we randomly generate 10,000 pseudo-absence records from all over the calibration area (i.e., in our case, the globe terrestrial surface). The random draw of pseudo-absence records was repeated three times, and equal weights were given in the models to presences and pseudo-absences. 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. S3). 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 (i.e. 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.S4).

Invasion impact considers not only the count of naturalized species but also their ratio to native ones. A region with 10 naturalized species among 100 natives may seem more invaded than one with 10 naturalized species among 1000, but the latter could face stronger negative effects, especially in regions rich in native and endemic species. Therefore, we also explored the relative distribution patterns of cultivated alien plants compared to the richness of native species in southern Africa. To do this, we extracted the projected numbers of native species in each grid cell in southern Africa (Cai, et al. 2023), and used these numbers to standardize the richness of cultivated alien plants in each specific grid cell (Supporting Information Fig. S10).

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. Species 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, respectively, in the climatically suitable area under climate change. 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 $SSP_{1\text{-}2.6}$ and $SSP_{5\text{-}8.5}$ 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 native origins and life forms

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 and life forms. 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 and life forms. Again to account for the fact that each species can be native to multiple continents and belong to multiple life form, we applied simple randomizations to determine whether the mean projected range size change of each geographical origin and life form deviated from those expected by chance ($p < 0.05$, two-tailed test; see Divíšek, 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 and life form. 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 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 the 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 Divíšek, 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.

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, for each grid cell (10' × 10') the number of cultivated species that find suitable climatic conditions there. We determined current invasion hotspots to be grid cells that were projected as suitable for at least as many cultivated plants as identified by the 90% percentile of grid cells under the current climate; this corresponds to grid cells that were projected to be suitable to 128 cultivated alien plants or more. To depict potential future contractions or expansions of invasion hotspots under warming scenarios, we identified the high-risk region under future climatic scenarios by applying cut-off value determined under current conditions (i.e. 128 alien species) to the future climatic scenarios.

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. S3), 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 $SSP_{1\text{-}2.6}$ and $SSP_{5\text{-}8.5}$ 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 S5) and native origins (Supporting Information Figure S6).

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.S7). The results reported below were consistent across all GCMs explored (Supporting Information Fig. S8). Across the 1,527 cultivated alien species, the number of projected suitable grid cells under current conditions varied from 0 to 9,244 (approximately 51% of southern Africa's area). As expected, the current area of suitable climate in southern Africa was positively related to the probability that a species has naturalized within the region (GLM: $z = 9.64$, $P \leq 0.001$; Fig. 1a, Supporting information Table S1). Under future climate scenarios, the area of suitable climate was predicted to decrease for most species ($SSP_{1\text{-}2.6}$: 72.8%; $SSP_{5\text{-}8.5}$: 85.6%). The strongest driver of suitability contractions was increasing Maximum Temperature of the Warmest Month across the region (Supporting Information Fig. S4). Under the moderate future climate scenario $SSP_{1\text{-}2.6}$, these contractions are projected to be less severe for already naturalized species (GLM: $z = 2.15$, $P = 0.031$; Fig. 1b, Supporting information Table S1). Under the worst-case scenario $SSP_{5\text{-}8.5}$, stronger declines in suitable area are expected in general, with similar changes for naturalized and non-naturalized species (GLM: $z = 1.87$, $P = 0.060$; Fig. 1c, Supporting information Table S1). While the average cultivated plant in southern Africa will experience a reduction of its potential range, we note that increases are projected for ~26.0% and 13.5% of species under the scenarios $SSP_{1\text{-}2.6}$ and $SSP_{5\text{-}8.5}$, respectively.

Across southern Africa, the number of species projected to encounter climatically suitable conditions under current climate varied geographically, ranging from 0 to 313 species per grid cell (approximately 20% of the modeled cultivated alien flora; Fig. 2a). Under climate warming scenarios ($SSP_{1\text{-}2.6}$ and $SSP_{5\text{-}8.5}$), numbers of species per cell were generally projected to decrease

(Fig. 2b-e). Changes in the number of potentially naturalized species varied across biomes, with patterns differing between climate change scenarios (Fig. 3). Notably, under moderate climate change ($SSP_{1-2.6}$), tropical and subtropical dry broadleaf forests and flooded grassland savannahs are expected to become climatically suitable for a higher number of potential invaders (Fig. 3a).

The area of suitable climate, current and projected future, also varied depending on species native geographic origins and life form. Species native to continents spanning primarily equatorial latitudes or located in the Southern Hemisphere (i.e., Pacific Islands, Australasia, Tropical Asia, and Southern America) generally had a higher current suitability and were projected to experience smaller contractions in suitable climate compared to those originating from Northern Hemisphere continents (Fig 4). Under moderate climate change ($SSP_{1-2.6}$), species native to the Pacific Islands and Australasia were even predicted to experience increases in suitable area (Fig 4a). Epiphyte and woody species were less likely to lose suitable area Under both climate scenarios. While climber, aquatic, and long-lived herb plants did not deviate from random expectations, short-lived herbs were expected to lose suitable area more than expected by chance (Supporting Information Fig. S9).

We defined the top 10.0% of grid cells in southern Africa that were climatically suitable for the highest number of cultivated alien species as invasion hotspots (i.e. a threshold of 128 species from the pool of 1,527 modeled cultivated aliens; Fig. 5a). However, when accounting for native richness, proportion of cultivated plants was reduced along the coastal area where native richness is higher (Supporting Information Fig. S10). Until the end of the century, the number of cells meeting this invasion hotspot criteria were predicted to decrease slightly under the $SSP_{1-2.6}$ climatic scenario (to 7.1%; Fig. 5b) but substantially under the worst-case climatic scenario SSP_{5-}

$_{8.5}$ (to 2.0%; Fig. 5c). Under increasingly severe climate scenarios, invasion hotspots were restricted further towards southern coastal regions.

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). In contrast, our results for the subtropical semi-arid region of southern Africa indicate that increasingly hotter and drier future conditions will result in reduced climatic suitability for the majority of already naturalized aliens and non-naturalized species that may escape cultivation. Suitability within the region is projected to decline more for species originating from continents of the Northern Hemisphere, but the effect will be less pronounced for cultivated aliens introduced from primarily tropical or subtropical continents, with climatic favorability even increasing for some of these species. Cultivated aliens that have already naturalized populations in southern Africa are also expected to maintain larger areas of suitable climate relative to non-naturalized species, indicating that these species will continue to threaten native species and ecosystems.

Our results are in line with projections for the world's 100 worst invaders that suggest suitability will decline across many tropical and subtropical regions for these species (Bellard, et al. 2013). Similarly, (Bezeng, et al. 2017) projected that climatically suitable areas for the majority of alien trees and shrubs in the country of South Africa will contract under climate change. Our assessment of the cultivated alien flora of southern Africa also parallel projections predicting that the native flora of this region 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 optimistic climate change scenarios (Broennimann, et al. 2006). We found that richness of alien cultivated plants is highest in areas with medium native richness, particularly within the Montane Grasslands & Shrublands biome (Fig. S10). This might be because this area presents milder climatic conditions compared to the harsh conditions in (semi-)arid biomes, coupled with lower competition from native plants in contrast to the Tropical biomes. This emphasizes the importance of considering interactions between biotic and abiotic drivers when assessing future invasion risks. Thus, further comparisons between native and non-native floras are required to better understand how plant communities across southern Africa will change as warming continues.

While we found that much of southern Africa will become less suitable for cultivated alien plants under future climate warming, the effects of climate change were not uniform across the different biomes and growth forms. We observed large variation among biomes; for example, climate change is predicted to cause fewer losses, or even gains, of potentially establishing alien species in some tropical biomes. In contrast, other biomes, such as semi-deserts, are expected to undergo significant contractions of potentially suitable area for many cultivated alien plants. Overall, we identified the southeastern region of southern Africa as the major invasion hotspot for the cultivated alien flora, currently and in the future (Fig. 5a-c). These patterns might be explained by higher predicted increases in temperature and aridity in the western parts of southern Africa (such as the Namib desert), which already experience extreme climatic conditions today and generally have low suitability for most aliens currently cultivated in southern Africa (Almazroui, et al. 2020). This is consistent with our results identifying Maximum Temperature of the Warmest Month as the most influential bioclimatic variable in determining climatically suitable areas of alien cultivated plants (Supporting Information Fig.S4). Similarly, temperature was found to be a major macroecological factor reducing diversity in native savanna flora of Kruger National Park, Republic of South Africa (Hejda, et al. 2022). We also found that woody and epiphyte species are predicted to experience less losses in climatic suitability compared to other growth forms (Fig. S9). Woody species are generally less sensitive to climate change compared to herbaceous species (Lin, et al. 2010, Wang, et al. 2020). Contrasting responses of woody and herbaceous species to climate change was also reported along dry lands in Africa (Verbruggen, et al. 2021) and the new world (Šímová, et al. 2018).

Overall, our study highlights that the potential distribution of the cultivated alien flora in southern Africa is unlikely to be amplified by future climate changes. In contrast, climatically suitable ranges are projected to shrink, particularly under severe climate change. The reduction in climatic suitability for cultivated alien plants in southern Africa can be attributed to increasingly hot, semiarid climates 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 climatic conditions, which could affect species distributions in unexpected ways (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).

Consistent with previously identified correlations between climatic suitability and naturalization success (Feng, et al. 2016, Haeuser, et al. 2018, Mayer, et al. 2017), naturalized plants currently have significantly larger climatically suitable areas in southern Africa than non-naturalized cultivated aliens. The species in our analyses that have not yet naturalized are expected to experience the most severe declines in suitability, indicating generally declining opportunities for future invasions from within southern Africa's cultivated flora. However, we note that between 15% and 8% of non-naturalized species (111 and 61 species; $SSP_{1-2.6}$ and $SSP_{5-8.5,}$ respectively) are projected to experience increased suitability under warming. Our results suggest that future invaders are most likely to originate from tropical or subtropical native regions and have Epiphyte and woody life forms, with southern Africa's tropical biomes most at risk. Plants originating from temperate continents have historically been prominent among introduced and naturalized aliens in the region (Omer et al, 2021). However, with declines in suitability projected to be steepest for these species (see also Pouteau et al. 2021), the composition of southern Africa's naturalized flora is likely to change under warming. These changes, and threats from future invasions more generally, are likely to become more pronounced as cultivators and farmers will use new species that are better adapted to future conditions than species introduced in the past, such as the ones examined in this study.

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Figures

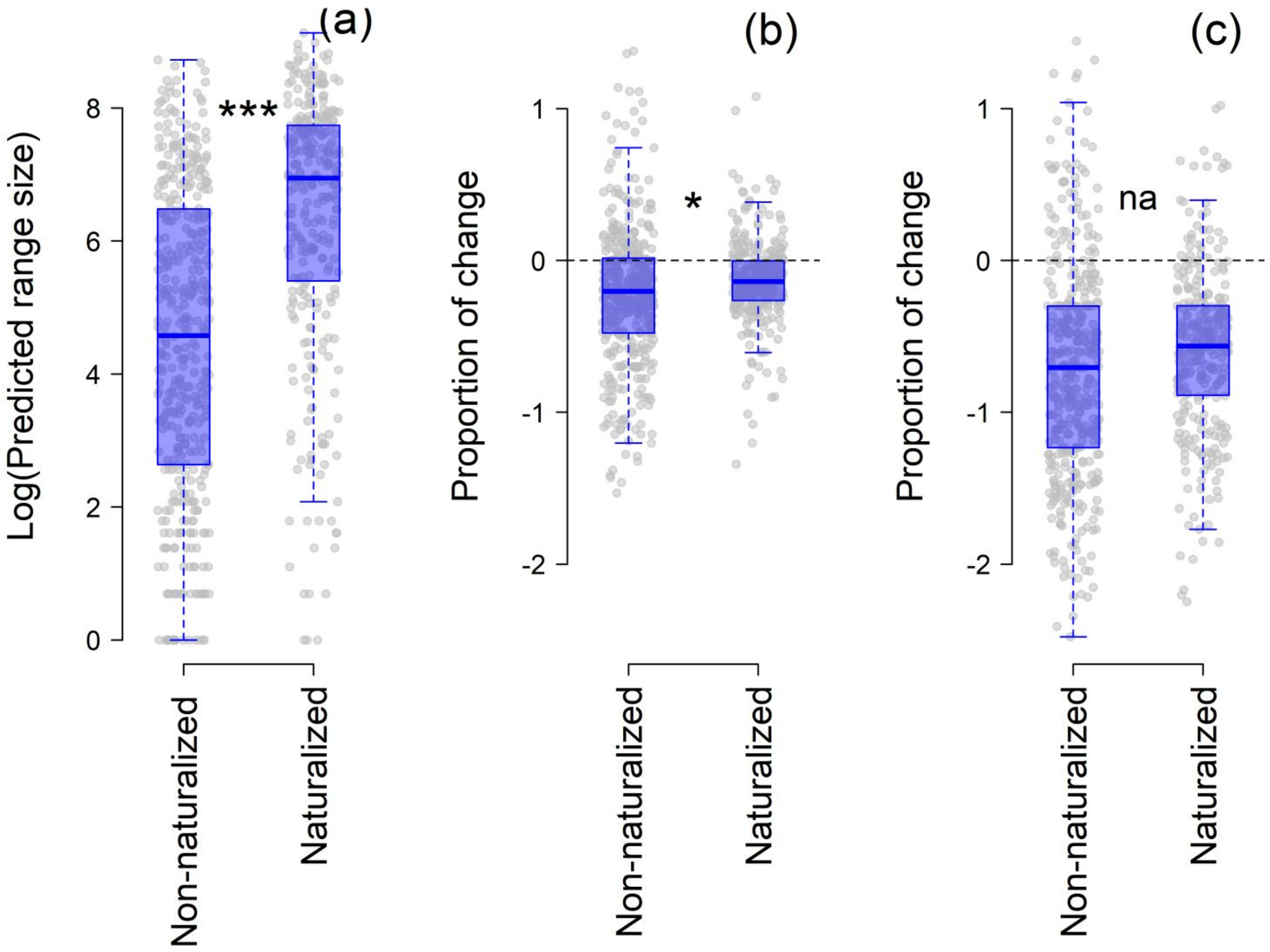


Figure 1: Current climatic suitability (number of grid cells; a) and predicted change to current climatic suitability under moderate ($SSP_{1\text{-}2.6}$) **(b) and severe** ($SSP_{5\text{-}8.5}$) **(c) climate change by 2081-2100 of cultivated non-naturalized and naturalized plants of southern Africa.** 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.

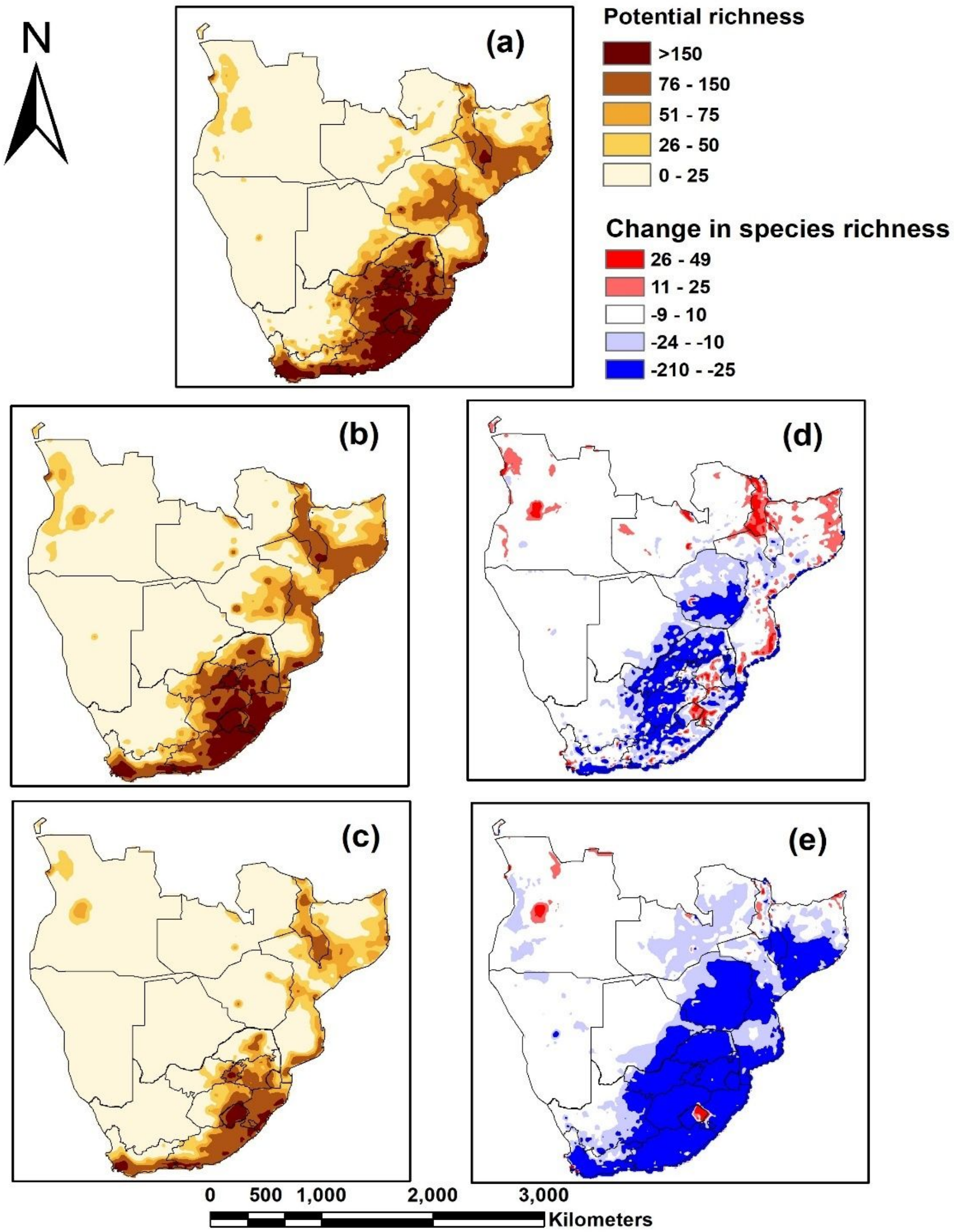


Figure 2: Current and future potential richness of cultivated alien plants of southern Africa. The maps show the predicted number of species that are expected to encounter suitable climatic conditions per 10′ grid cell under current climatic conditions (a), moderate future climate change ($\text{SSP}_{1\text{-}2.6}$) (b) and severe climate change ($\text{SSP}_{5\text{-}8.5}$) by the end of the 21st century (2081-2100). (c) and the expected change to current species richness under future climate change scenarios; $\text{SSP}_{1\text{-}2.6}$ (d) and $\text{SSP}_{5\text{-}8.5}$ (e).

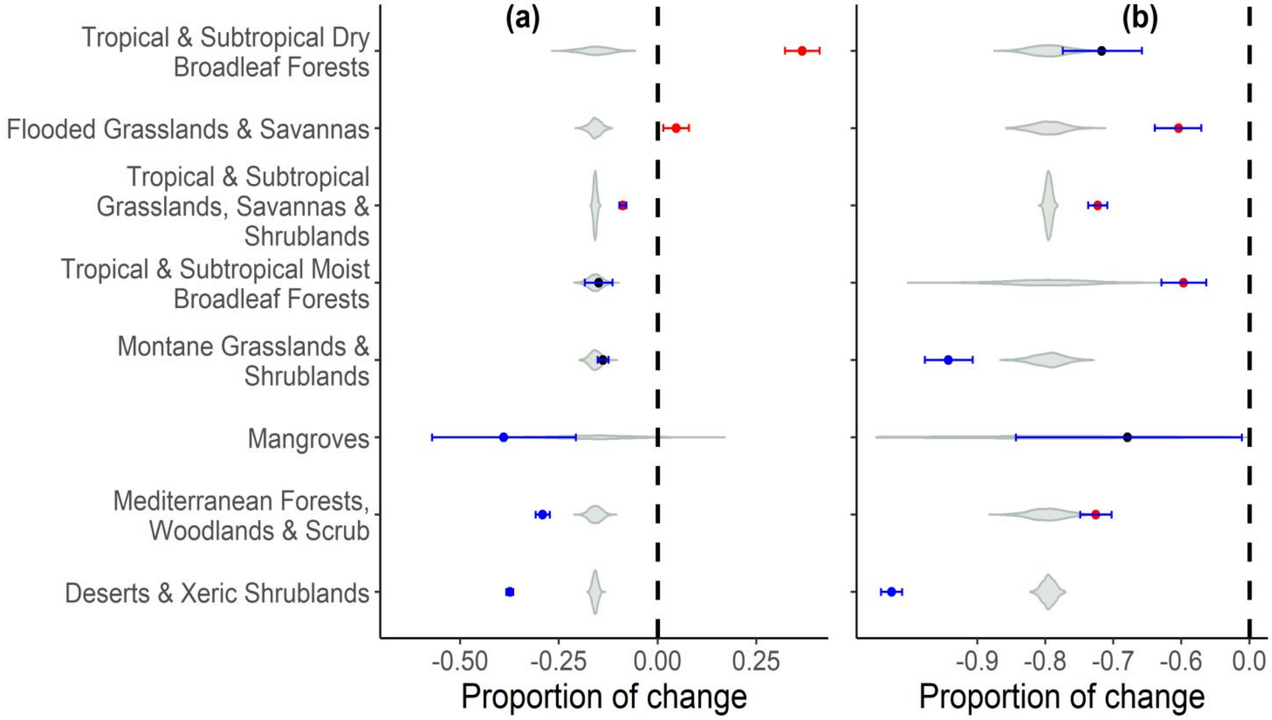


Figure 3: Predicted change in current climatic suitability under moderate future climate change ($\text{SSP}_{1\text{-}2.6}$) (a) and severe climate change ($\text{SSP}_{5\text{-}8.5}$) (b) of cultivated alien plants of southern Africa by 2081-2100 separated by their biomes. The dots represent the mean 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 means of the predicted change are significantly higher, lower, or not different from the random expectations, respectively.

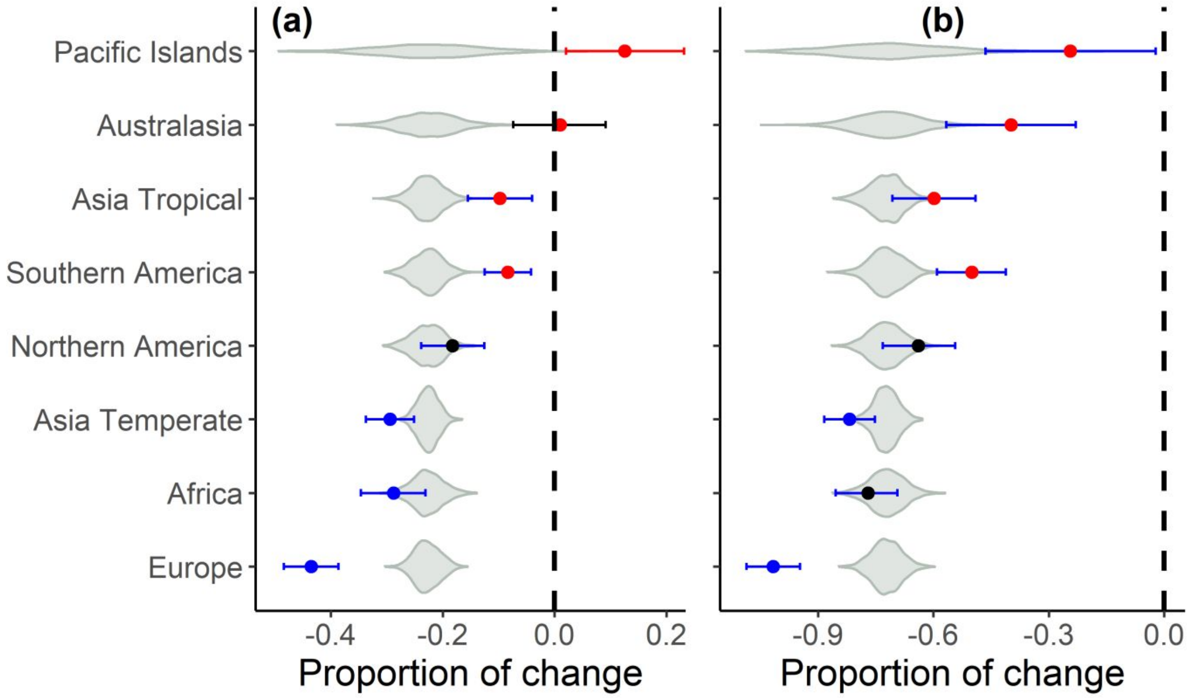


Figure 4: Predicted change in current climatic suitability under moderate (SSP$_{1\text{-}2.6}$) **(a) and severe climate change** (SSP$_{5\text{-}8.5}$) **(b) by 2081-2100 of cultivated alien plants of southern Africa separated by their native origins.** The dots represent the mean of the predicted 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 means of the predicted change are significantly higher, lower, or not different from the random expectations, respectively.

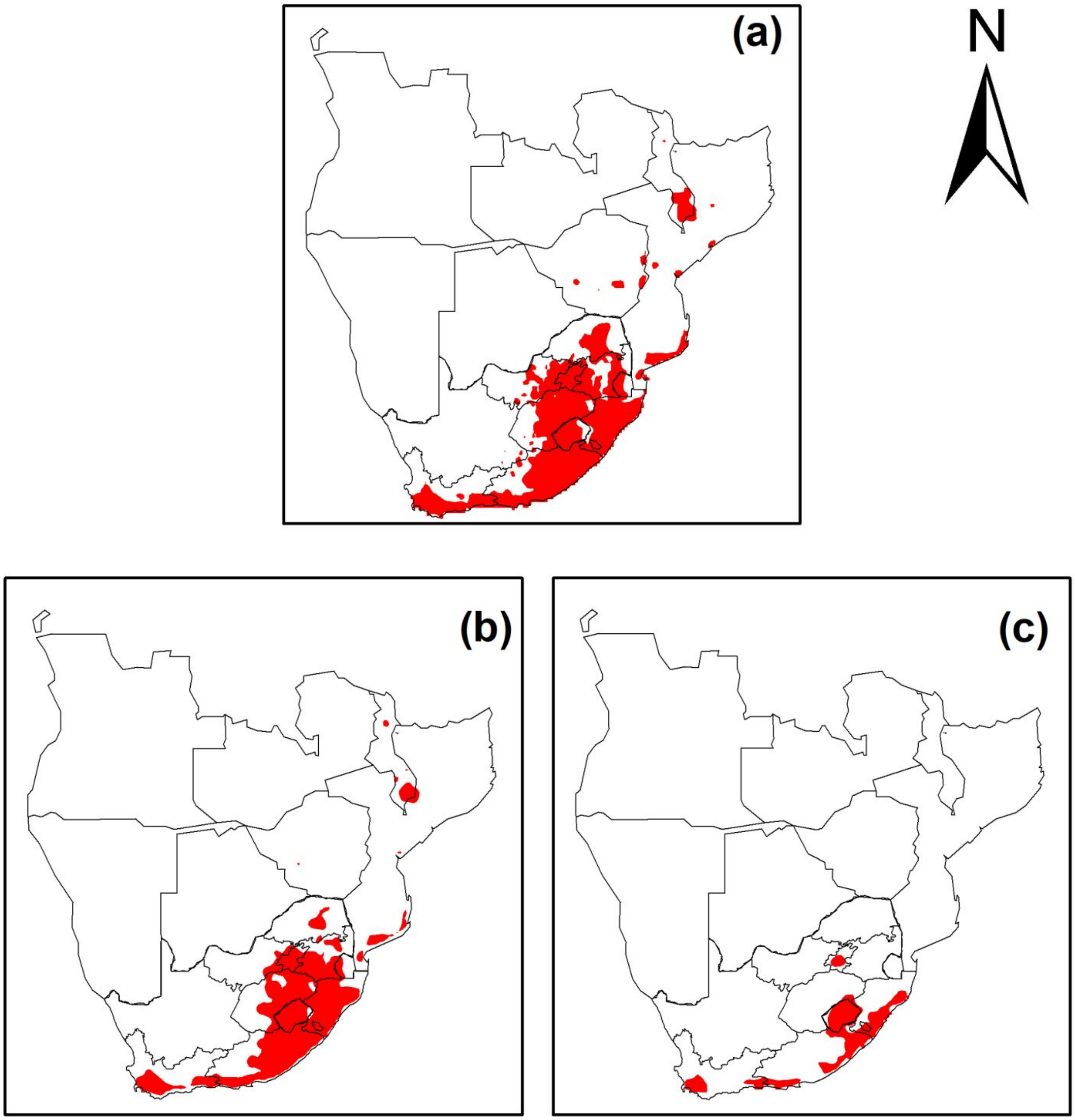
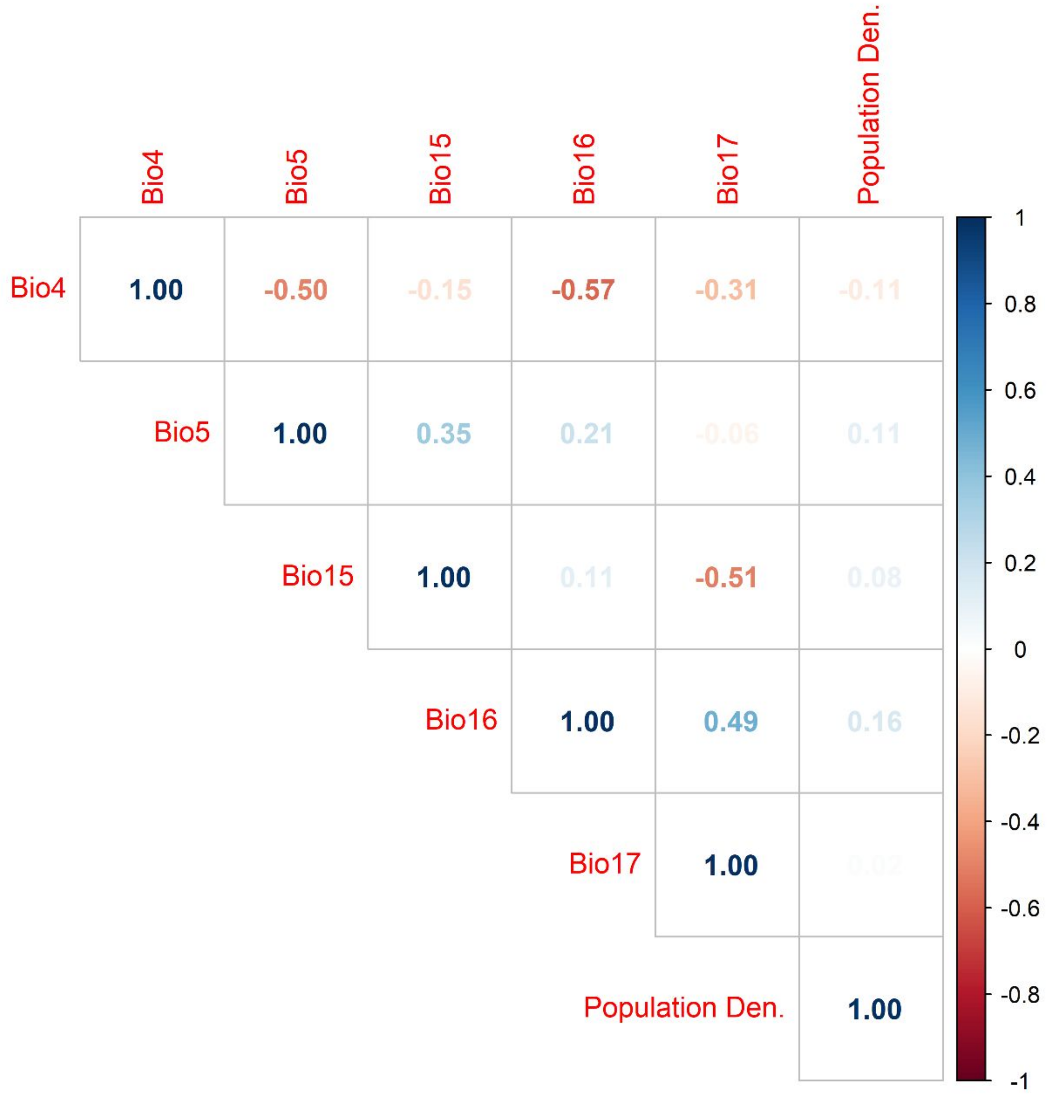


Figure 5: Current and future potential invasion hotspots of cultivated alien plants in southern Africa. The maps represent current climatic conditions (a), moderate future climate change ($SSP_{1\text{-}2.6}$) (b), and severe climate change ($SSP_{5\text{-}8.5}$) by the end of the 21st century (2081-2100). 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.

Table S1: Results of the binomial generalized linear models (GLMs) testing the relationship of the naturalization success (measured as naturalization occurrence in at least one region in southern Africa) of cultivated plants to predicted current climatic suitability and predicted change to current climatic suitability under moderate (SPP1) and severe (SSP5) climate change by 2081-2100. Predictor variables were standardized to a mean of 0 and a standard deviation of 1.

Predictors	Estimate ± SE	Z	P
Intercept	-2.48 ± 0.24	-9.99	< 0.001
Current	0.3 ± 0.04	9.64	< 0.001
Intercept	-0.25 ± 0.08	-3.14	0.001
Current -SSP1	0.38 ± 0.17	2.15	0.031
Intercept	-0.19 ± 0.10	-1.89	0.058
Current -SSP1	0.20 ± 0.10	1.87	0.060



	Bio4	Bio5	Bio15	Bio16	Bio17	Population Den.
Bio4	1.00	-0.50	-0.15	-0.57	-0.31	-0.11
Bio5		1.00	0.35	0.21	-0.06	0.11
Bio15			1.00	0.11	-0.51	0.08
Bio16				1.00	0.49	0.16
Bio17					1.00	0.02
Population Den.						1.00

Figure S1: Correlation coefficients between bioclimatic variables and human population density used to predict the potential distributions of the cultivated alien plants in southern Africa.

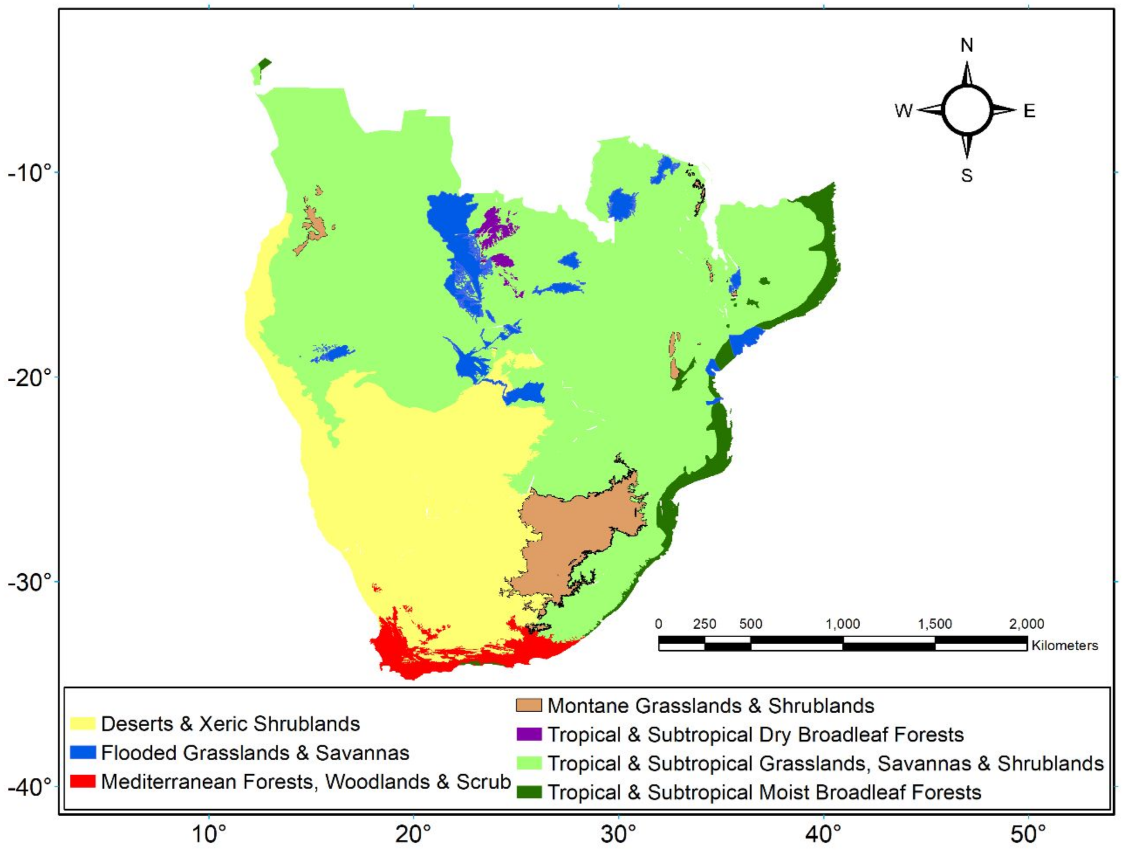


Figure S2: Map showing the distribution and locations of the different biomes in southern Africa, following the biome categories defined by Dinerstein, et al. (2017).

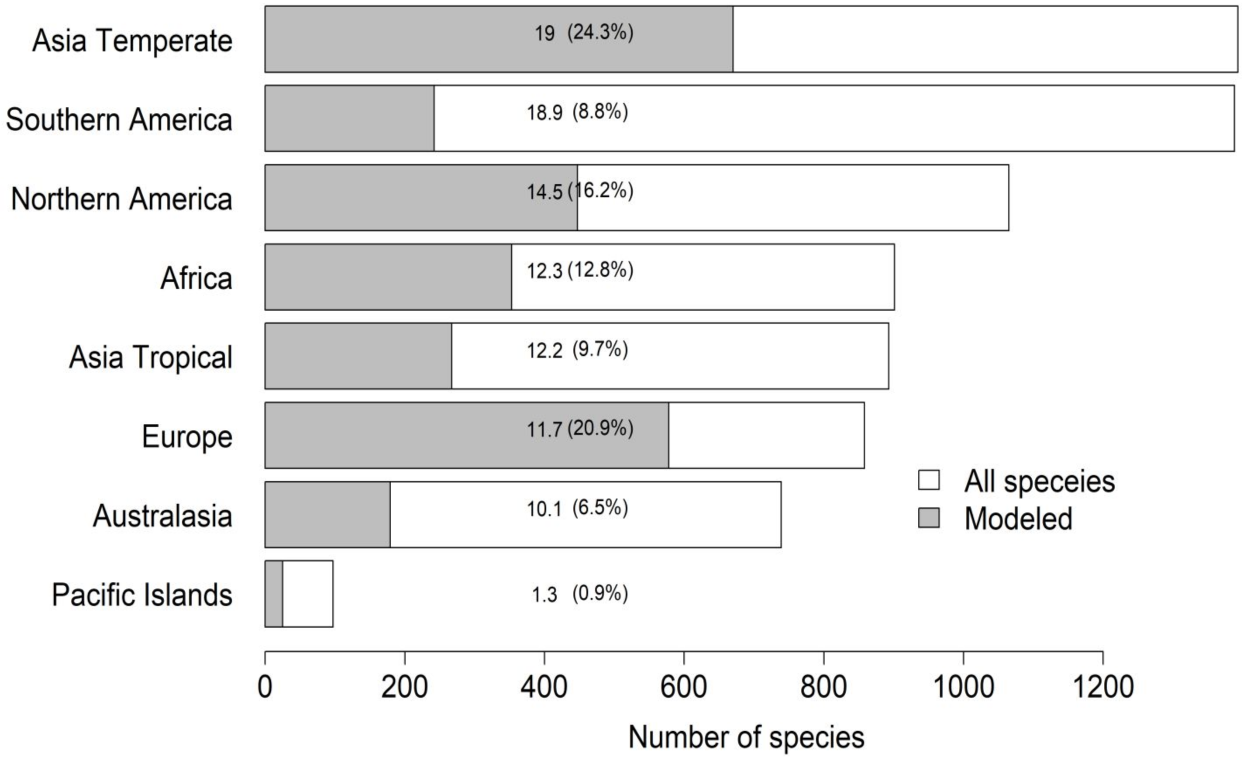


Figure S3: Numbers of introduced cultivated plant species in southern Africa according to their continents of origin. The cultivated species that have been modelled are indicated in grey. A species could be native to multiple origins. Numbers outside and inside parentheses are percentages of cultivated species from different native origins and species that have naturalized have been modelled, respectively.

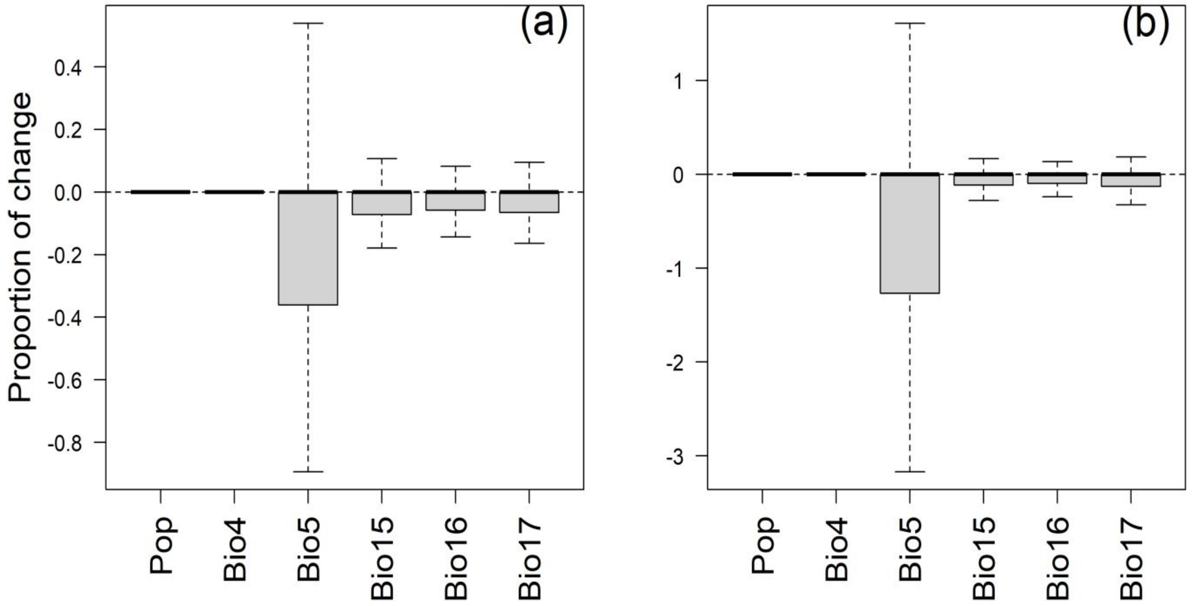


Figure S4: Difference in the number of suitable cells between future projection under moderate (SSP1) (a) and severe (SSP5) (b) climate change scenarios by 2081-2100 compared to the same future projections when one of the bioclimatic variables is held to its historical (1979-2000) value. A predictor variable has more impact the more the two projected future distributions differ. Boxplots indicate median of proportional changes in climatic suitability between future scenarios and the same scenarios when one of the bioclimatic variables is held to its historical value and interquartile range (i.e., 25th percentile and 75th percentile), with whiskers corresponding to 1.5 times the interquartile range. Key: Pop = human population density; Bio4 = Temperature Seasonality; Bio5 = Max Temperature of Warmest Month, Bio15 = Precipitation Seasonality, Bio16 = Precipitation of Wettest Month; Bio17 = Precipitation of Driest Month.

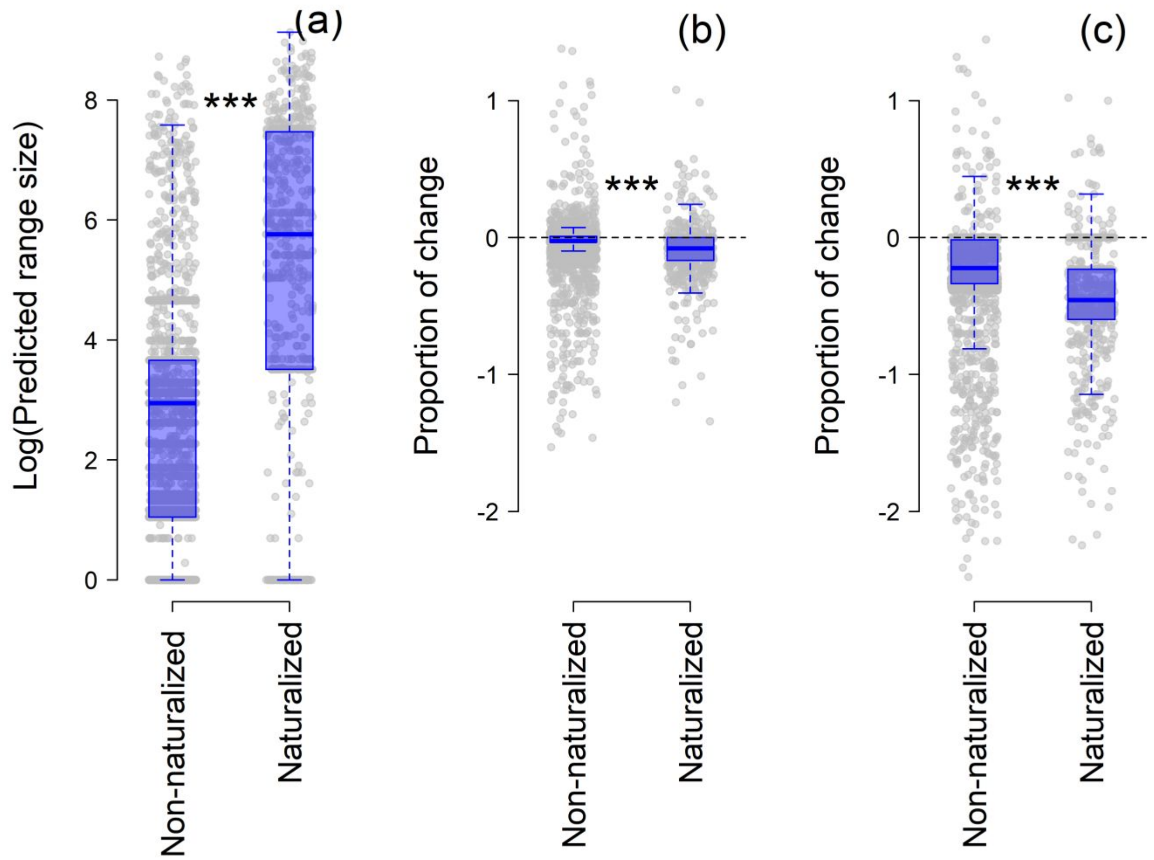


Figure S5: Current climatic suitability (number of grid cells; a) and predicted change to current climatic suitability under moderate (SPP1) (b) and severe (SSP5) (c) climate change by 2081-

2100 of cultivated non-naturalized and naturalized plants of southern Africa using the entire pool of cultivated species. 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.

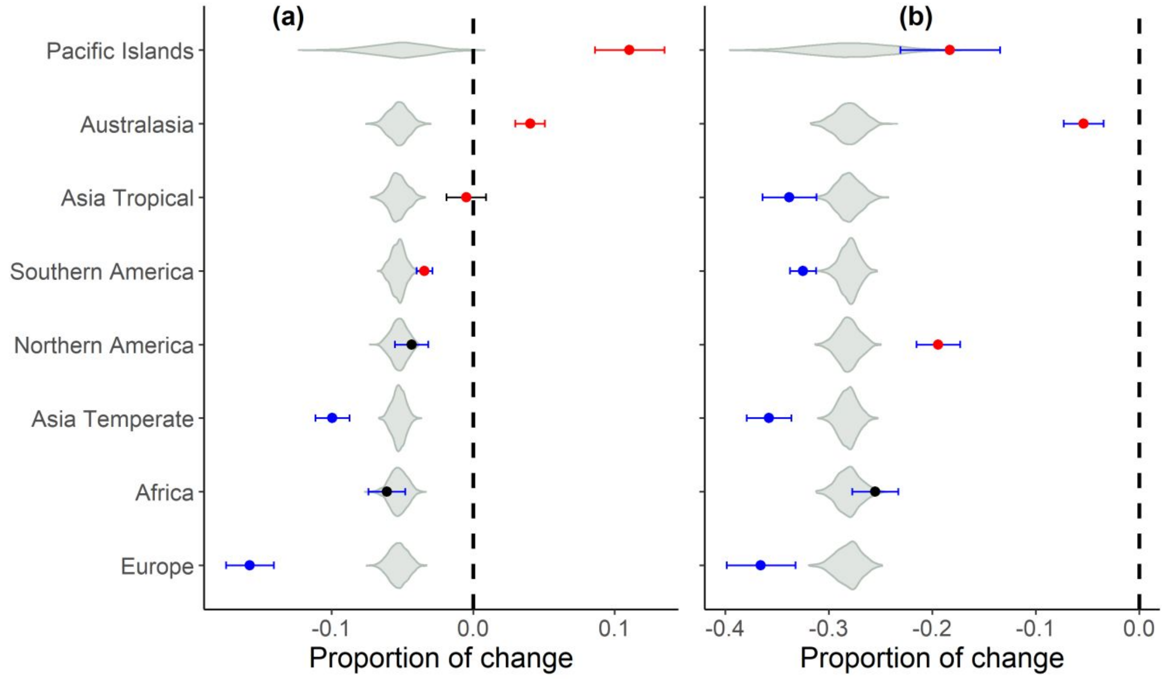


Figure S6: Predicted change in current climatic suitability under moderate (SPP1) (b) and severe (SSP5) (c) climate change by 2081-2100 of cultivated alien plants of southern Africa separated by their native origins using the entire pool of cultivated species. The dots represent the mean of the predicted 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 means of the predicted change are significantly higher, lower, or not different from the random expectations, respectively.

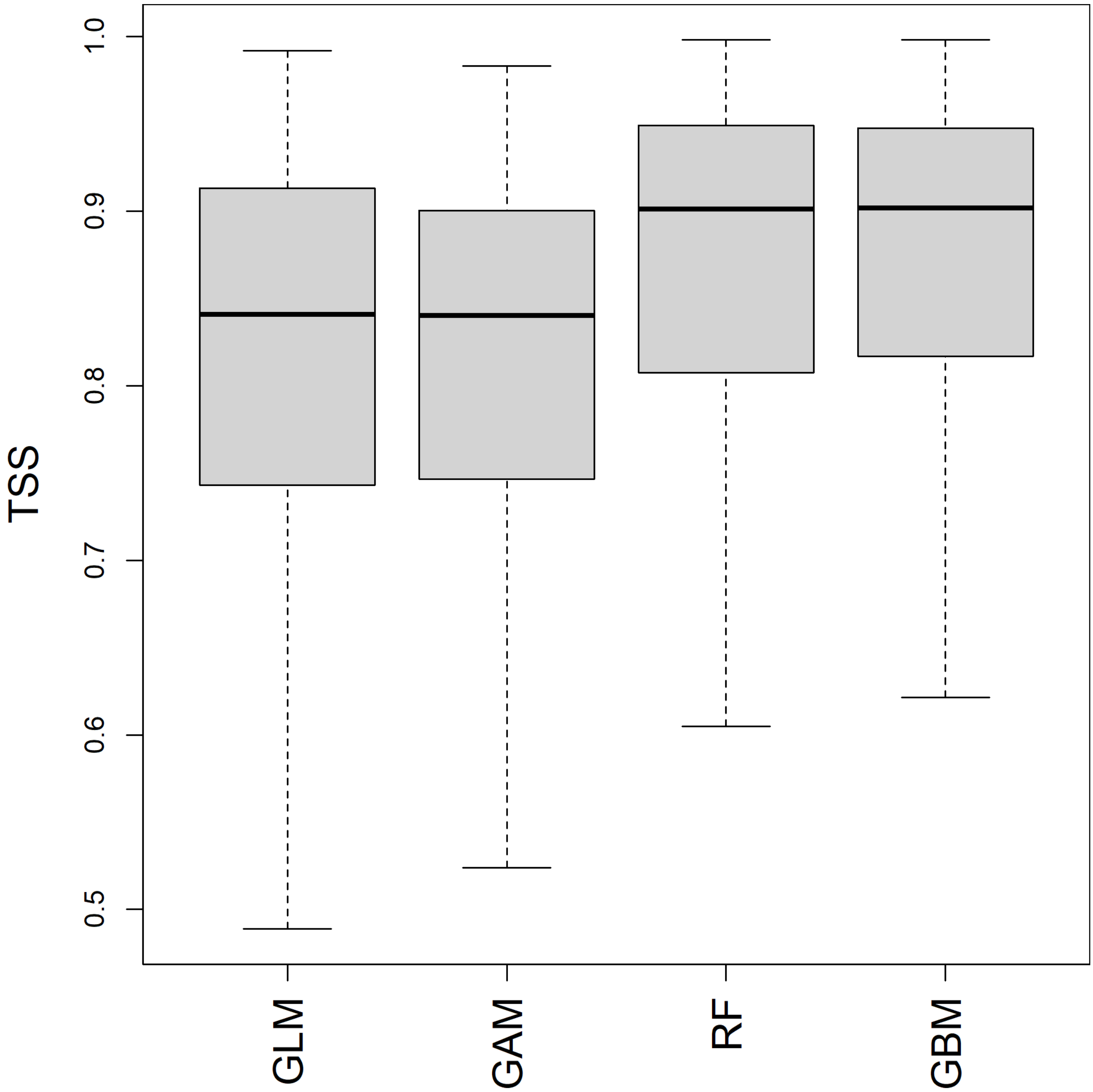


Figure S7: Performance of the 1,527 species distribution models for four different algorithms: generalized linear model (GLM), general additive model (GAM), random forest (RF) and boosted regression trees (BRT). Performance was measured with true skill statistics (TSS). Boxplots indicate median TSS of each algorithm and interquartile range (i.e., 25th percentile and 75th percentile), with whiskers corresponding to 1.5 times the interquartile range.

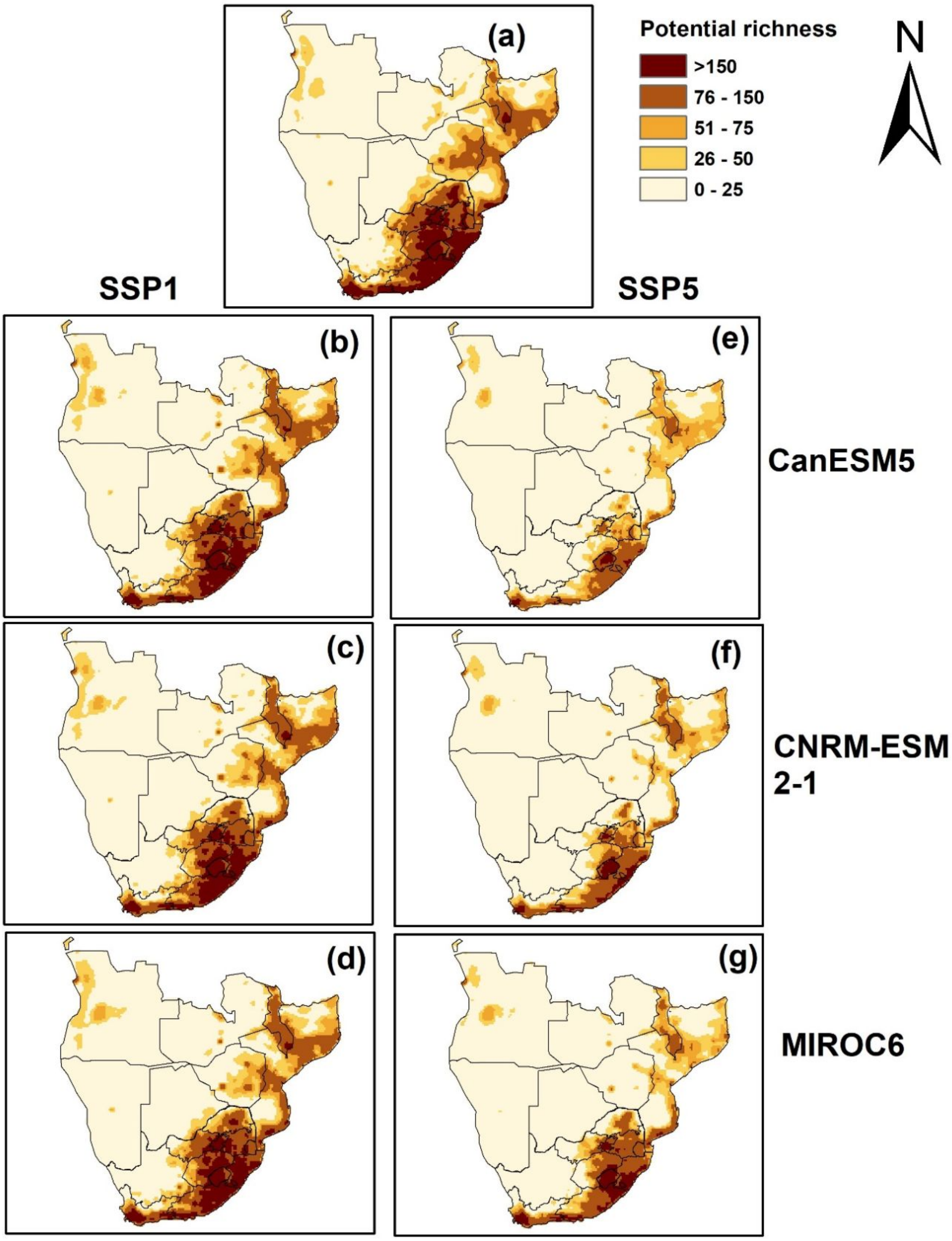


Figure S8: Current and future potential richness of naturalized cultivated alien plants of southern Africa. The maps show the predicted number of species that are expected to encounter suitable climatic conditions per 10′ grid cell under the current climate (a), moderate (SSP1) (b, c, d) and severe (SSP5 (e, f, g) climate change (by 2081-2100) across three different global circulation models.

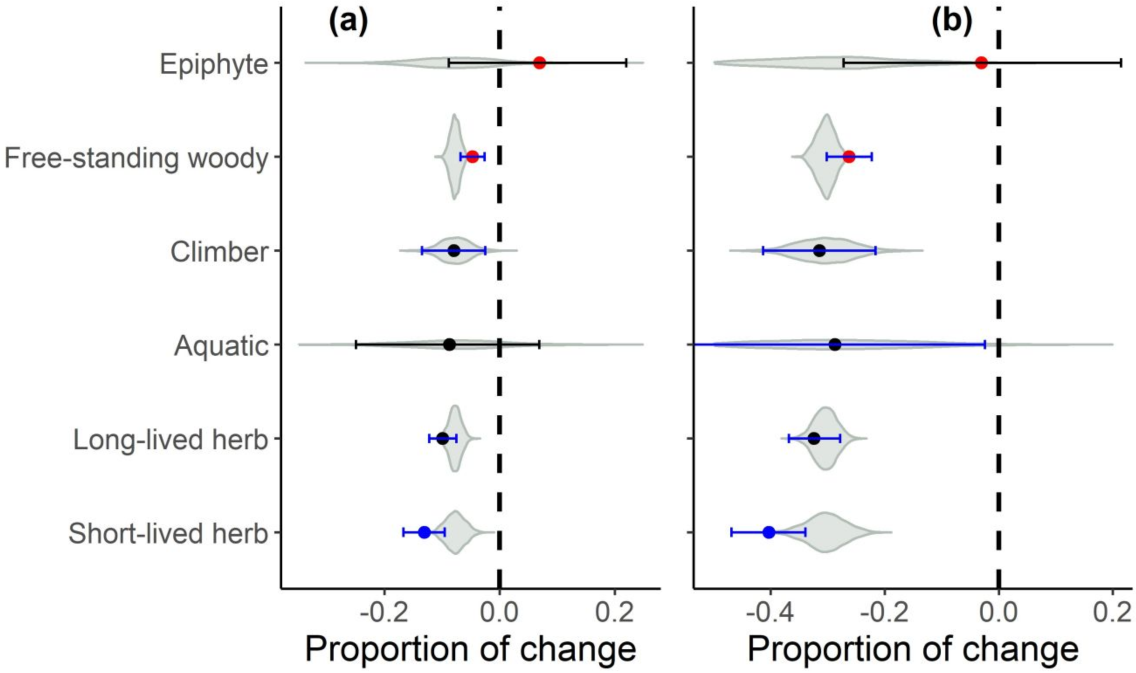


Figure S9: Predicted change in current climatic suitability under moderate ($SSP_{1\text{-}2.6}$) (a) and severe climate change ($SSP_{5\text{-}8.5}$) (b) by 2081-2100 of cultivated alien plants of southern Africa separated by their life forms. The dots represent the mean of the predicted change of a 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 means of the predicted change are significantly higher, lower, or not different from the random expectations, respectively.

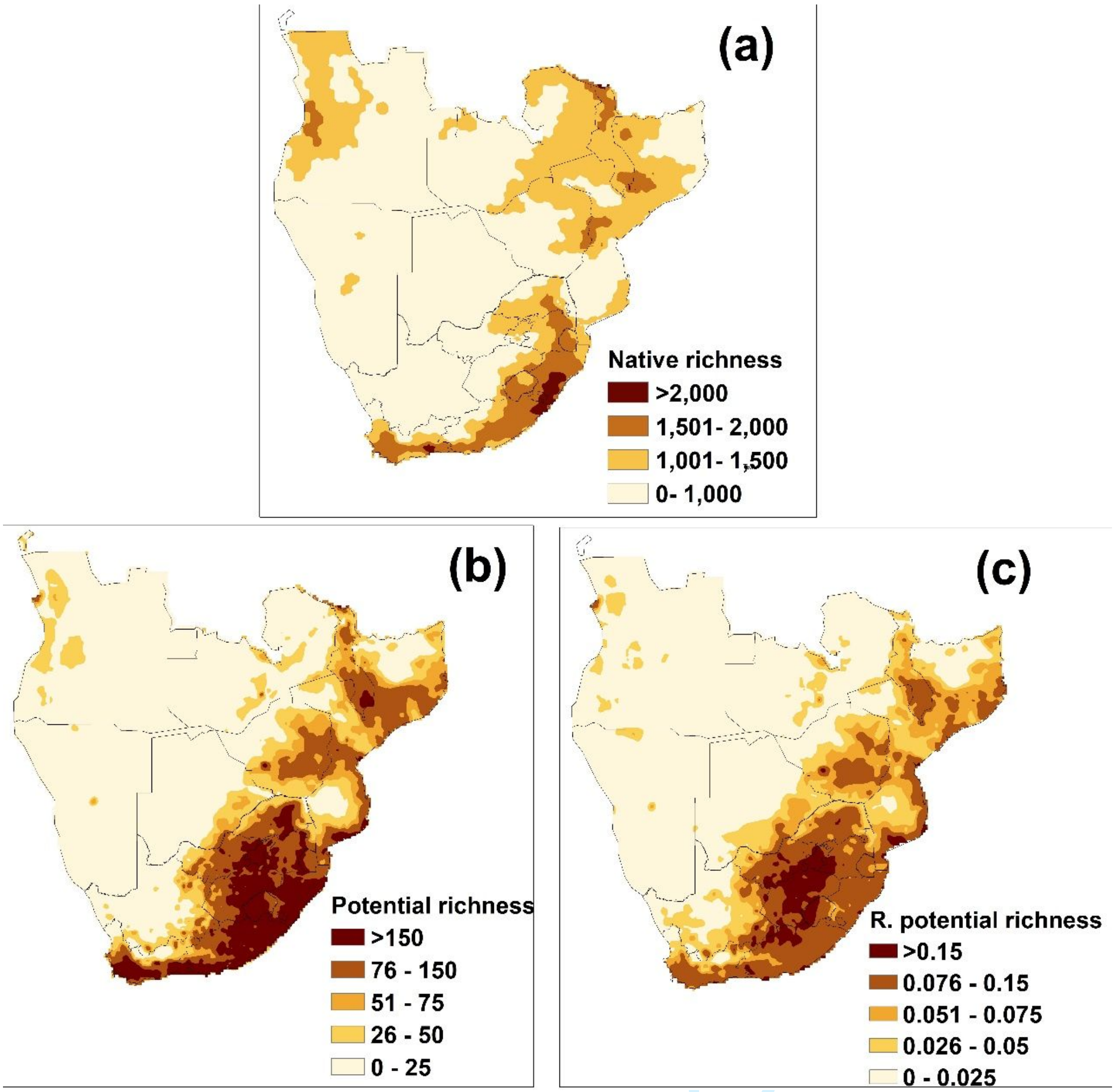


Figure S10: Current potential richness of native and cultivated alien plants of southern Africa. The maps show: (a) the projected number of native species in southern Africa according to Cai, et al. (2023), (b) the predicted number of cultivated alien plant species that are expected to encounter suitable climatic conditions per grid cell under current climatic conditions and (c)) the predicted number of cultivated alien plant species that are expected to encounter suitable climatic conditions per grid cell under current climatic conditions relative to the numbers of native species in that particular grid cell.

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