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Mapping potential environmental impacts of alien species in the face of climate change

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Abstract Risk maps are a useful tool to prioritise sites for management and allocate resources where they are most needed as they can show us where impacts of biological invasions are most likely to happen or expected to be largest. Given the pace of global changes, we need to understand not only the risks under current conditions, but future risks taking these changes into account. In this study, we use Australian acacias alien to South Africa as a case study to model their potential distribution under future climate change to map their potential impacts at the middle and end of the century and the uncertainty related to three socio-economic pathways and five climatic models. The resulting risk maps across South Africa are a pioneering attempt to combine impacts of alien species with potential future distributions. We found

that although climatic suitability and therefore the risk is predicted to decrease under climate change in 51,4% of the country's area, the opposite is predicted for 26% of the area and the highly vulnerable fynbos biome remains an area with high projected impacts. Such risk maps can help us prioritise management actions and aid the development of suitable plans to protect biodiversity under current and future climate conditions. However, they have to be interpreted with caution and we highlight some shortcomings around species distribution models in general, vulnerability of ecosystems to the potential impacts, data gaps on impacts, as well as currently benign or unknown invaders, which are not included in the projections.

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Introduction

Biological invasions and climate change are two of the main drivers of global biodiversity loss (Master and Norgrove 2010; IPBES 2023). Impacts of biological invasions are manifold, including changes to ecosystem functions such as fire regimes and hydrology and changes to biodiversity including extirpations and extinctions of native species (Vilà et al. 2011, 2024; Smith 2020; IPBES 2023). Similarly, climate change can have severe impacts on native species, for example increasing their risk of extinctions (e.g., Thomas et al. 2004; Manes et al. 2021) and causing range changes (e.g., Lenoir et al. 2008; Doak et al. 2010). While these drivers can act in isolation, climate change can also affect the invasion of alien species as climatic conditions play an important role in the growth, survival and distribution of species (Master and Norgrove 2010). Climate change can not only lead to changes in native species distributions, but also those of alien species (Bellard et al. 2013).

Member states of the Convention on Biological Diversity (CBD) are mandated to improve the protection of natural resources under the Kunming-Montreal Global Biodiversity Framework (GBF) (Decision 15/4, CBD/COP/DEC/15/4 2022). Target 1 asks to minimize the loss of areas with high biodiversity. To achieve this, we need to understand the pressures on these areas from drivers such as climate change and biological invasions, and map them to prioritise control. Risk maps have been used for various purposes in invasion science. For example, they can be useful to improve detection of new incursions or individuals of species with limited populations (Kaplan et al. 2014). They have also been used to map the potential impacts to assess sites experiencing the highest current or potential impact, translating to sites at risk of invasion impacts (Nentwig et al. 2010). However, as species' distributions are expected to change with climate change, considering only current climatic conditions in such risk maps does not prepare us well for future risk scenarios. Therefore, to improve our ability to manage biological invasions, as stipulated under

Target 6 of the GBF, we need to understand how biological invasions and their impacts could change under climate change. Simultaneously, this addresses Target 8, which aims to minimize the effect of climate change on biodiversity. Still, climate change is not routinely included in risk assessments for alien taxa (but see Marchioro and Krechmer 2021 for some insect pests).

Correlative species distribution models (hereafter SDM) are popular in various fields of ecology and are increasingly used in invasion science (Guisan et al. 2014). They are statistical methods which correlate known occurrences of species with environmental variables and predict a species' potential distribution in other regions over space and time (Guisan and Zimmermann 2000). The advantages of SDMs are manifold as they are easy to implement and can cover large geographic areas. Therefore, they are widely used to produce maps of potential invasion by delineating areas based on climatic suitability for a species (e.g. Bradley et al. 2010; Tingley et al. 2017). Despite known limitations (see for example Hui 2023), they have shown potential for accurate prediction of alien species spread (Barbet-Massin et al. 2018) and response of biological invasions to climate change (Sheppard et al. 2014) if properly calibrated.

We selected, as a case study, Australian acacia species (*Acacia* Mill. sensu stricto – synonym: *Acacia* subg. *Phyllodineae* (DC.) Searge) which are alien in South Africa. This includes 33 species (Magona et al. 2018; Jansen and Kumschick 2022; Supplementary Material Appendix S4.1), of which three species (*Acacia crassiuscula*, *A. acuminata* and *A. koa*) had to be excluded from all analysis because they had less than 10 presence records globally after the filtering steps detailed in the Methods section. Acacias are among the most highly impacting alien taxa in South Africa with a diverse range of impacts on native biodiversity (le Maître et al. 2011; Kumschick & Jansen 2023). The fynbos biome, which only occurs in the Western and Eastern Cape provinces of the country, is a megadiverse shrubland containing thousands of plant species which occur nowhere else and is particularly susceptible to invasion of alien trees such as acacias (e.g., Wilson et al. 2014).

In this study, we assess (i) the current distribution of the acacia species and their potential impacts in South Africa, (ii) the potential distribution under current climate, and (iii) the projected future distribution

under climate change scenarios. We fitted SDM models per species that were then used to project the habitat suitability across South Africa per time horizon, accounting for various climatic scenarios. Then, we aggregated an impact score from the species-wise SDM projections and the documented impacts per species. By overlaying the outputs of the models with the species potential impacts, we produced risk maps for current and projected future climatic conditions and assessed potential change in impacts risk for protected areas of the Western Cape Province in South Africa.

Methods

Occurrence data

We gathered distribution data from the native and introduced ranges of the 30 acacia species, and used it along with bioclimatic variables to build individual ensemble models which were then projected based on current and future climate in South Africa. For each species, worldwide occurrence data were obtained from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>) using the `rgbif` package (Chamberlain et al. 2022). For this extraction, we kept all records which had complete coordinates, which were tagged as “presence”, and which were either human or machine observations or coming from the literature. No time limit was specified. Then we filtered occurrences to reduce the uncertainty arising from questionable records and only kept records which came from a list of 65 trusted GBIF datasets. This list was previously developed for the global distribution of acacia species (Botella et al. 2023) and is composed of datasets which include at least one documented step of taxonomic verification in the recording of the occurrences. The documented native and introduced countries of each species were also obtained from that study. Besides, we extracted the global land cover raster (approx. 300 m resolution) from the European Space Agency GlobCover product. We excluded records located outside the native and introduced countries of the species (obtained from Botella et al. 2023) or whose 4 km × 4 km cell was located in urban areas based on the GlobCover 2009 global land cover raster (ESA and UCLouvain

GlobCover 2009 Project, last accessed 29/01/2024). The latter step was implemented to exclude planted trees. More precisely, we excluded cells classified as “Artificial surfaces and associated areas (Urban areas > 50%)” by GlobCover. We then kept only up to one record per 4 km × 4 km cell for each species to reduce the spatial autocorrelation and the over-sampling of some areas (Boria et al. 2014). We obtained a total of 37,940 filtered records (Figure S4.1 and S4.2). The number of filtered records were imbalanced across the 30 considered species, with 27 for the least sampled (*A. adunca*) and 3,738 for the most sampled (*A. dealbata*).

Climate variables

To estimate the climatic suitability for each acacia species from their occurrence data, we extracted four bioclimatic variables from the Climatologies at High Resolution for Earth’s Land Surface Areas database (CHELSA, Karger et al. 2017). We chose the mean annual air temperature (bio1), mean diurnal air temperature range (bio2), annual precipitation (bio12) and precipitation seasonality (bio15) as environmental variables as they are likely to affect plant productivity and survival across the landscape (Mod et al. 2016), and the correlation between each of these variables was moderate (Pearson’s $|r| < 0.55$). These data are available globally at a 4 km × 4 km resolution for the period 1981–2010.

Then, we predicted the suitable climatic range of each species per time period in South Africa. The “current” South African climate was derived from the 1981–2010 period and the “future” climate was decomposed in two horizons: mid-century (2041–2070) and end of the century (2071–2100). For both time horizons, we extracted the four climatic variables based five global climate models from CHELSA (“gfdl-esm4”, “ipsl-cm6a”, “mpi-esm1”, “mri-esm2”, “ukesm1”) for three shared socio-economic pathway scenarios (“ssp1.26”, “ssp3.70” and “ssp5.85”) for the South African region: ssp1.26: scenario with low greenhouse gas (GHG) emission; ssp3.70: scenario with high GHG emission; ssp5.85: scenario with very high GHG emission (Fig. 1 and Supplementary Material, Appendix S1). This selection covers a wide range of different predictions and was defined to maximise the different degrees of

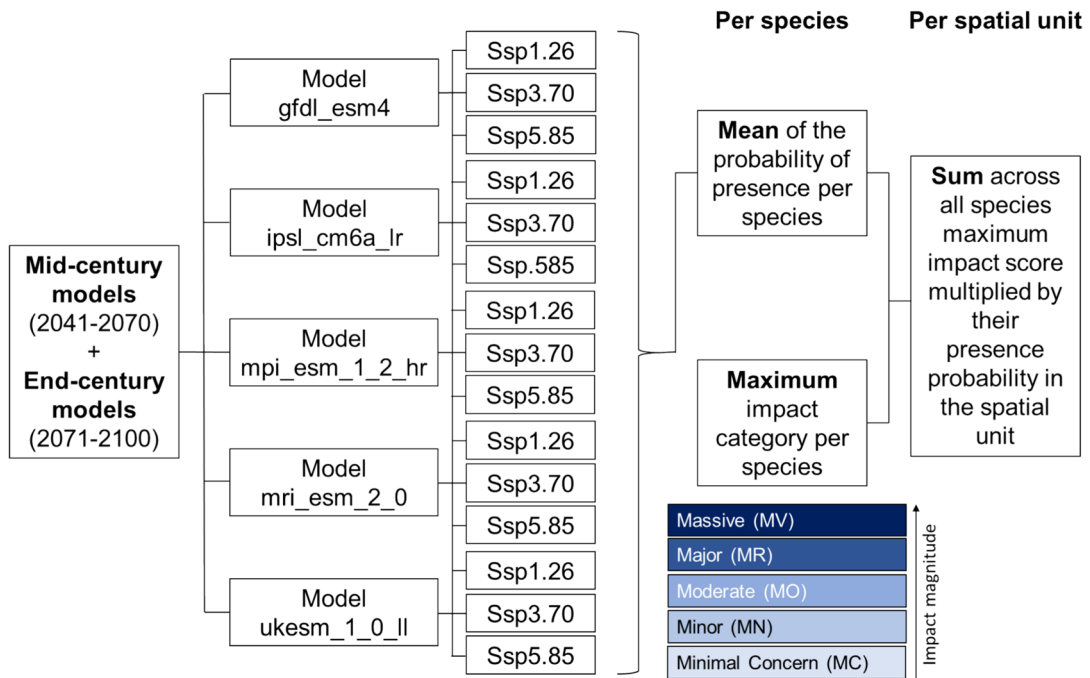


Fig. 1 Step by step explanation of the development of the models and maps for future climate projections. Five climate models were selected, and three shared socio-economic path-

way scenarios (ssp) modelled. For details on the models and variables selected, see text

predicted climate change. Specifically, the selected global climate models have different equilibrium climate sensitivity values (a measure of the change in equilibrium global mean surface temperature after a doubling of atmospheric CO₂ concentration) ranging from 2.8 °C to 5.1 °C.

Species distribution models

Pseudo-absences selection

For each species we drew ten datasets of pseudo-absences composed of the same number of pseudo-absences as presences. For species with less than 100 presences, we increased the number of pseudo-absences to 100 in each dataset, to reduce the variance (over-fitting) of each model. These pseudo-absences were drawn in the countries being part of the native and introduced ranges of the species assuming that the species likely had an opportunity to establish at pseudo-absence locations. Following recommendations of Barbet-Massin et al. (2012), pseudo-absences were selected based on the surface range envelope

method (Busby 1991), by randomly selecting pseudo-absences outside the usual climatic range of the species occurrences (Thuiller et al. 2009). Given that pseudo-absences were drawn in the native and introduced ranges but outside of the climatic envelope where the species occurrences were recorded (PA.sre.quant=0), we can assume false absences to be rare. Therefore, the final model predictions will approximate the probability of presence conditional to the species presence in the area, i.e. an establishment probability.

Model implementation

For each species we built a species distribution model using functions and workflow of the biomod2 package (Thuiller et al. 2009). All codes are available on GitHub (Supplementary Material, Appendix S2). We applied a random forest classifier (Liaw and Wiener 2002) on the presence/pseudo-absence datasets and the four climatic variables to decipher which climatic conditions are suitable for each species. Each forest was composed

of 500 trees, where each branch tests two randomly picked variables ($m_{try}=2$, i.e. the square root of the number of predictors, as generally recommended for classification), and we impose a minimum of five sampled presence/pseudo-absences per terminal node to limit tree-level over-fitting and computational costs. We implemented a step of cross-validation for which the presence/pseudo-absence dataset was divided into four blocks along the longitude axis with presences equally balanced between each block (Wenger and Olden 2012). Then, three blocks were used for model training and one for testing. This approach allows for spatial and environmental independence between training and testing sets. Kappa and TSS metrics were computed each time on the testing dataset. As we had ten pseudo-absence datasets and four blocks, we computed 40 random forest models for each species.

For each species we kept only the random forest models with a Kappa and a TSS over 0.7, indicating a robust predictive capacity, and which we refer to as sub-models. We then derived for each species an ensemble of its sub-models that was a “committee averaging” of the binarized responses given by the sub-models to reduce the error of individual sub-model predictions (Thuiller et al. 2009). We used a probability threshold of 0.5 to binarize each sub-model response, corresponding to a majority vote among trees of the corresponding random forest. Committee averaged values are the proportion of sub-models predicting the species as present, and a value near 0 or 1 mean that sub-models tend to agree to predict absence or presence, respectively. Here, we considered that committee averaged values can be regarded as a proxy for the probability of a species to establish. Thus, we obtained one projection of establishment probability for South Africa under the current climate and 15 scenarios (five global climate models x three socio-economic pathways) for each time horizon (2041–2070 and 2071–2100) as represented in Fig. 1. So, for each time horizon and each spatial cell, we averaged the 15 establishment probabilities of the 15 scenarios to obtain the final establishment probability of the species in that cell. This final establishment probability gives an equal weight to the 15 plausible scenarios. Finally, for each time horizon, we produced a potential acacia species richness map summing

the 30 species establishment probability maps, and an associated uncertainty map. The uncertainty map shows standard deviation of the potential richness estimate based on the variability standard deviation of the predicted establishment per species and its variability across the 15 scenarios.

Risk maps

As we aimed to map the accumulated risk of acacia species potentially causing impacts in different regions in South Africa, we firstly derived a potential impact score per species based on its documented impacts. Data on the impacts of the acacia species were taken from Jansen and Kumschick (2022). They assigned categories of Minimal Concern to Massive to each species, based on the impacts reported in the literature and following the International Union for the Conservation of Nature (IUCN) standard for impact classification, the Environmental Impact Classification for Alien Taxa, EICAT (Blackburn et al. 2014; Hawkins et al. 2015; IUCN 2020a, 2020b; Volery et al. 2020). We used the maximum impact category per species as a precautionary measure, which is the recommended approach used by the IUCN EICAT Standard (IUCN 2020a; Kumschick et al. 2024), noting that other calculation methods are possible depending on the aim of the study (see also Kumschick et al. 2024, Boulesnane-Genguant et al. in prep). We transformed the impact categories into numerical values as follows: Minimal Concern (MC)=0, Minor (MN)=1, Moderate (MO)=2, Major (MR)=3, Massive (MV)=4. 19 species classified as Data Deficient (DD), i.e. no data on impact was found in a comprehensive literature search, and they were excluded from the impact risk maps (assigned NA) (Supplementary Material Appendix S4.1).

As a prediction of local impact risk per species, we multiplied the predicted establishment probability derived from the SDMs in each grid cell by the species impact score. Finally, we summed up the local impact risks across species in each grid cell to obtain the impact risk map (see also Nentwig et al. 2010). Hence, each species occurring adds to the risk of the potential impacts actually manifesting at that site, again using a precautionary approach. Our maps therefore do not represent sites where impacts are definitely going to occur, as the potential establishment

of each species alone does not necessarily happen and, even if it does, it does not necessarily result in the worst impact documented for that species. Other factors such as the recipient community and the abundance of the alien species play important roles in the manifestation of impacts. Note also that even if data deficient species are present, they do not affect the impact risk value, as for species whose maximum impact is MC. This might underestimate the impact of some species which actually cause higher impacts but which have not been studied.

Changes in impact risk in protected areas

To assess the specific change in risk across time on protected areas, we assessed the potential changes of impact risk for protected areas in the Western Cape Province of South Africa. For each protected area, we calculated the mean impact risk score and compared it under current and future (2071–2100) projected climate. To see whether differences could be found based on the protected area status, we also calculated the mean impact risk score per protected area type. In the Western Cape, protected areas are classified as follows (with increasing level of protection): private nature reserves, provincial nature reserves and national parks. We obtained protected areas data from the South African National Biodiversity Institute (www.bgis.sanbi.org).

Results

Firstly, we present a method to map the potential cumulative impacts of alien species under climate change projections (Fig. 1, Supplementary Material, Appendix S1). It combines the recorded impacts alien species have had with the projected species richness. Applying this method to acacia species in South Africa, we find that across all species currently present in the country, the suitable area declines over time and only the south coast in the Eastern Cape province and parts of the Western Cape province still remain suitable for a considerable number of species (Fig. 2). Large parts of the north eastern (NE) part of the country are predicted to become unsuitable for most acacias in future. Indeed, while the current projected impact score lies between 15 and 25 in a relatively large part of the NE area, it is inferior

to 5 in nearly all of the area for the end of the century (Fig. 2). When computing the number of spatial cells where the projected impact score changed, we found that impact risk increased in only 26.7% (324'224 km²) of the area of South Africa by the end of the century, but decreased in 51.4% (625'115 km²) of the country. Yet, this decrease should be interpreted with caution, as the standard deviation of the end-of-century impact score, due to the variability across socio-economic pathways and climate models, is around 2 in the NE area that currently shows a high risk (Figure S3). Comparing the current impact risk map to a risk map based on actual records for acacia species (Fig. 3), the general pattern looks similar to potential impacts under current climate, with a less continuous distribution along the east coast, and a marked region of high risk in the Gauteng province. The latter is probably due to the fact that in the map showing impacts based on recorded occurrences, urban areas were not excluded, and much of the Gauteng province would fall under this category (Fig. 3). Furthermore, a positive sampling bias in this highly populated area might be responsible for higher detection rates of the species present and explain the relatively high impact risk when based on actual occurrences.

Although species richness of acacias is not projected to be as high in the southwestern part of the country as along the south coast, the projected risks are similar in both areas (Fig. 2). That shows that the areas around Cape Town and Hermanus, although not suitable for as many species, might remain suitable for the high impacting species. The impact score in this area remains most likely high compared to other areas even when considering its standard deviation (Figure S3).

We found that potential impacts would decrease under climate change within protected areas of the Western Cape. Our results showed a lower impact risk with climate change for protected areas along the coast line, almost no change for northern protected areas and a higher impact risk in few isolated protected areas (Fig. 4). However, the impact risk differed according to the protection status. The impact risk remains high in areas of high protection status (such as national parks) and low for private protected areas (with lower protection status).

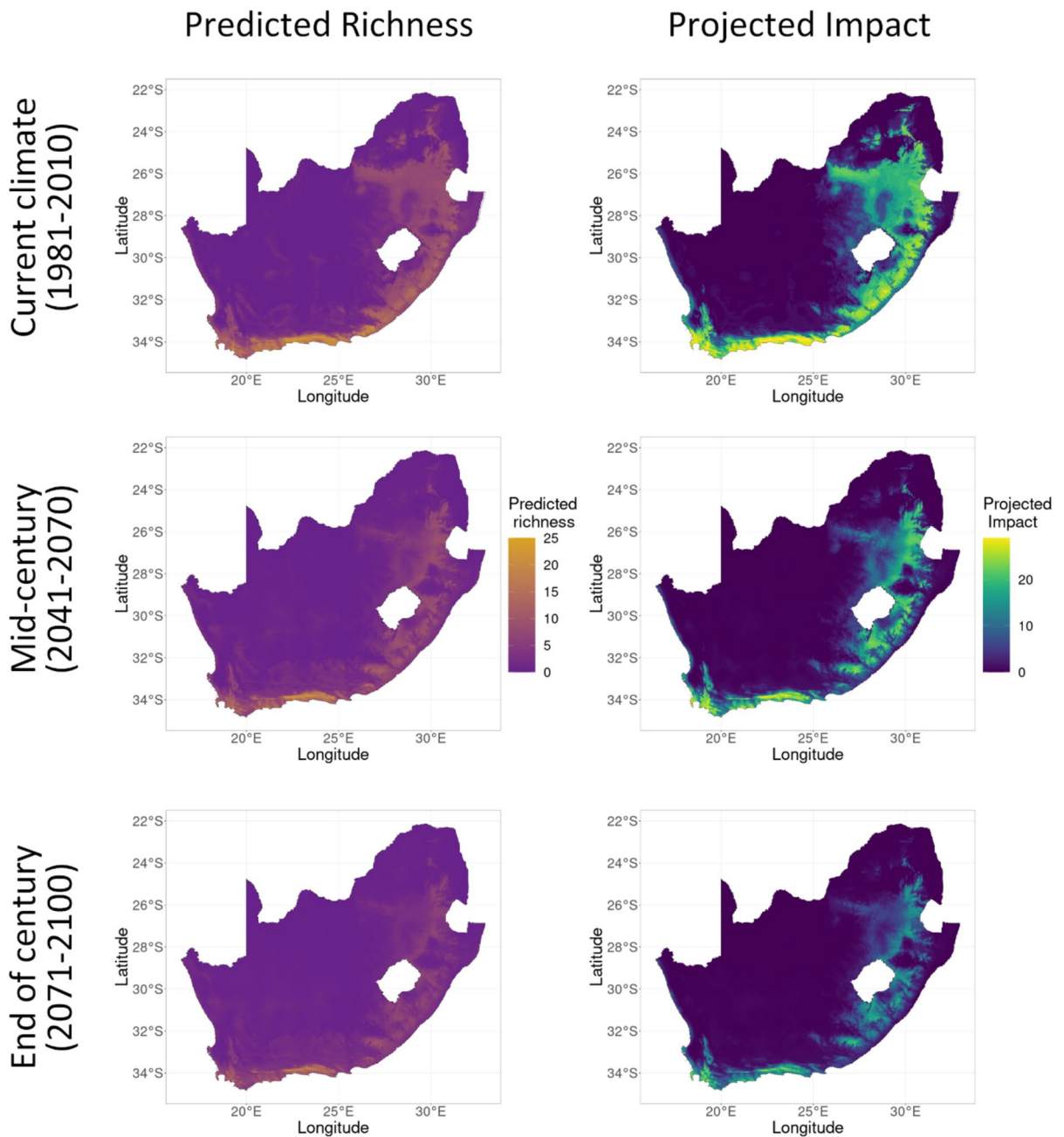


Fig. 2 Cumulative probability of presence ranging from zero (no species projected to establish) to thirty (all species with the highest probability to establish) of alien acacias (left) and projected impacts (right) based on the maximum recorded impacts of the species present over three time horizons. The cumulative probability of presence on the left is the sum of single species

establishment probability. Each species probability is a mean across combinations of global climate models and socio-economic scenarios. The right hand column shows the sum of species maximum impact weighted by their establishment probability

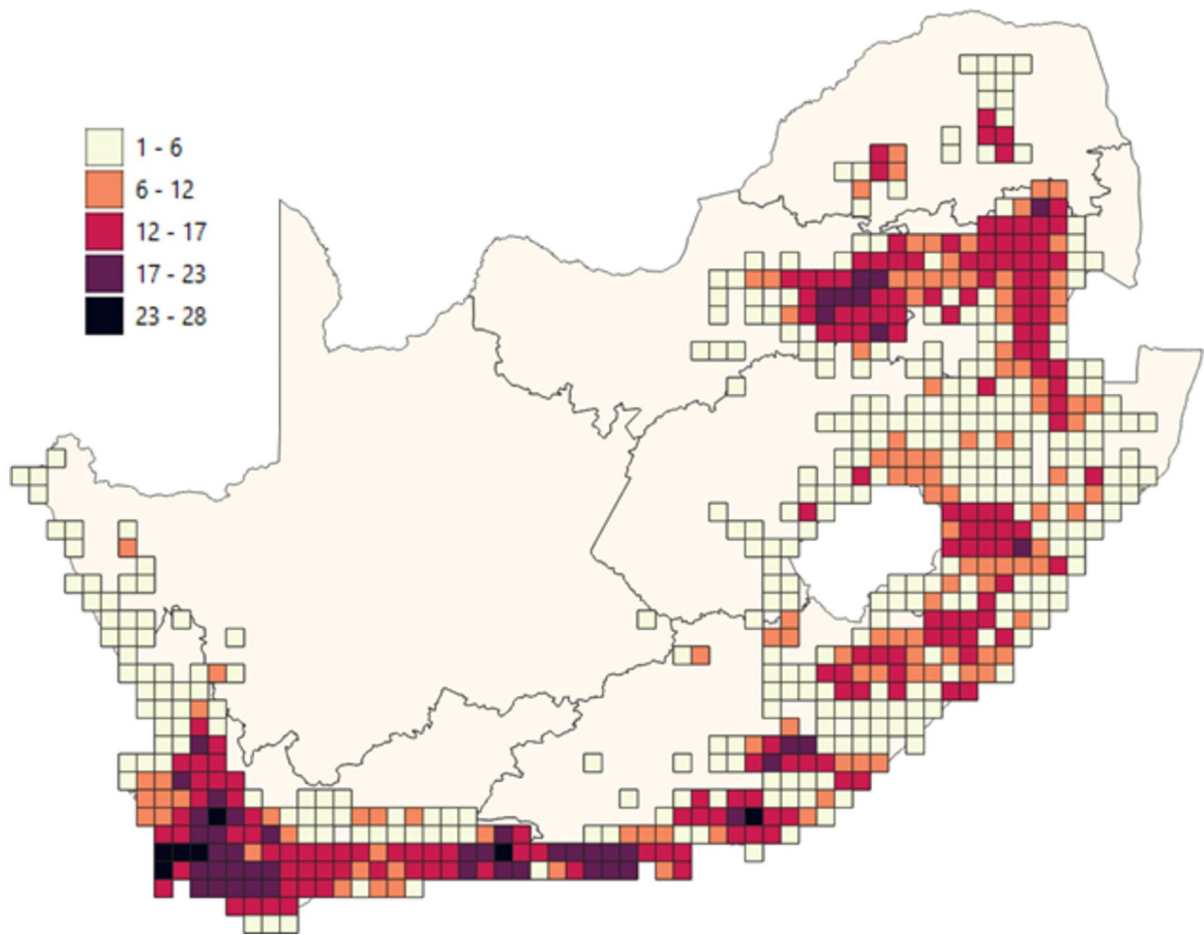


Fig. 3 Sum of maximum recorded impacts across acacia species based on EICAT records in Jansen & Kumschick (2022) occurring per Quarter Degree Square (QDS; 25 km × 25 km) grid cell. This map is based on actual occurrence records of acacia species in South Africa taken from the database of

Botella et al. (2023), with sum of impacts overlaid. Contrary to the projected maps in Fig. 2, no records were excluded (including urban areas). The darker the red color, the higher the impact sum of the species occurring in these cells

Discussion

This study presents, to the best of our knowledge, a first attempt at combining impacts of alien taxa with their projected distribution under climate change to produce risk maps for future climatic scenarios. Our results indicate that the projected suitable areas for alien acacia species in South Africa are reduced in half of the country under climate change (Fig. 2). This is similar to a study looking at *A. mangium* and *A. auriculiformis* in Brazil, where they found a shift in potential distribution and a reduction in suitable area (Heringer et al. 2019). More generally, this is in line with Bellard et al. (2018) who showed in a

review of 71 papers covering 423 alien species that climate change is more frequently projected to contribute to a decrease in range size than an increase. However, to assume that the problem of acacia invasions is going to sort itself out over time might be a bit too optimistic. For once, the sites at highest risk are also the regions where the highly vulnerable fynbos biome is located. This biome is already under pressure from the effects of climate change, including increased temperature and drought, and therefore more vulnerable to other pressures (Slingsby et al. 2017). Protected areas are set up to safeguard biodiversity and ecosystem services for the future. We show that for the Western Cape

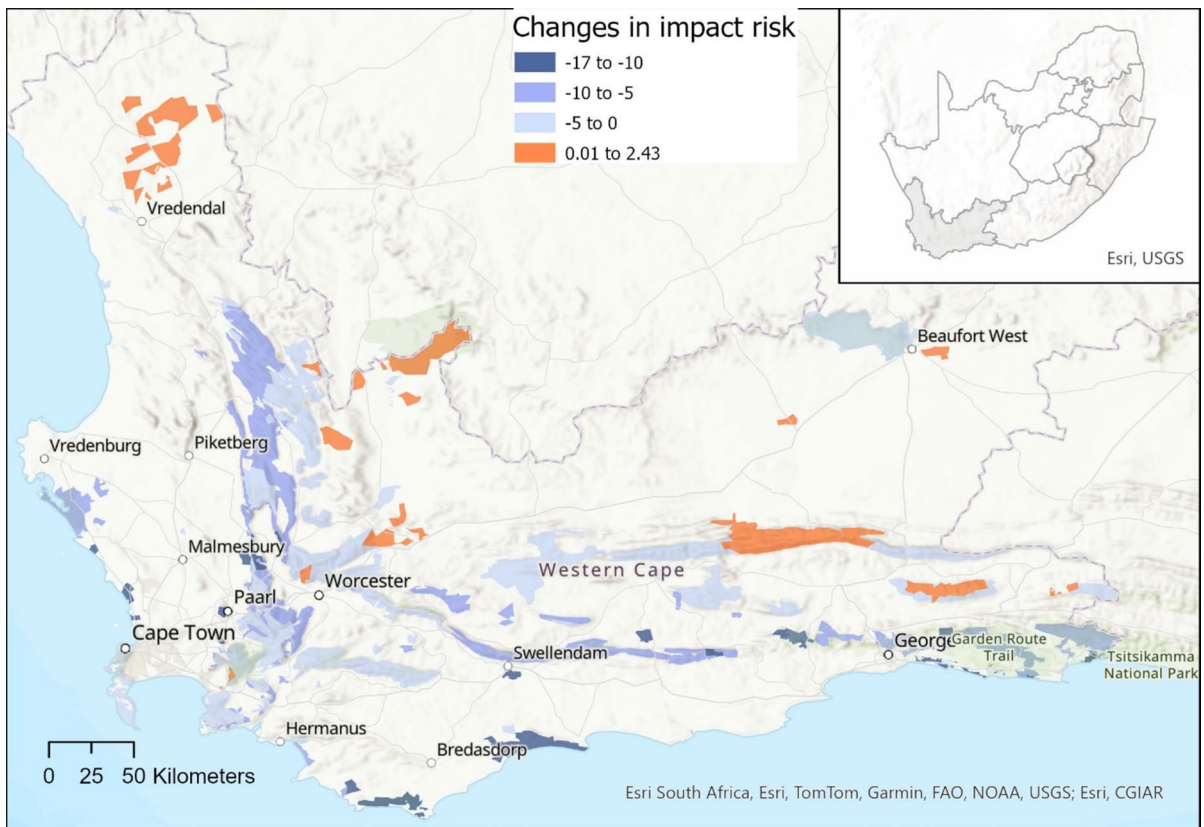


Fig. 4 Projected changes in impact risk of acacia species under future climate for protected areas of the Western Cape province. For each protected area, we compared the mean impact risk under current climate and end-of-century (2071–

2100) climate. Negative values (in blues) indicate a reduction in impact risk, while positive values (in red) indicate an increase in impact risk

province, most protected areas should experience less impact risk in future, but some protected areas experience increased or similar impact risk (Fig. 4). Controlling of harmful acacias now and preventing the arrival of new acacias in these areas is crucial to reduce the loss of high biodiversity areas, as stipulated in the GBF Target 1.

Furthermore, acacia species which are not currently alien in the country (not yet introduced) were not modelled in this study. That means that other species not in our dataset might behave differently from what we present here. Therefore, this does not exclude the possibility of other acacia species, and other alien species in general, becoming more problematic in future (see also Sheppard et al. 2016). Furthermore, acacias and trees in general are long lived species which can result in a long lag between reduced climate suitability and decline in populations or

observed reduction in impacts, and they often exhibit lag phases of several decades before the beginning of an invasion (Robeck et al. 2024). Hence, several acacia species could still be in a lag phase preceding an invasion in South Africa, and this invasion debt was not accounted for in the trends presented here (e.g., Rouget et al. 2016).

As with any model, there are uncertainties linked to the projections. SDMs are based on several strong assumptions (Guisan et al. 2017; Hui 2023). First, occurrence records should reflect the true performance of the species. However, sampling biases are present in most if not all record databases (Beck et al. 2014). Moreover, low sample size can highly impact the performance of SDMs and data available may not be sufficient to fully inform the models (Wiszniewski et al. 2008). To address these shortcomings, we designed a conservative methodology to keep only

the most trustworthy records and limit oversampling in some areas. We also kept records from both the native and the alien range (Broennimann and Guisan 2008). Even though we did not set a time constraint in our records filtering, the vast majority of records kept were collected after 1981, partly matching the period of the climate rasters used for SDM building (1981–2010). Yet, a significant portion of records were collected after 2010, a period that might have already shown the imprint of climate change on these tree species. Besides, our future projections are an average over a range of global climatic models and socio-economic pathways which can substantially impact projections of a species climatic suitability (Petrosyan et al. 2023). Even though the standard deviation of our richness and risk projections (Figure S3) is low relative to their mean values (Fig. 2), an analysis of the sensitivity of the impact risk to the climate scenarios and models might enable us to attribute the causes of this uncertainty.

Second, the species' performance should respond directly to the variation of the selected predictors. In this study we chose four climate variables for their known link with plant species survival and development (Mod et al. 2016) and their availability in both fine spatial and temporal scales. Moreover, Shepard et al. (2014), showed that predictions of similar SDMs of the response of three invasive plant species to climate change was highly correlated with field experiments. However, SDMs are correlative and may yield incorrect estimates of habitat suitability if climatic variables are correlated to other unknown variables in the training area (e.g., Guisan et al. 2017). Future projections from our fitted models of climatic suitability could be biased by potential confounding factors of climate, as we do not take into account other factors which determine the success of alien species in a new region, such as dispersal capabilities and biotic interactions. Our model fitting procedure implicitly assumed that a species had the opportunity to colonise a large part of any country where it was recorded. Regarding interactions, Australian acacia species often have competitive advantages over native plant species and tend to become dominant among plant communities, especially after disturbance (Morris et al. 2011), suggesting that the spatial extent of the realised niche would not be strongly restricted by competitive interactions compared to the potential niche. Yet, other interactions, such as mutualistic and

trophic interactions with soil fungi (Birnbaum et al. 2018) may contribute to constrain the actual range of acacias and act as confounding factors of climate in fitted SDMs, inducing bias in future projections. Furthermore, factors such as topography could be taken into account to improve the models (Bradley and Mustard 2006). Thus, our model predictions could be improved by considering non-climatic drivers (such as soil composition) if these variables were available at a fine resolution.

Third, the species' distribution, represented by recorded occurrences, should be stable and fill any available niche in the study environment. Several studies have shown violations of the niche conservatism hypothesis during invasion with niche shifts between the native niche and the introduced niche (e.g. Parravicini et al. 2015; Guisan et al. 2014). Moreover, predictions based on extrapolations on a new territory and with future climatic conditions may not be robust because the data used for model parameterization cannot represent all conditions in the extrapolated region (e.g., Elith and Leathwick 2009). Thus, it must be kept in mind that our suitability and risk maps may be underestimated and should not be taken as a prediction of true future species richness and impacts.

Fourth, some future climatic conditions may not have an analogue amongst the historical climates of the study area (Williams & Jackson 2007). Yet, SDMs cannot predict exactly how species will respond to conditions that were not used for calibration (Pouteau et al. 2021). This could partly explain why most alien species including acacias alien to South Africa, are projected to experience a decrease in the size of their potential range according to our current knowledge (Bellard et al. 2018). Future work should consider the identification of novel climates to avoid putting too much confidence in climates with no current analogues.

Caution is also advised when interpreting the risk maps including the sum of potential impacts of acacias. Firstly, there are many ways to aggregate impacts, both, within species (calculating one impact value taking into account all impact records for the species) and across species (calculating an impact score for a site where several alien species are present) (Boulesnane-Genguant et al. in prep). Some of the most prominent methods to get one impact value per species have been to sum scores

(e.g., Nentwig et al. 2016), to calculate a mean value (e.g., Rumlerova et al. 2016), and to take a maximum value (e.g., Blackburn et al. 2014) (see also Kumschick et al. 2024). They each come with underlying assumptions which can affect the results. The maximum score per species, as used here, was chosen for range shifting species in the US to anticipate if any high impacting invaders are likely to arrive under climate change (Rockwell-Postel et al. 2020). However, the applications of scores aggregated across species are scarce (for an example, see Nentwig et al. 2010).

Furthermore, climate change can not only affect the potential distribution of species, but also modify their invasion behaviour and impacts (e.g., Le Maitre et al. 2020). Changes to fire regimes could have large impacts on alien species and native ecosystems, especially in the fynbos biome of South Africa where fires have been increasing in frequency and intensity due to alien invasions and climate change (Le Maitre et al. 2020; Slingsby et al. 2017). Furthermore, CO₂ concentration could lead to woody plant densification, which is already shown for native woody plants in some southern African habitats (Skowno et al. 2017). In the fynbos biome, increased CO₂ could also favour the alien acacias as they are nitrogen fixers as opposed to the native flora which are adapted to low nitrogen conditions (Richardson et al. 2000). In other examples, the synchronisation of the flowering period of native and alien plants may favour the latter, through increased interactions with pollinators to the detriment of the pollination of native species. This is the case in New Zealand with *Calluna vulgaris* whose greater phenological plasticity compared to the native species *Dracophyllum subulatum* means that it can reproduce more easily in areas with a high floral density (Giejsztowt et al. 2020). Morphological responses to climate change can also increase the competitiveness of alien species. For example, milder winter temperatures in China facilitate the survival of the water hyacinth *Pontederia crassipes*, and also allow it to develop a greater biomass, forming denser foliage that excludes submerged native plants the following season (You et al. 2013). In terrestrial environments, rising temperatures can also encourage the development of alien plants, reducing the availability of water for native plants, which are then at a disadvantage when it comes to coping with dry spells. This is the case with *Tamarix* spp. introduced in the United States, which develop greater capacity to capture and

use water resources than native riparian species under the effect of drought (Hellmann et al. 2008).

Given all these potential interactions between climate change and impacts of alien species, what we are showing here is not an accurate representation of sites with future impacts of alien acacia species in South Africa. However, risk maps like these of sites where impacting species could occur under climate change projections can be valuable in helping us prioritise sites for future protection from invasion impacts. Despite the potential shortcomings of the models presented here, our study contributes to our understanding of the impacts of climate change on the risk of alien acacia invasions, including their impacts. Furthermore, it can aid the prioritisation of clearing actions for alien acacia species in South Africa and feed into strategies for protected area management and expansion (e.g., Department of Environmental Affairs 2016). Understanding where some of the most damaging invaders might occur under climate change is important so our management is tackling not only current, but also potential future problems.

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Author contributions SK and MR conceptualised and designed the study. CB provided distribution data. CB, LJ, OBJ and MR performed the data analyses. The first draft of the manuscript was written by SK and all authors contributed to the writing of the submitted draft, the revisions, and read and approved the final manuscript.

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Data availability All data used in this publication have been published previously and are available in the primary sources. Impact data was taken from Jansen & Kumschick 2022, species records were downloaded from GBIF.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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