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Spatially-Differentiated Regulation of Alien Species Can Be Improved Using Species Distribution Models: *Psidium guajava* in South Africa as a Case Study

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ABSTRACT

Aim: Biological invasions can generate conflicts between those who benefit from alien taxa and those threatened by subsequent invasions. Ideally, regulations should be proportionate to the level of threat—regulations perceived as unwarranted are likely to result in conflicts. We explore options for spatially differentiated regulation of alien species using *Psidium guajava* as a case study.

Location: South Africa.

Methods: Using various sources, we mapped sites across the country where guava is cultivated, naturalised, and has formed invasive monocultures. We identified areas under threat of invasions using species distribution models (SDMs).

Results: Our models predict that guava invasions are likely along South Africa's east coast. However, the niche dynamic indices indicate a larger cultivated niche than a naturalised niche, suggesting that there are areas in South Africa suitable for guava cultivation where invasions are unlikely. Our SDMs suggest that almost half the area regulated at the provincial level does not require regulation; this spatial over-regulation could be reduced to ~20% if regulations were at the next lower political level.

Conclusions: We recommend that current regulation of guava be aligned to the level of threat. For example, guava is currently regulated in the North-West province, but we found no records of naturalisation and SDMs suggest the climate is not suitable. However, we note a trade-off between the resolution of the regulations and enforceability. We argue that: at lower levels there will be dispersal of fruits between unregulated and regulated areas as the distances between areas will be short; the SDMs produced here are not of sufficient resolution to accurately predict local conditions; and very localised variations in regulations will be complicated to enforce. Although SDMs can easily be over-interpreted, we believe that their judicious use provides a valuable method of interpreting field information in a form useful for regulators so conflicts can be avoided.

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1 | Introduction

Hundreds of tree species have been moved around the world and cultivated for diverse purposes, including forestry, agroforestry, ornamentation and to provide food (Richardson and Rejmánek 2011). Due to their high propagule pressure, extensive plantings and strong human associations, some of these tree plantings have become invasive (Donaldson et al. 2014). Consequently, invasions of alien trees are an increasing problem in many parts of the world (Richardson et al. 2014), with huge negative impacts on agriculture, human health and biodiversity (Pyšek et al. 2020). Research on such invasions and expensive efforts to control them are underway worldwide. Global guidelines were developed recently to facilitate the sustainable use of alien trees, with the aim of preventing invasions and mitigating their impacts (Brundu et al. 2020). One of these guidelines is to ‘Be aware of and comply with international, national and regional regulations concerning non-native trees’. The challenge for regulators is to ensure that such regulations are proportionate, transparent and acceptable, particularly in cases where conflicts of interest complicate management (van Wilgen and Richardson 2014). In this study, we use species distribution models (SDMs) to profile areas under threat of invasions, and that therefore should be prioritised for regulation.

With the increasing number of alien species that potentially threaten the environment and the limited resources for managers to cope with the resulting negative impacts, there is a need for methods that increase the efficacy of invasive species management activities (Kuebbing and Simberloff 2015; Jarnevich et al. 2023). SDMs are used to inform a range of ecological, biogeographical and conservation applications (Sánchez-Mercado et al. 2010). In invasion biology, SDMs have been used to identify areas where species are likely to establish under present and future climatic scenarios (Peterson et al. 2003), predict the rate of spread of invasive species (Wang and Wang 2006), prioritise management efforts (Jarnevich et al. 2023; Guillera-Aroita et al. 2015; Sofaer et al. 2019) and provide background evidence for pest risk analysis (Kumschick et al. 2020). Furthermore, SDMs that incorporate fine-scale environmental data can be used to inform local policies related to the management of invasive alien species by identifying areas where invasive species are likely to establish or spread, thereby aiding in the prioritisation of control and monitoring efforts (Guisan et al. 2013; Lodge et al. 2016).

Here we focus on *Psidium guajava* (guava), an important fruit tree native to tropical America (Naseer et al. 2018). Due to the nutritional value and popularity of the fruit, the plant is commercially grown in many regions of the world. Guavas were introduced to South Africa in the 1860s (Pereira et al. 2017) and the first commercial guava orchard was established in Paarl in the Western Cape in 1890 (<https://guava21.co.za/>, accessed April 2022). In 2024, South Africa produced approximately 26,641 t of guavas (with an estimated market value of USD 3.06 million), according to the Guava Producers' Association (GPA) (<https://guava21.co.za/>, accessed May 2025). Because of South Africa's long history of guava cultivation (Willemse 2021), the species has been widely disseminated. People use the plant for food, fire and medicinal purposes (Ruwanza and Thondhlana 2022; Msomi 2008). Guava has become invasive in South Africa, with

invasions found mainly along roadsides, watercourses and forest margins (Ruwanza and Dondofema 2020; Henderson 2020). It is listed as a ‘widespread-abundant’ invader in South Africa (Nel et al. 2004) and as a ‘signature’ species in ‘alien plant species assemblages’ in moist tropical parts of the country (Richardson et al. 2020). Due to its benefits and invasiveness, guava is recognised and categorised as a potential conflict-generating species in South Africa (Zengeya et al. 2017). *Psidium guajava* has been regulated as an invasive plant in South Africa since 2001, with detailed regulations promulgated in 2014. These regulations were developed following extensive consultations with experts. Public feedback on draft proposals also played a role in shaping the final listings. This approach recognises that any control measures must balance the economic and livelihood benefits of guava with the level of threat it poses, ensuring that regulation remains proportionate and context-sensitive. However, the rationale underlying these recommendations was never clearly articulated nor were they apparently based on specific analyses (Wilson and Kumschick 2024).

This study assesses the potential for SDMs to form part of a rational, defensible and repeatable approach for regulating species differently in different parts of a country and at different political levels. Specifically, we explore different regulatory approaches for the management of guava in South Africa based on: (1) the current distribution of guava across the country; (2) climatic niches and areas that are vulnerable to guava invasions under present climate; and (3) environmental and socio-economic impacts posed by guava in South Africa. We then combined all the information to provide specific actionable recommendations.

2 | Methods

2.1 | Determining Current Distribution of Guava in South Africa

We collated localities where guava is growing from the Southern African Plant Invaders Atlas (SAPIA; accessed: March 2020), the Global Biodiversity Information Facility (GBIF; <https://doi.org/10.15468/dl.azbacf>, accessed: May 2022) and iNaturalist (www.inaturalist.org; accessed: March–April 2020). We contacted the Guava Producers' Association and the Agricultural Research Council for information on guava farmers in the country. As guava is known to occur in high numbers in the Eastern Cape, KwaZulu-Natal, Mpumalanga and Limpopo provinces, we selected these provinces for field surveys. We included the Western Cape in our field surveys because this province is one of the biggest guava farming regions in the country (Willemse 2021). As the species is recorded only in low numbers in Gauteng province (iNaturalist; accessed June 2022), we chose not to physically sample there. We conducted field surveys between April 2019 and March 2021. At each site, we recorded the locality of plants using a hand-held Global Positioning System (GPS Garmin GPSMAP 64S).

2.1.1 | Field Surveys

We mapped guava across the country to identify sites where the species is cultivated, where it has naturalised, and where it has

formed invasive monocultures (we used this category as a proxy for where regulation is warranted). We categorised planted sites as those with individuals that are not yet naturalised (established and self-sustaining). We noted whether these plants occurred in gardens or on farms. We categorised naturalised sites as those with self-sustaining populations with no obvious and direct intervention by humans, such as irrigation and addition of fertiliser. We categorised sites as invasive monocultures if plants were growing at considerable distances from parent plants and close enough together that they formed closed canopies over several metres (albeit in the understory in some cases). Our classification of sites is based on the definition of Groom et al. (2019) and criteria proposed by Wilson et al. (2014).

2.1.2 | Questionnaires

We sent questionnaires to people known or assumed to have guava trees on their property anywhere in the country (see Table S1 for the questionnaire). We sent questionnaires out at the end of March 2020 and recorded responses up until the end of May 2022 (see Table S1 for more information on the questionnaire).

2.1.3 | Historical Data

We used Google Earth and Google Street View to assess populations with geographic coordinates on GBIF that we did not visit in person. Similarly, for records on iNaturalist that we did not visit, we assessed images associated with the records. In most cases, we could not categorise the sites to a level higher than naturalisation from the images provided.

2.2 | Niche Dynamics: Cultivated vs. Naturalised vs. Invasive Monocultures

To uncover how *Psidium guajava* adapts and shifts its ecological niche across different stages of invasion in South Africa, we conducted a multidimensional niche dynamics analysis prior to building SDMs. We took this approach because: (1) it provided us with an understanding of guava's ecological behaviour in the climatic space during the process of invasion; and (2) the outputs of the Principal Components Analysis (PCA) helped us to select variables for the subsequent SDMs.

We used the hypervolume framework described by Blonder et al. (2018), implemented in the R package 'Hypervolume', to estimate the species' realised niche in a high-dimensional environmental space. Unlike traditional two-dimensional methods, this method allowed us to directly measure the niche dynamics in high-dimensional space, offering a more ecologically realistic representation of niche structure.

To delineate niche boundaries, we applied the Support Vector Machine (SVM) method, which is well suited for estimating realised niches, in contrast to Kernel Density Estimation typically used for fundamental niches. Our analysis was based on the 19 bioclimatic variables from WorldClim (version 2.1; Fick and Hijmans 2017) at a 2.5-min spatial resolution and using

occurrence records from our field work, questionnaires and historic data from iNaturalist. We reduced dimensionality using PCA and used the first three components (that accounted for approximately 85% of the total variance) to construct the hypervolumes. We then performed pairwise comparisons between cultivated, naturalised and invasive monoculture populations, calculating the total niche size and overlapping and non-overlapping components. Lastly, we calculated Jaccard's Index to quantify niche similarity between cultivated, naturalised and invasive monoculture populations. We selected Jaccard's Index for this study due to its effectiveness in quantifying niche similarity based on occurrence points and climatic data. It offers a straightforward interpretation, with values ranging from 0 (no overlap) to 1 (complete overlap), making it particularly suitable for comparing ecological niches. This metric is widely used in ecological modelling to assess the degree of shared suitable habitat between species or populations, especially in the context of invasion biology and niche dynamics (Qiao et al. 2019; Gonçalves et al. 2023). This analysis not only enhanced the ecological realism of our models but also provided us with insights into guava's potential for spread and establishment under varying climatic conditions.

2.3 | Species Distribution Models

We selected MaxEnt (Maximum Entropy Modelling) as the algorithm for SDM in this study. MaxEnt estimates the suitability distribution of maximum entropy (i.e., the most spread out or uniform distribution) constrained by the environmental conditions at known presence locations, making it well-suited for ecological niche modelling. Various analyses have found MaxEnt to be a reliable predictive approach that often outperforms other methods in terms of the accuracy of the predictions, particularly for those related to biological invasions (Elith et al. 2006; Merow et al. 2013). For example, Valavi et al. (2021) conducted a comprehensive study comparing multiple SDM algorithms and found that MaxEnt consistently performed among the best in terms of predictive accuracy, especially when models were properly evaluated. Similarly, Merow et al. (2013) provided a practical guide to MaxEnt, emphasising its popularity and performance advantages, particularly its ability to handle complex interactions between environmental variables and its flexibility in model tuning. Lastly, Phillips et al. (2006), demonstrated the theoretical robustness and practical use of MaxEnt in ecological applications. MaxEnt uses species presence data as well as formulated background data as a substitute for true absences. This is particularly useful if true absences are not available due to a lack of systematic surveys (Phillips and Dudík 2008; Fourcade et al. 2014), as is the case in our study.

To examine the spatial dynamics of past invasions and to predict potential guava invasions, we developed an array of SDMs using MaxEnt. We constructed sequential SDMs throughout the invasion continuum and assessed how well these predicted guava invasions in South Africa. Six different models were constructed (Table 1). Firstly, we constructed a native model to assess how good SDMs were in predicting potential invasions given native range records only. Pre-empting invasions before they occur is often an effective strategy for managing biological invasions (IPBES 2023). We hypothesised, however, that these models would not be able to accurately identify

TABLE 1 | Details of the species distribution models (SDMs) that we developed for sequential stages of the invasion continuum.

Name	Description	Number of records used	Model evaluation and important predictor variables	Interpretation for South African regulations
Native model	We created a model only using records from the native range to assess if the SDMs could predict where guava has become invasive in South Africa (providing some indication of whether there may have been a realised niche shift).	3341 (7324 before cleaning)	The model showed low performance (AUC = 0.605; Continuous Boyce Index (CBI) = 0.614) but identified the areas where guava invasions have been found as suitable (Figure S2A). Key predictors included annual precipitation, mean temperature of the coldest quarter and precipitation of the driest quarter.	NA
Global model (-SA)	We created a model that used records from the native and alien ranges (excluding South Africa). We did this to assess whether the SDMs would correctly predict invasions in South Africa (providing some indication of whether there may have been a realised niche shift).	7103 (14,599 before cleaning)	The model performance was slightly better than the native model (AUC = 0.638; CBI = 0.639). The model identified areas as suitable along South Africa's coastline where invasions have been recorded (Figure S2B). The most influential variable was mean temperature of the coldest quarter, contributing over 90% to the model.	NA
Global model (+SA)	We created a model that used all records of guava to predict current invasions in South Africa.	10,315 (17,465 before cleaning)	The model performed well (AUC = 0.835; CBI = 0.724), predicting suitable areas along South Africa's coastline and inland from Mpumalanga to Limpopo (Figure S2C). The most influential predictors were precipitation of the driest quarter and mean temperature of the coldest quarter.	NA
^a Cultivated in SA model	We wanted to evaluate where in South Africa is suitable for guava cultivation based on where it is currently cultivated. Data were collated from our field work, questionnaires and Google Street View surveys. Only records where there was cultivation in South Africa were used.	34 (6005 before cleaning)	The model performed very well (AUC = 0.996; CBI = 0.608) and predicted that the coastline of South Africa is suitable for guava cultivation, and further inland from Mpumalanga to Limpopo (Figure 3D). Precipitation of the driest quarter and mean temperature of coldest quarter were the most important predictor variables for this model.	If there are areas suitable for cultivation that are unsuitable for invasion, then these areas could be exempt from regulation.

(Continues)

TABLE 1 | (Continued)

Name	Description	Number of records used	Model evaluation and important predictor variables	Interpretation for South African regulations
^a Naturalised in SA model	We wanted to evaluate where guava could establish, without obvious and direct human interventions (e.g., irrigation, fertilisation or seedling removal). Data were collated from our field work, questionnaires and Google Street View surveys. Only South African records of naturalised populations were used.	441 (32,845 before cleaning)	The model performed very well (AUC = 0.982; CBI = 0.754). The model predicted that the coastal areas (from the west coast through the east coast) of South Africa are suitable for guava naturalisation (Figure 3E). The most important variables for this model were precipitation of driest quarter, annual precipitation and mean temperature of coldest quarter.	While sites of naturalisation are of concern, the presence of recruitment close to parental plants is arguably not, in itself, enough to warrant wholesale bans. If plants are found surviving and recruiting far from the putative points of introduction, the concern will be greater. However, in neither case is it clear that there would be important negative impacts. Nonetheless such sites should be monitored, noting that the residence time of the site will determine the level of concern (cf. Brock and Daehler 2020). Proactive management might be judicious if the site is close to suitable areas (e.g., riparian areas).
^b Invasive monocultures in SA model	We wanted to evaluate sites where there is evidence of negative impacts and predict where else such negative impacts might occur in South Africa. Data were collated from our field work. Only South African records of invasive monocultures were used.	80 (8800 before cleaning)	The model performed the best of all the models (AUC = 0.997; CBI = 0.856). It predicted that coastal areas (from the west coast through the east coast) of South Africa are suitable for guava monocultures to form (Figure 3F). The most important variables for this model were mean temperature of coldest quarter, precipitation of driest quarter and annual precipitation.	Any locations where monocultural stands of guava are forming are likely to be having Moderate negative environmental impacts (i.e., guava is out-competing native plants). Populations need to be managed to prevent invasions and negative impacts from increasing. Cultivation is not recommended at such sites unless any spread from such cultivated sites can be prevented or effectively controlled.

Note: Naturalised and invasive monocultures are hierarchical categories, and populations could transition between these categories over time (see Brock and Daehler 2020). We classified populations into categories as per the unified framework for biological invasions (Blackburn et al. 2011) and as modified in the Darwin Core (Groom et al. 2019) using the guidelines proposed by Wilson et al. (2014). We used occurrence data for the native, global and global-SA models from the Global Biodiversity Information Facility (GBIF). For South African models, the ^adenotes that the data were from our own field work, questionnaires, iNaturalist and GBIF; and the ^bdenotes data from our field work only.

areas under threat of guava invasions since the records used likely come from only a part of the fundamental niche. Second, we constructed a global model using records from the native and global alien range, but excluding South Africa, to assess the effectiveness of SDMs in predicting invasions (i.e., based on global records for a species not yet introduced to the country). We hypothesised that using records from the native and global alien range should provide a better prediction compared to the model using native records alone. This is because these records should provide a better estimate of the fundamental niche. We constructed an additional model (global-SA model) with global records (including South African records) to predict the distribution of guava in South Africa, based on the current situation (Table 1). Finally, we constructed three South African models using occurrence records solely from South Africa. We believe that using only South African data was valid, because guava has had a long residence time in South Africa (at least 161 years; Pereira et al. 2017; Willemse 2021) and has been widely planted (Richardson and Potgieter 2024). We, therefore, believe it is reasonable to assume that guava has experienced the breadth of suitable environmental conditions available in South Africa. We constructed three South African models using records from cultivated (cultivated-SA model), naturalised (naturalised-SA model) and invasive monoculture populations (invasive monocultures-SA model).

2.3.1 | Occurrence Records

We downloaded 7324 records for the native model, 14,509 for the global and 17,465 for the global-SA model from GBIF (Table S5). We assessed the occurrence records and cleaned them using the 'Biogeo' package (Robertson et al. 2016) in R version 4.1.0. We removed erroneous records; this included records with no coordinates, records that fell in the sea, duplicate records and records that are environmental outliers (i.e., records that were far away from the rest of the records in environmental space, such as records of ephemeral populations, or where there are errors in the co-ordinates that could not be easily corrected, Robertson et al. 2016). The total number of occurrence records in the cleaned datasets was 3341 for the native model, 7103 records for the global model and 10,315 for the global-SA model (Table 1). Our three South African models (cultivated-SA model, naturalised-SA model and invasive monocultures-SA model) were based on records from South Africa only (see Table 1 for data sources). In total we collated 6005 records for the cultivated-SA model, 32,845 for the naturalised-SA model, and 8800 for the invasive monocultures-SA model. After we implemented the cleaning processes described above, we used 34 records for the cultivated-SA model, 441 for the naturalised-SA model and 80 records for invasive monocultures-SA model to build the models (see Table 1).

2.3.2 | Selection of Predictor Variables

To model the potential distribution of *Psidium guajava*, we selected a set of ecologically relevant climatic variables that reflect the species' physiological tolerances and environmental preferences. These included annual mean temperature (BIO1), maximum temperature of the warmest month

(BIO5) and minimum temperature of the coldest month (BIO6), which together represent the species' thermal tolerance and seasonal extremes. We chose precipitation-related variables—annual precipitation (BIO12), precipitation of the wettest month (BIO13) and precipitation of the driest month (BIO14)—to represent overall water availability and seasonal moisture variability. We obtained bioclimatic variables from the WorldClim v2.1 database (Fick and Hijmans 2017). We believe the chosen variables are particularly relevant for guava, as it is a species that thrives in warm, moderately humid environments and is sensitive to both drought and excessive rainfall (Arévalo-Marín et al. 2021; Fischer and Melgarejo 2021; ul Haq et al. 2022).

We checked the selected variables for collinearity using the Pearson correlation coefficient, as collinearity can be detrimental to the accuracy of SDM predictions (Petitpierre et al. 2017). In instances of substantial collinearity ($r > 0.75$; Elith et al. 2010), we retained the most ecologically relevant variable (as per Arévalo-Marín et al. 2021; Fischer and Melgarejo 2021; ul Haq et al. 2022). Consequently, we used four climatic variables to model the distribution of guava: mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation and precipitation of driest quarter.

2.3.3 | Generating Background Points

Selecting appropriate background points is a crucial step for ensuring accurate model performance and reliable predictions in SDMs with no absence records (Phillips et al. 2009; Daniel et al. 2020). Poorly chosen background points can introduce bias, inflate model performance metrics or misrepresent the species' ecological niche (Phillips et al. 2009; Castillo and Higa 2025). To minimise such issues, we generated background points for the native, global and global-SA models from a restricted area that was environmentally similar to sites where *Psidium guajava* occurs, as identified using a map of the Köppen-Geiger climate zones (Kottek et al. 2006). We selected background points for the three South African models using a different method. We did this because we believe that some areas where the species is currently cultivated in South Africa are not climatically suitable for guava to naturalise (e.g., parts of the Western Cape). In such cases, human intervention (e.g., irrigation, nutrient supplementation and the removal of competing vegetation) is essential for guava to survive and so identifying background records from such areas would mis-inform the models. We therefore selected background points for the South African models from areas that are not suitable for cultivation based on the global plant hardiness zones (i.e., a geographic areas with certain average annual minimum temperature—a factor that influences the survival of many plants) (as outlined by Magarey et al. 2008 and shown in Figure 1). It is suggested that guava grows best in hardiness Zones 10 and 11, sometimes in Zone 9 (with care) (Naik et al. 2021). The majority of our guava cultivated occurrence records in South Africa fell within hardiness Zones 10 and 11. It is recommended that sites from which background records are selected should be unsuitable for the species, but be near enough to the limit of what is suitable. As such, we selected background points for South African models from hardiness Zone 9 (in South Africa) because only one record from our surveys fell within this

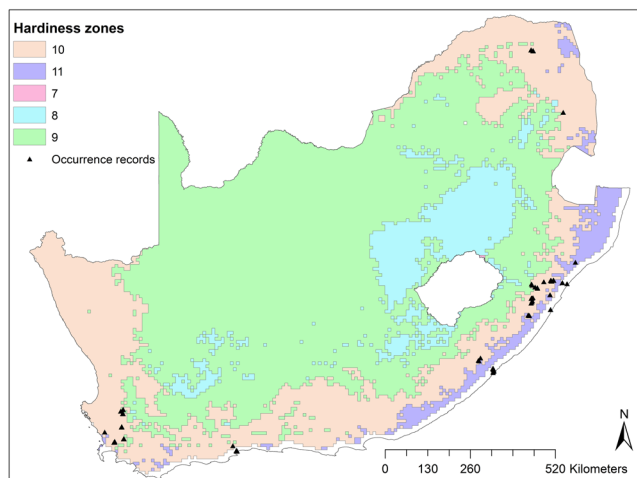


FIGURE 1 | Hardiness zones for *Psidium guajava* in South Africa, adapted from Magarey et al. (2008). Zones 10 and 11 represent areas where guava occurrences were recorded in this study, indicating suitable conditions for growth. Zone 9 indicates areas where background points for the South African species distribution models were generated. These zones reflect climatic suitability, and we used them to inform model calibration and interpretation (see Figure 3).

zone, and most importantly this zone is environmentally close to the zones (10, 11) where the species is currently cultivated. We selected 1000 background points for the South African models and 10,000 background points for the native, global and global-SA models using the package ‘dismo’ and function ‘randomPoints’ in R (Hijmans et al. 2015).

2.3.4 | Model Performance

We evaluated model performance through cross validation (with the data split five times), and by calculating the average area under curve (AUC) statistic and Continuous Boyce Index (CBI). Furthermore, we evaluated models by examining multivariate environmental similarity surface (MESS) maps (Ramampandra et al. 2023) and the ecological plausibility of the response curves. We used the Jack-knife test in MaxEnt to gauge the relative contribution of each environmental predictor in the models.

2.4 | Assessing Options for Regulating Guava in South Africa

The regulation and management of alien species, especially those with strong human affiliations, such as ornamental plants or culturally significant animals/plants often lead to social conflict (Estévez et al. 2015). Such conflicts highlight the importance of understanding not only the ecological impacts of alien species but also the social dimensions of their presence. Overlooking these human connections may risk alienating stakeholders which may in turn reduce compliance, and ultimately undermine conservation goals. Therefore, integrating stakeholder perceptions into decision-making processes is essential for developing socially acceptable and ecologically effective management and regulation.

To identify strategic approaches for managing *P. guajava* in South Africa, we adapted the framework proposed by Novoa et al. (2015). The framework emphasises the importance of stakeholder engagement, policy alignment and adaptive management. We believe that this framework is particularly applicable to this case as there are complex socio-ecological dynamics regarding the cultivation of guava and the management of guava invasions. We identified and assessed six different regulatory approaches: (1) regulate guava throughout the country; (2) regulate guava only in provinces where it is recorded as invasive; (3) regulate guava in provinces where it is recorded as invasive with the provision for issuing permits; (4) municipal-level regulation with no provision for issuing permits; (5) a ‘wait and see’ approach (i.e., regulating the species through the application of bylaws rather than national regulation in response to demonstrable impacts); and (6) no regulation (the numbers here correspond to the rows in Table 2). We evaluated each approach using six criteria: (1) level of understanding or amount of information required for the approach; (2) costs of acquiring the information; (3) number of populations regulated where a threat is not posed; (4) number of populations not regulated where a threat is posed; (5) public acceptance; and (6) costs of implementing the regulations based on the approach (the numbers correspond to the columns in Table 2). We considered current and potential distribution of guava in South Africa in the evaluation of each approach.

2.5 | Determining the Administrative Scale for Regulation in South Africa

To assess and determine the administrative level at which *P. guajava* should be regulated in South Africa, we used the output of the SA-invasive monocultures SDM that estimates the suitability of habitats for *P. guajava* across the country (in Figure 2 we outline a conceptual framework developed to guide the evaluation of regulatory options for *P. guajava* in South Africa). To facilitate decision-making and spatial prioritisation, we converted this continuous output into a binary map (suitable/unsuitable) using a threshold. We chose the threshold based on a precautionary approach, that is, we used the lowest suitability value at which a true presence was correctly predicted as present. This is a conservative approach suitable for risk analyses of invasive plants. In such cases, the cost of failing to predict a true presence (i.e., a false negative) can be significantly higher than the cost of overpredicting suitability (i.e., a false positive). By prioritising sensitivity over specificity, our choice of threshold aims to minimise the risk of underestimating the area suitable for the species. We overlaid the binary map onto political boundaries at four different administrative levels (arranged from highest to lowest): national, provincial, municipality and ward (Figure 2). We then calculated the percentage of grid cells within administrative boundaries of South Africa that are predicted to be likely suitable for guava. We used the ‘extractr’ (Baston 2023) package in R for geo-processing.

2.6 | Risk Analysis Using the RAAT Framework

To evaluate the potential environmental and socio-economic risks posed by *Psidium guajava* in South Africa, we conducted a comprehensive risk analysis using the Risk Analysis for Alien

TABLE 2 | Our evaluation of options for regulating *Psidium guajava* (guava) in South Africa using a framework proposed by Novoa et al. (2015).

Approach	Level of understanding required	Cost of getting the information	Number of populations regulated where a threat is not posed	Number of populations not regulated where a threat is posed	Public acceptance	Cost of implementation
1. National regulation	Low: based just on records of invasion.	None: information exists already (Figure 3A–C).	High: the species is not invasive in all South African provinces, though there might be range expansion due to climate change.	None	Low: we anticipate resistance from commercial, small-scale farmers and people with guava trees in their gardens. Many people would lose a source of income.	High: Guava would have to be controlled across the whole country. Enforcing the removal of trees from private gardens would be difficult and costly.
2. Provincial regulation (if a province is climatically suitable for a guava invasion, then guava should be regulated in the whole of the province)	Low: invasion status of guava per province (cf. Table 3).	Low: costs involved in conducting fieldwork to confirm status (e.g., as performed here).	High: there are areas within these provinces where the species is not invasive, but only in cultivation and the climate seems to be unsuitable for naturalisation (Figure 3A–C).	None	Low: There would be resistance from commercial and small-scale guava farmers in provinces where regulations are in force.	High: Access to private land would be difficult. This approach would also be costly for farmers in provinces where guava is invasive.
3. Provincial regulation with provision for issuing permits (if permit conditions are effective in preventing spread from guava plantations, then restricted activities could be allowed. The plantings should be away from natural forests, roads and not in areas with high climatic suitability)	High: data are needed for current distribution, species distribution models need to be created, and data interpreted in risk analysis. The conditions under which permits can be issued need to be tested or at least justified.	High: costs involved to conduct fieldwork, species distribution models and risk analysis.	High: there are areas within provinces where guava is cultivated but it is not invasive and the climate is unsuitable for an invasion (Figure 3C,F).	None	Medium: permits can be expensive, and potentially time consuming to obtain, but we anticipate some level of public acceptance for this approach.	Medium: This is the current approach. Costs attached to this include awareness campaigns for the permitting procedures (noting the cost of permits do not cover all permitting costs).

(Continues)

TABLE 2 | (Continued)

Approach	Level of understanding required	Cost of getting the information	Number of populations regulated where a threat is not posed	Number of populations not regulated where a threat is posed	Public acceptance	Cost of implementation
4. Municipal-level regulation (no provision for issuing permits in areas with high climatic suitability, close to open forests and riparian areas)	Medium: data are needed for current distribution, species distribution models and risk analysis.	High: costs involved to conduct fieldwork, species distribution models and risk analysis.	None	None	Medium: from both users and conservation community, though concerns might be expressed about the complexity of the system.	Medium: for conservation community and invasion managers in terms of publishing and communicating complex regulations.
5. Wait and see (a reactive approach, no permits are required until guava invasions with demonstrable impacts are recorded in a given locality, local regulation, e.g., through bylaws, are then implemented)	None: no information is initially needed to implement it. though guidelines for monitoring and deciding when an invasion is of concern are needed.	None	None: only listed if impacts seen at a site.	High: by virtue of the reactive approach.	High: users. Low: conservation community as it allows for impacts.	High: for conservation community and invasion managers. It is not easy or cheap to control an invasion after it has started.
6. No regulation	None	None	None	None	High: guava users. Low: conservation authorities and invasion managers, as impacts do not stop.	None: no direct costs to implementing agents in terms of regulations. High in terms of management and damage costs, noting that justification might be needed to clear unregulated invasions.

Note: Each option was scored for each criterion as none, low, medium or high.

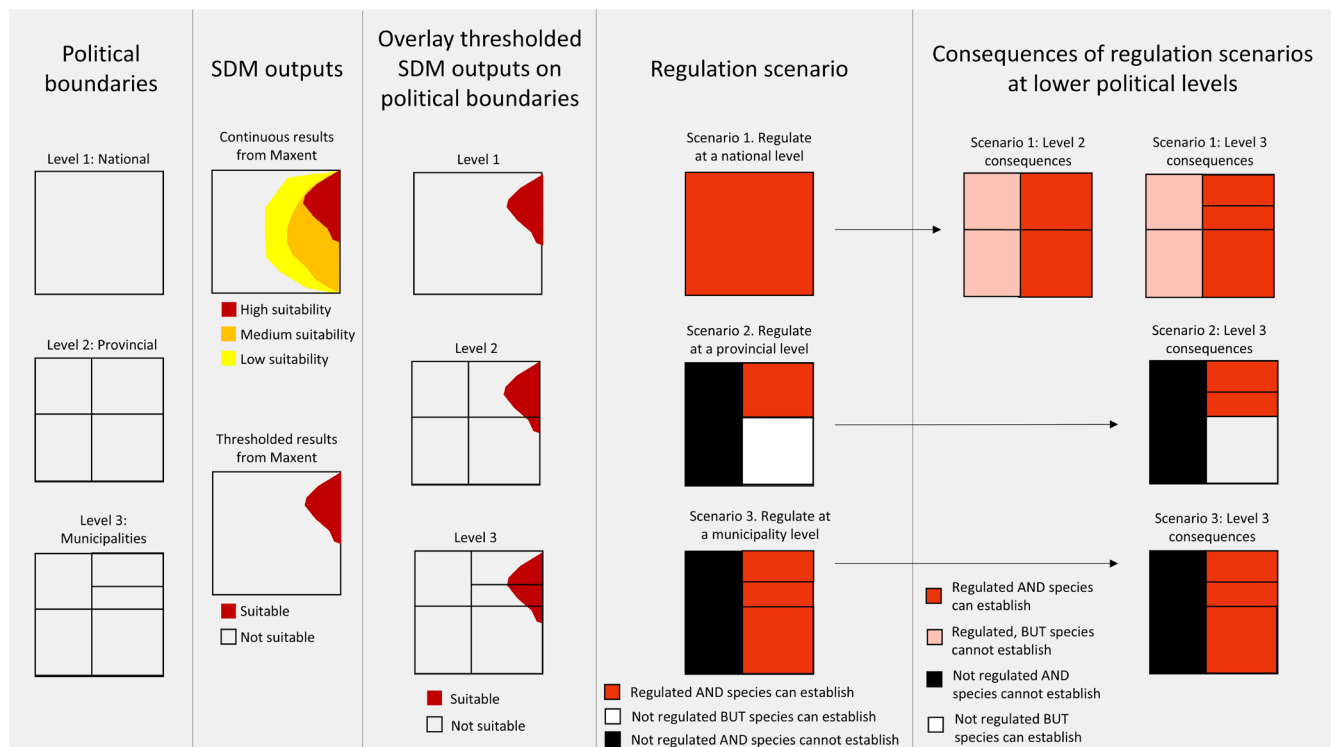


FIGURE 2 | Our proposed procedure to allow for spatially-differentiated regulation of alien species. Ideally both the area not regulated where the threat is acceptable (i.e., where the species is unlikely to establish) and the area regulated where the threat is unacceptable (i.e., where the species is likely to establish) should be maximised. However, invasions are very difficult to stop once they start and the decision might be to only maximise the area regulated where the threat is unacceptable. Regulation at lower political levels will likely be more costly to implement, more easily misunderstood and ultimately less effective. A buffer around suitable areas might also be needed to allow for dispersal from unregulated to regulated areas. We applied the procedure to determine how guava (*Psidium guajava*) should be regulated in South Africa (Figures 3 and 4).

Taxa (RAAT) framework developed by Kumschick et al. (2020). This framework provides a standardised approach for assessing the risks of alien species, including high environmental and socio-economic impacts. Using this framework, we systematically scored and categorised the risks associated with *P. guajava* based on available empirical data, and expert knowledge (Data S2). Furthermore, we collated information on climate and habitat suitability, likelihood of entry and spread, and impacts from various sources including the ISI Web of Knowledge, Google Scholar, websites addressing biological invasions, databases such as the Global Invasive Species Database (www.iucngisd.org/gisd), scientific publications and the grey literature. We used synonyms, common names in English and scientific names when searching for impacts.

3 | Results

3.1 | Current Distribution and Degree of Establishment of Guava in South Africa

We recorded guava cultivation at 34 sites, naturalised populations at 441 sites and invasive monocultures at 80 sites (Figure 3A–C, Table 1). We found cultivated and naturalised sites across the country, whereas invasive monocultures occur mostly in KwaZulu-Natal (Figure 3C). Most of our cultivated records in KwaZulu-Natal, Limpopo and Mpumalanga were of individual trees planted in gardens (Figure 3A). We recorded naturalisation across the country, mainly from KwaZulu-Natal, Mpumalanga and Limpopo

(Figure 3B). We also recorded five sites of guava naturalisation in the Western Cape (Figure 3B), some of which were along riparian zones and one of which was by a hot spring (a site where the broad climatic conditions did not reflect microsite conditions).

3.2 | Niche Dynamics: Cultivated vs. Naturalised vs. Invasive Monocultures

The first PCA axis of our niche dynamics model explained 47% of the variance, while the second and third axes explained 21% and 17% of variance, respectively (Table S2). Our niche hypervolume analysis suggested that the cultivated niche is the largest, and the naturalised niche is much smaller and forms a subset of the cultivated niche (with proportions of 75% and 0.8%, respectively) (Table S3; Figure S1A), with a niche overlap of 24% (Table S3). Similarly, there was niche overlap for cultivated populations and invasive monocultures, but a larger part of these niches did not overlap (Figure S1B).

3.3 | Species Distribution Models

3.3.1 | Model Performance and Variable Contribution

For our native, global and global-SA models AUC values ranged between 0.60 and 0.84, indicating moderate to good performance. Our three South African models had AUC values ranging between 0.85 and 0.99 indicating good to high performance,

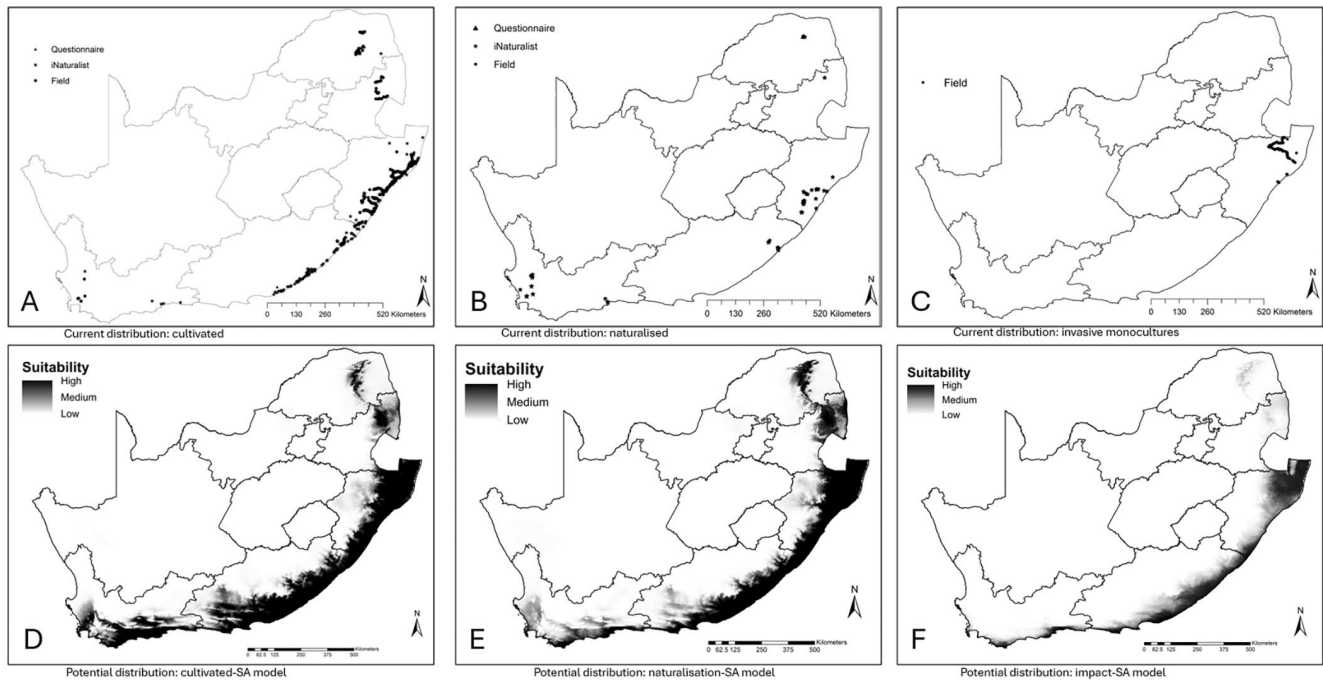


FIGURE 3 | Distribution and modelled suitability of *Psidium guajava* populations across South Africa. We mapped occurrence records for (A) cultivated populations, (B) naturalised populations (excluding invasive localities) and (C) invasive monocultures. We compiled these records from historical sources, questionnaire responses and field surveys (Table 1; Table S5). Average suitability maps from our models show where the climate in South Africa is likely suitable for *P. guajava* to be, (D) cultivated, (E) naturalised and (F) form invasive monocultures (Table 1).

and CBI values of >0.60 (Table 1). Our invasive monoculture model had the highest AUC (0.997) and CBI values (0.85). We took this to mean that the predictions were consistent with the observed distribution. We found that most of the response curves were plausible and aligned with expectations of species–environment relationships (Figure S3). However, we found some inconsistencies. Notably, the response curves for two predictors (mean temperature of the coldest quarter and mean temperature of the warmest quarter) in the Native and Global models displayed ecologically implausible shapes, suggesting potential overfitting or limitations in predictor representation. Additionally, the response curve shapes for annual precipitation differed between our South African and Global models, which may reflect regional differences in environmental gradients, species behaviour or sampling bias. We concluded that these patterns highlight the importance of contextualising model outputs within ecological and geographic frameworks. The MESS maps for each of our models indicated that the models did not extrapolate into novel environments in South Africa. We found that, based on the Jack-knife test of variable contribution, the most important predictors differed among our models (Table 1). Mean temperature of the coldest quarter proved important for our global model, contributing more than 90%. On average, precipitation of the driest quarter contributed the most to our South African models (Table 1).

3.3.2 | Potential Distribution: Native vs. Global Alien vs. South African Models

Our native, global and global-SA models predicted large areas of South Africa as climatically suitable for the species. Our models indicated that sites threatened by guava invasions occur

along the coastline of the country, primarily along the east coast (Figure S2A–C).

Our predictions based on the SDMs are that: a suitable climate for guava cultivation in South Africa extends from the Western Cape along the south and east coasts of the country into Mozambique and inland into Mpumalanga and Limpopo (Figure 3D); areas that are climatically suitable for guava naturalisation occur mostly along the east coast of the country and into Mozambique (Figure 3E); sites that are suitable for invasive monocultures are along the coast, especially the east coast (Figure 3F); and that the western part of the country is unsuitable for guava invasions, except for some areas along the coast (Figure 3F). All three of our South African models suggest areas along the coast of the country are likely suitable, but there are also areas suitable for cultivation inland that are likely unsuitable for naturalisations or invasive monocultures (Figure 3D–F).

3.4 | Options for Regulating Guava in South Africa

We assessed a national-level regulation of guava (approach one) in South Africa as neither feasible nor desirable. This is primarily because guava is already widespread across the country and does not exhibit invasive behaviour in all regions (Figure 3A–C). Furthermore, large areas of the country are likely to be climatically unsuitable for guava establishment and invasion (Figure 3D–F). Our second approach (regulate guava in provinces where the species is already recorded as invasive) would, we argue, result in a low number of populations that are regulated but will not become invasive, but would likely be met with a low degree of public acceptance. This is mainly because

of the overlap between the guava producing areas (Figure 3A) and regions where the species is recorded as naturalised in the country (Figure 3B). Most commercial guava production is in the Western Cape, Limpopo and Mpumalanga provinces; and small-scale farmers are clustered primarily in KwaZulu-Natal and the Eastern Cape (Figure 3A). We suggest that modifying approach two to accommodate provision for issuing permits (i.e., approach three: regulate the guava in provinces where it is recorded as invasive with the provision for issuing permits) offers a more workable option. This is the approach currently used to regulate guava in South Africa (Table 3). We feel that public acceptance for this approach is likely to be high, because several guava farmers seem to be aware of the invasion risk that the species poses to native biodiversity. A problem, though, is that some of the permitted plantings are near natural forests and riparian areas—habitats that are highly susceptible to guava invasions. Moreover, there are areas within the provinces where guava is not invasive (Figure 3C). Our fourth approach (municipal-level regulation-with no provision to issue permits) provides an option more closely attuned to the risks—the species is regulated in only the affected areas (Figure 4C). Our fifth approach (‘wait and see’, that is, regulate the species through bylaws in response to demonstrable impacts) is reactive. We believe that acceptance of this option would be high from guava farmers, but it would receive low support from the conservation community, mainly because controlling an invasion after it has started is expensive and often ineffective. Our final approach (i.e., approach six: no regulation of guava in the country) would result in more widespread guava invasions across the country and exacerbated threats to native biodiversity.

3.5 | Determining Administrative Scale for Guava Regulation in South Africa

The socio-economic importance of guava to human livelihoods presents a significant challenge to its effective management as an invasive species. Given this, and based on our SDM results, we recommend a spatially-differentiated regulatory approach. Specifically, we recommend that: (1) guava be regulated differently in different regions of the country; and (2) the level of regulation is proportionate to the level of ecological threat in each area. We illustrate the spatially differentiated regulatory scenarios evaluated for South Africa in Figure 4A–D.

Results from our SDMs suggest that provincial-level regulation would result in approximately 49% of the area being subject to control, despite no threat being currently posed or detected in many of these areas. Currently guava is regulated at the provincial level in South Africa (Table 3, Figure 4A). To improve efficiency and reduce unwarranted regulation, we recommend implementing regulation at the municipal level (Figure 4C, Table 2). While ward-level regulation could reduce the regulated area by about 14% (Figures 2 and 4D, Table 3), regulation at this smaller political-level presents three key problems: (i) long-distance seed dispersal by frugivores (Le Roux et al. 2020), could facilitate spread from unregulated to regulated areas; (ii) the SDMs would need to be at such fine spatial resolutions that they have limited predictive accuracy; and (iii) the regulations would become very detailed,

potentially confusing stakeholders and making them onerous to enforce. Finally, although ward-level regulation reduces the total area under regulation, the benefit is not very large (20% of the area of South Africa is regulated at the municipal level and 14% at the ward level, Table 3). This benefit is unlikely to outweigh the significantly higher administrative costs and the risk of under-regulating areas that may become threatened. There is, we argue, a key trade-off between regulatory resolution and practical enforceability.

3.6 | Risk Analysis

We found that South Africa has habitat and climatic conditions suitable to grow and support self-sustaining populations of *Psidium guajava*. In terms of impacts, we scored *P. guajava* as having Moderate impacts globally, with competition being the most frequently recorded impact mechanism. In Eswatini, *P. guajava* trees grow very tall and close to each other, forming dense continuous canopies that smother native plants, outcompeting them for light (Mamba and Singwane 2019). In India, guava is found growing in forested areas and along roadsides (Semwal et al. 2024). We argued that the potential impacts, if left unmanaged, could be Major in South Africa (as outlined in Table S4). Based on our scoring of the likelihood of establishment, the potential for range expansion and the impacts of *P. guajava*, we consider the species as high-risk for the country, and so some form of regulation is warranted. Therefore, we recommend that *P. guajava* be regulated as category 2 (a permit is required to carry out restricted activities, such as trade) in South Africa, with specific exemptions for the consumption of fruit. Furthermore, we recommend provision for permits for commercial production given the size of the industry and the demand in the country. However, we note that as guavas are dispersed by birds and mammals, it is unlikely that permits will be effective in stopping invasions where the threat of invasion and/or impacts is high (i.e., next to open forests, riparian zones, and areas where *P. guajava* is recorded as invasive and/or is predicted to become invasive) (see Table S4 for more information).

4 | Discussion

Invasive species are costly to manage and, with limited resources available, managers and policy makers must prioritise species and sites for intervention (McGeoch et al. 2016; Richardson et al. 2010). This is a core aspect of Target 6 of the Global Biodiversity Framework. Alien species that confer benefits to some stakeholders but cause damage to others (so called conflict-generating species; Zengeya et al. 2017) present special challenges. We collated data on the distribution of guava in South Africa from a combination of historical sources, in-field sampling, citizen science, questionnaires and Google Street View. We used these data to inform species distribution models, models of niche dynamics, and a risk analysis. Our model species (*Psidium guajava*) occurs along a climatic gradient with different uses and degrees of establishment; providing us with a good opportunity to identify areas that should be prioritised for management and resource allocation, and assess whether alien species can be spatially regulated.

TABLE 3 | Area of South Africa where we recommend guava regulation to limit invasions at different spatial scales.

Level of South African governance	Area regulated	Percent of South Africa regulated where no threat is posed	Percentage area not regulated where a threat is posed	Summary and implications of the approach
(Level 1) National	~1,220,813 km ²	80	0	Regulating the species at a national level is inappropriate because more than half of South Africa is probably not suitable for guava naturalisations and invasions. Most naturalised populations of guava are recorded in two provinces (Eastern Cape and KwaZulu-Natal). We recorded invasive monocultures in KwaZulu-Natal (Figure 3C).
(Level 2) Provincial (current regulations as of 2020)	~570,458.2 km ²	47	11	Current regulation. There are both provinces of South Africa where guava is regulated, but that are not suitable for guava naturalisations and invasions (e.g., North-West Province), and provinces of South Africa where guava is not regulated, that are suitable for guava naturalisations and invasions (Western Cape) (Figure 4A,B).
(Level 2) Provincial level (proposed based on SDMs)	~595,038 km ²	49	0	Though areas that are likely climatically suitable for guava cultivation extend from Cape Town along the southern and eastern coasts of South Africa and then inland to Mpumalanga and Limpopo provinces, areas that are likely climatically suitable for guava naturalisation occur mostly along the east coast of South Africa (Figure 3D–F). This suggests that most of the inland areas are likely not suitable for guava invasions. Therefore, regulating the species at the provincial level (specifically those where the species is already invasive) seems disproportionate to the level of threat as there are areas within these provinces where naturalisations are not predicted.
(Level 3) Municipality (proposed based on SDMs)	~233,696 km ²	20	0	We recommend regulating the species at the municipality-level where there is demonstrable need for management. Guava is invasive and has demonstrable impacts in several municipalities of KwaZulu-Natal (Figure 4C). The models also predicted that most of these municipalities are likely to be climatically suitable for the species to expand its invasive range.
(Level 4) Ward (proposed based on SDMs)	~162,363 km ²	14	0	Regulating the species at ward level would mean less area under regulation (about 14% of the country). However, seeds of guava are dispersed by several frugivores and this can sometimes be over long distances (i.e., from unregulated to regulated wards). Given the size of wards, regulating the species at this level, would also likely be bureaucratically complicated and confusing for stakeholders.

Note: The percentage areas shown are based on the proportion of South Africa (at a 0.5° grid cell scale) that our species distribution models (SDMs) predicted as likely suitable for a guava invasion with impacts.

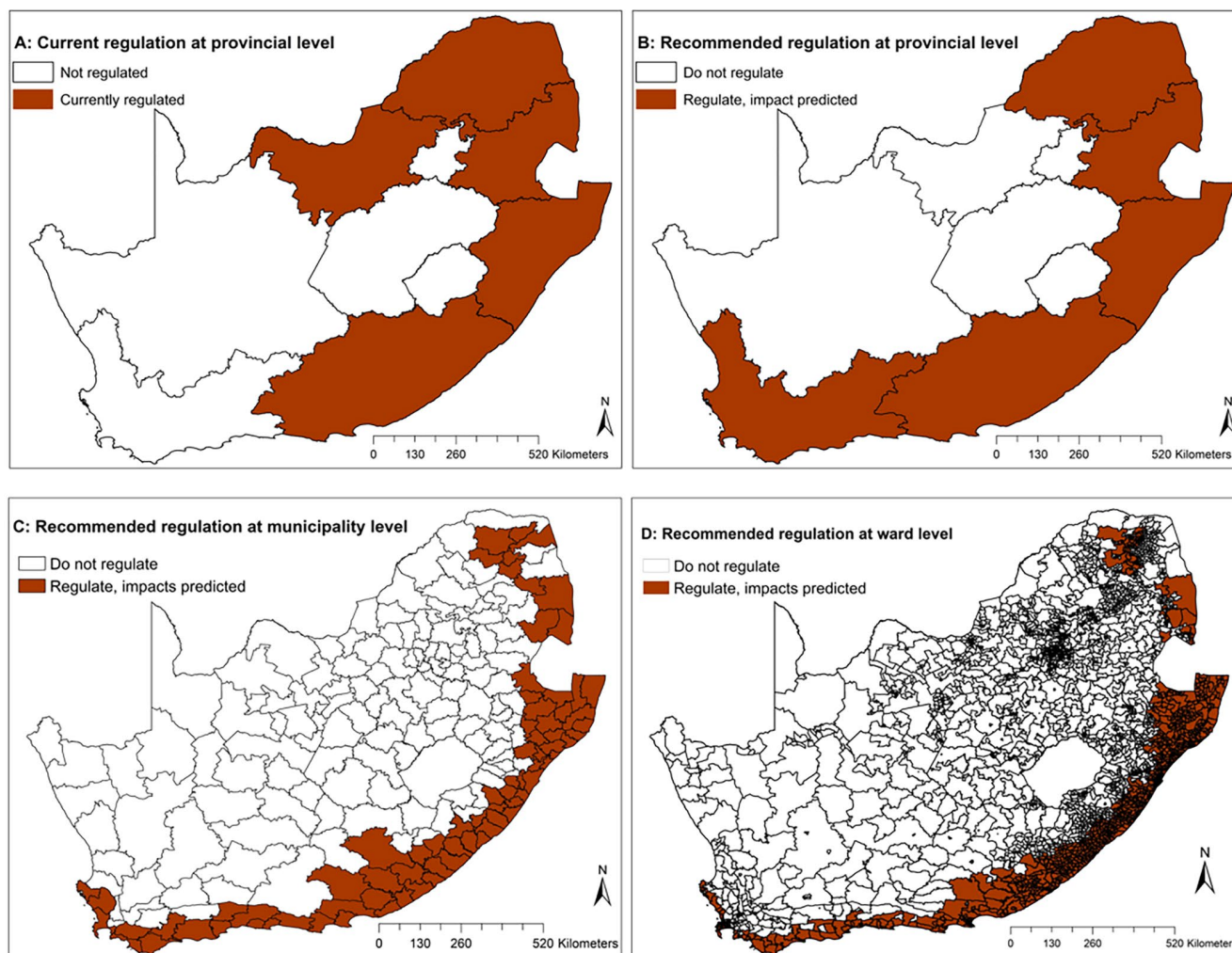


FIGURE 4 | Options for spatially differentiated regulation of *Psidium guajava* in South Africa to limit harmful invasions. Panel A shows current regulations at the provincial level. Panels B–D show recommended regulations at the level of provinces (Panel B), municipalities (Panel C), and wards (Panel D), based on areas we predict will be impacted by *P. guajava* according to the invasive monocultures-SA model (Figure 3F). White areas are predicted to be unsuitable for *P. guajava* impacts (Panels B–D) or where the species is not currently regulated (Panel A). To generate the binary suitability maps used in this figure, we applied a precautionary threshold, that is, the lowest predicted suitability value at which a true presence was correctly classified. This conservative method prioritises sensitivity over specificity to reduce the risk of underestimating the suitable area for the species. We discuss the details of the implications of these options (e.g., proportion of area where the regulatory option is inappropriate) in Table 3.

The current distribution of guava in South Africa is primarily along the coastline of the country, from the south coast to the eastern parts of the country. The low number of cultivated populations (guava farms in particular) recorded in Mpumalanga and Limpopo can be attributed to the presence of guava wilt that has resulted in many orchards being cleared (S. Willemse, pers. comm.). Also, land use practices in these regions have changed, particularly in Limpopo. Naturalised guava plants are being cleared for plantations of more profitable crops such as macadamia nuts. This might explain the low extent of naturalisations we recorded in these regions. However, our models predicted that these regions are climatically suitable for guava invasions. A recent study by Ruwanza and Dondofema (2020) in Limpopo showed that guava invasions alter some soil properties, creating favourable conditions for its growth. This region therefore needs to be monitored to gain a better understanding of guava invasion ecology. The other areas that our SDMs suggest are climatically suitable are primarily within the subtropical coast of the country,

and are characterised by medium to high rainfall (650–1000 mm per annum) (Borrel et al. 2011; Mucina and Rutherford 2006) and annual temperatures in the range of 20°C–30°C. Precipitation is vital for guava production (see Fischer and Melgarejo 2021). The need for water is particularly important for guava seedling survival (Fischer and Melgarejo 2021). Drier conditions with low rainfall can lead to seedling death, and so irrigation is necessary for guava cultivation in regions that experience drought. Large parts of the Western Cape (currently the largest guava-producing region in South Africa; Willemse 2021) have a Mediterranean-type climate with a pronounced summer drought (Mucina and Rutherford 2006), and thus are suitable for irrigated cultivation, but not for invasions (Figure 3A vs. Figure 3C; the exception that we feel demonstrates this was a site by a hot spring in the Western Cape where we recorded guava naturalising). Moreover, most guava farms we recorded in the region are in urban areas, with no natural forests or vacant land in close proximity to plantings to provide opportunities for naturalisations. We recorded

naturalisations and invasive monocultures along roadsides and natural forests elsewhere across the country. Guava thrives in such habitats (Henderson 2020), and plant invasions in disturbed areas including roadsides are documented in South Africa for other fleshy-fruited invasive plants (Ruwanza and Mhlongo 2020). It seems that climatic suitability and microsite conditions together define the potential range of guava in South Africa.

Since *P. guajava* is only likely to be invasive at certain sites in the country, regulating guava at a national level would not be proportionate to the level of threat posed. We therefore recommend guava is regulated only in municipalities where it poses a significant invasion threat, and that no permits are issued in those municipalities. We anticipate a relatively high degree of public acceptance for this approach, which is an important consideration when regulating invasive species (Brody 2003). Collaboration and coordination with municipalities is crucial for successful management of guava invasions in South Africa. Most naturalisations occur along roadsides and seem to be triggered and sustained by mowing of grass and clearing of other vegetation. *Psidium guajava* is a vigorous resprouter after ineffective manual control (when stumps are cut but not treated with herbicide) and after fire (field observations; KwaZulu-Natal). Management strategies in these areas should consider integrated control efforts with the management of roadside vegetation and other types of vegetation management.

4.1 | Caveats of the Study and Next Steps

Our study provides insights into the potential distribution of alien species using SDMs, contributing to the growing body of research aimed at understanding and managing biological invasions. However, one of the limitations of our study is the inherent uncertainty associated with predictions from SDMs, particularly when applied to alien species (Elith et al. 2010; Thomas et al. 2024, and references therein). SDMs are built on occurrence data and environmental variables, assuming that the species' ecological niche remains constant across space and time (Elith and Leathwick 2009; Elith et al. 2010). However, alien species often undergo shifts in their realised niches as they exploit ecological opportunities unavailable to them in their native ranges (Battini et al. 2019). This can lead to over- or underestimation of suitable habitats, especially when models are transferred across regions or climates (Elith et al. 2010). Moreover, the quality and completeness of occurrence data can significantly influence model accuracy. Alien species are frequently underreported in newly invaded areas, and data may be biased toward easily accessible or well-surveyed locations. This spatial bias can skew model outputs and obscure the true potential for invasions. Numerous studies have highlighted the sensitivity of SDMs to both data quality and modelling choices. For instance, Farashi and Alizadeh-Noughani (2023) emphasise that uncertainties can arise from various sources, including species detectability, spatial resolution and the ecological relevance of predictor variables. Similarly, Rathore and Sharma (2023) provide a comprehensive review of SDM performance across ecological contexts, underscoring the variability introduced by different algorithms and data availability.

Lastly, research by Guisan and Thuiller (2005) and Elith and Leathwick (2009) further elaborate on the assumptions underlying SDMs and the challenges of projecting species distributions under novel conditions.

While species distribution models have limitations (as outlined above), our study demonstrates how a multi-source, integrative approach can help mitigate some of these limitations. By incorporating historical herbarium records, systematic field sampling, citizen science observations, structured questionnaires and remote sensing via Google Street View, we developed a spatially and temporally diverse dataset that should enhance model calibration and ecological inference. In constructing our SDMs, we took care to incorporate both the ecological characteristics and the invasion history of the focal species. We took this approach to try to ensure our models are not only statistically robust but also ecologically meaningful. By integrating these dimensions, our models aim to provide more realistic and actionable predictions of invasion risk for management. This aligns with recent recommendations in the literature, which emphasise the importance of ecological context and invasion dynamics in SDM applications for alien species (Hui 2023). Furthermore, given that our models are intended to inform decisions at moderate to large spatial scales, the influence of fine-scale uncertainties is likely to be minimal. As such, while local-scale variation may exist, it is unlikely to significantly affect the broader management recommendations we derived from our results.

We recognise that model transferability, data completeness and enforcement feasibility remain challenging, particularly at sub-national scales where dispersal dynamics and administrative boundaries intersect. Nonetheless, our findings provide a robust framework for aligning regulatory decisions with ecological evidence. The SDMs identified areas of high invasion risk and revealed mismatches between current regulatory designations and predicted climatic suitability—for example, in the North-West Province, where guava is regulated despite no evidence of naturalisation and low modelled suitability. These results underscore the potential of SDMs, when applied judiciously, to inform adaptive, spatially explicit management strategies. Ultimately, our approach contributes a replicable and policy-relevant methodology for improving the precision and effectiveness of alien species regulation.

Secondly, we did not include an analysis to assess the potential influence of climate change. Projections and recommendations need to be given over a timescale that is defensible and relevant to key stakeholders. In the context of guava cultivation, trees may live for 30–35 years, but commercial orchards typically begin fruiting after 3 years and are often replaced every 20 to 25 years due to declining productivity and increasing management challenges (Kanwal et al. 2016). Spatial models can and should be updated as conditions change and as the understanding of guava invasion ecology improves. Regulatory lists are currently updated every 2–4 years, but with new processes in places, more regular updating is feasible and desirable (Wilson and Kumschick 2024). Given it is important to landowners and businesses that regulations are not constantly changing, we recommend that the maps are updated every 10 years. This is in line with the proposal that the lifespan of risk analyses on alien taxa in South Africa should be 10 years (Kumschick et al. 2025).

Lastly, we have not yet engaged with stakeholders (e.g., municipality managers) to gauge the acceptability of our proposal. While there is provision in legislation for national-scale invasive species management plans, regulation of alien species has rarely been done at a municipal level in South Africa (Zengeya and Wilson 2023). We realise that this will present challenges for both legislation and implementation. We also have not quantified the costs of inaction, the costs of reactive control or the benefits guavas provide to different sectors. These are important aspects to consider when attempting to manage conflict generating invasive species. We hope our proposal will form a solid foundation upon which such analyses can be added.

Author Contributions

T.M., J.R.U.W., and D.M.R. conceived the idea. T.M. conducted the field-work. T.M., A.D., and K.T.F. analysed the data. T.M. led the writing of the manuscript draft, with input from all co-authors.

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Ethics Statement

The questionnaire was conducted under ethical clearance (SU project number: 10598) issued by Stellenbosch University.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All relevant data is contained in the manuscript's [Supporting Information](#).

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70102>.

Biosketch

This research team focuses on biodiversity, particularly in the context of invasive plant species and their ecological impacts. Our work explores the pathways and drivers of biological invasions, the role of human activity in shaping invasion dynamics and the development of tools to support decision-makers. By integrating ecological modelling, risk analysis and policy-relevant research, we aim to strengthen the scientific foundation for managing invasions and informing biodiversity conservation strategies.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ddi70102-sup-0001-DataS1.docx. **Table S1:** Responses to questions relating to the invasion of guava (*Psidium guajava*) in South Africa. We sent out the questionnaires at the end of March 2020, but, as not much feedback was received before the initial deadline (end of May 2022), the deadline was extended (until the end of July) and a reminder sent out in June 2022. We received a total of 18 usable responses by the end of the deadline. For most responses we could not categorise the sites to a level higher than naturalised (see Table 1 for data points that came from the questionnaires). **Table S2:** Principal component analysis (PCA) results showing the importance of each component. The table reports the standard deviation, proportion of variance explained and cumulative proportion of variance for the first eight principal components (PC1–PC8). PC1 explains the largest proportion of variance (47.28%), followed by PC2 (20.81%) and PC3 (17.13%), with decreasing contributions from subsequent components. **Table S3:** Pairwise niche overlap indices for *Psidium guajava* across cultivated, naturalised and invasive monoculture ranges. We calculated niche volumes, unique and shared components and centroid distances to assess overlap between cultivated populations and those that have naturalised or formed invasive monocultures. The table reports niche volume estimates, proportions of unique and overlapping space, Jaccard indices and centroid distances for each pairwise comparison. Cultivated populations occupy the largest niche space, with minimal overlap observed with invasive monocultures. **Figure S1:** Climatic niche overlap between cultivated, naturalised and invasive *Psidium guajava* populations. **Figure S2:** Average suitability maps showing the potential distribution of *Psidium guajava* across South Africa based on different occurrence datasets. Panel A uses records from the native range only. Panel B includes global occurrence records (including native) but excludes records from South Africa. Panel C incorporates global records (including native) along with records from South Africa. These maps illustrate how the inclusion of different data sources influences predicted climatic suitability. **Figure S3:** Response curves for each SDM model we constructed. Curves show how each environmental variable affects the Maxent prediction and how the predicted probability of presence changes each environmental variable is varied, keeping all other environmental variables at their average sample value. **Data S2:** ddi70102-sup-0002-DataS2.pdf. **Data S3:** ddi70102-sup-0003-DataS3.xlsx.