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Predicting the potential distribution of a previously undetected cryptic invasive synanthropic Asian house rat (*Rattus tanezumi*) in South Africa

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Abstract

Three species of *Rattus*, Norway rat (*R. norvergicus*), black rat (*R. rattus*) and Asian house rat (*R. tanezumi*) are currently known to occur in South Africa. The latter two species are cryptic and form part of the *Rattus rattus* species complex. Historically, *R. norvegicus* has been reported to occur along the coast and in urban centres, *R. rattus* is widespread in most urban areas, except in the drier areas, while *R. tanezumi* was only recorded to occur in the country (and Africa) *ca.* 15 years ago, and its distribution remains unknown. The aim of this study was to predict the potential distribution of *R. tanezumi* in South Africa and assess how it overlaps with that of *R. norvegicus* and *R. rattus* using species distribution modelling. *Rattus tanezumi* was predicted to mainly occur in most inland urban areas and along the coast. The distribution of *R. rattus* was as expected, in contrast, the predicted range of *R. norvegicus* was not restricted to the coast but also included inland urban areas. All three species showed broad potential distributional ranges that overlapped extensively indicating that their establishment and spread may be influenced by similar factors such as proximity to urban areas and a wet and moderate climate. These results allow insights into assessing their risk of establishment and for formulating appropriate intervention strategies for their management and control.

Key words: invasive rodents, rats, *Rattus*, commensal species, niche overlap, invasive range

Introduction

Three invasive synanthropic species of *Rattus*: the Norway or brown rat (*R. norvegicus*), the black, roof, house or ship rat (*R. rattus*) and the Asian, Oriental or Tanezumi house rat (*R. tanezumi*) are known to occur in South Africa (Bastos et al. 2011). The three

species may have been unintentionally introduced into South Africa and elsewhere globally, as stowaways on ships (Atkinson 1985; Long 2003). The advent of modern and extensive transport networks may also have facilitated recent introductions and dispersal through bridgehead invasions (Bastos et al. 2011; Lack et al. 2012). *Rattus norvegicus* is native to eastern Siberia,

northern China and Japan, *R. rattus* to India and southern Asia, and *R. tanezumi* to south-east Asia, Japan and Fiji (Aplin 2003; Musser and Carleton 2005).

Rattus norvegicus was first recorded in South Africa after the arrival of the first Europeans in 1832, while archaeological evidence from the Iron Age suggests that the occurrence of *R. rattus* may have preceded the arrival of Europeans (Davis and Fagan 1962; Avery 1985). *Rattus tanezumi* was first recorded to occur in South Africa (and Africa) *ca.* 15 years ago through a small mammal genetic profiling initiative (Bastos et al. 2011). It was already well established in several urban areas around the country and probably remained undetected because it is morphologically similar to *R. rattus*. The two species are part of the cryptic *R. rattus* species complex and are difficult to distinguish apart without genetic profiling (e.g. cytogenetic and DNA sequence data). In contrast, *R. norvegicus* is morphologically distinct from *R. rattus* and *R. tanezumi* because it has a relatively larger body size.

Historical distribution records of the three *Rattus* species in South Africa indicate that *R. norvegicus* is likely confined to urban areas along the coast while *R. rattus* is widespread in most urban areas around the country, except in drier regions (De Graaf 1981; Meester 1986; Skinner and Smithers 1990). The distribution of *R. tanezumi* in South Africa is largely unknown and an earlier attempt to predict its distribution using species distribution modelling (SDM) was unsuccessful because of low sample size and incomplete sampling in its native range (Bastos et al. 2011). There are few occurrence records of *R. tanezumi* available in South Africa mainly from urban areas (Bastos et al. 2011; Jassat et al. 2013; Archer et al. 2017, 2018; Julius 2013; Julius, Schwan, and Chimimba 2018; Julius et al. 2021a).

The three *Rattus* species are synanthropic and are known to live near, and benefit from human settlements. This synanthropic relationship with humans is believed to have evolved multiple times in south-east Asia because of their pre-adaptation to environmental disturbances caused by agricultural activities (Aplin et al. 2011). Several factors influence the proliferation of invasive rodent species in urban areas and these include provision of harbourage, lack of sanitation, readily available food and water, poor socio-economic and environmental conditions in some areas (e.g. informal settlements) that lead to over-crowding, poor quality housing, and inadequate public services such as waste disposal that often provide food and shelter for rodents (Feng and Himsworth 2014). In addition, invasive rodents have adaptive life-history traits such as high reproductive rates and relatively short periods to attain sexual maturity that have allowed them to successfully colonise modified habitats that characterise urban areas (Aplin, Chesser, and Have 2003).

The commensal relationship between invasive rodents and human settlements raises several concerns because the invasive rodents have been implicated in causing several health, environmental and socio-economic impacts (Hagen and Kumschick 2018). For example, several *Rattus* species are known to be reservoirs for zoonotic diseases (e.g. rat-bite fever, plague and leptospirosis; Kosoy et al. 2015; Julius et al. 2021b), are vectors of parasites [e.g. cestodes (*Hymenolepis diminuta, Hymenolepis nana* and *Inermicapsifer madagascariensis* and acanthocephalans (*Moniliformis moniliformis*; Julius 2013; Julius, Schwan, and Chimimba 2018; Julius et al. 2021a], cause damage to agricultural products (Kay and Hoekstra 2008), contaminate foodstuff (Singleton et al. 2003), cause damage to infrastructure (Kay and Hoekstra 2008) and have caused the extinction of indigenous biodiversity, especially on island ecosystems (Harris 2009). As a result, there have been several initatives to monitor and control rodent infestations in some urban areas in South Africa (e.g., de Masi, Vilaça, and Razzolini 2009; Jassat et al. 2013) but as observed elsewhere in the world, most of the interventions have been largely ineffective in part because of gaps in knowledge in the ecology, distribution, and impacts of the rodents in areas of introduction (e.g., Himsworth et al. 2013; Parson et al. 2017).

A major requirement for such control initiatives is baseline data on the distribution of invasive rodent species, which is essential to inform appropriate management interventions (Maas et al. 2020). SDM is a tool that can be used to gain insights into the risk of establishment and inform on decisions on how to manage and control invasive species (e.g. Sofaer et al. 2019). For example, SDM can be used to highlight areas with known introductions and the extent of the invasion, identify areas suitable for establishment but are still invasion-free that should be monitored for early detection (Lübcker et al. 2014; Khosa et al. 2019). SDM can also be used to facilitate the prioritisation of interventions targeting particular pathways, species and/or sites and provide foundational information required to inform regulations and policies to manage biological invasions (e.g. Faulkner et al. 2014). The aim of this study was therefore to predict the potential distribution of *R. tanezumi* in South Africa and assess how it overlaps with the known distributions of *R. norvegicus* and *R. rattus* in the country. It was predicted that *R. tanezumi* is likely to have a broad distributional range that overlaps extensively with that of *R. rattus* and *R. norvegicus* because the establishment and spread of the three species is influenced by similar environmental conditions such as proximity to urban areas and a wet and moderate climate.

Materials and methods

Environmental data sources

The dataset of environmental variables in this study comprised 19 bioclimatic variables (Table 1) that have been widely used in SDMs of invasive species (Hijmans et al. 2005; http://www.worldclim.org). These bioclimatic variables represent annual trends (e.g. mean annual temperature and annual precipitation), seasonality (e.g. annual range in temperature and precipitation) and either extreme or limiting environmental factors (e.g. temperature of the coldest and warmest months and precipitation of the wet and dry quarters). *Rattus* species are synanthropic and to account for the possible effects of human activities on their distribution, an additional variable, 'human footprint' was also included in the SDM process (Table 1). The human footprint dataset was acquired from 'The Last of the Wild' website (http://sedac.ciesin.columbia.edu/data/collection/wildareas-v1). It includes data on human population densities, infrastructure and access via roads and railways into populated areas. The predictive ability of SDMs is sensitive to the selection of environmental variables used to build the models and various procedures have been suggested to pre-select variables (e.g. Peterson and Nakazawa 2007; Zengeya et al. 2013; Lübcker et al. 2014). The current study took advantage of the in-built method of regularisation in MaxEnt that deals with the selection of environmental variables (regulating some to zero), and this application has been shown to perform well, and is considered to out-perform other pre-selection procedures (Elith et al. 2011).

Table 1: Environmental variables and their contribution (%) to model performance for the predicted distributional range of *R. norvegicus*, *R. rattus* and *R. tanezumi* in South Africa

Climatic variables	*R. tanezumi*	*R. norvegicus*	*R. rattus*
BIO1 = Annual mean temperature	0.9	0.2	4
BIO2 = Mean diurnal range (mean of monthly (max temp—min temp))	0.1	1.9	0.3
BIO3 = Isothermality (BIO2/BIO7) (*100)	27.1	3.6	6.7
BIO4 = Temperature seasonality (standard deviation * 100)	0	3.5	7.2
BIO5 = Max temperature of warmest month	1.2	1.9	0.4
BIO6 = Min temperature of coldest month	0.2	6.7	2.1
BIO7 = Temperature annual range (BIO5-BIO6)	3.0	11.5	8.2
BIO8 = Mean temperature of wettest quarter	0	0.1	0.8
BIO9 = Mean temperature of driest quarter	0.2	2.5	0.5
BIO10 = Mean temperature of warmest quarter	0	0.6	16.5
BIO11 = Mean temperature of coldest quarter	1.3	0.6	1.5
BIO12 = Annual precipitation	0.6	1.3	4.2
BIO13 = Precipitation of wettest month	0.3	0.3	0.1
BIO14 = Precipitation of driest month	43.3	3.2	0.8
BIO15 = Precipitation seasonality (coefficient of variation)	0.2	2.2	0.2
BIO16 = Precipitation of wettest quarter	0.8	0.1	0.2
BIO17 = Precipitation of driest quarter	0.1	2.1	0.4
BIO18 = Precipitation of warmest quarter	0.7	0.1	0.8
BIO19 = Precipitation of coldest quarter	1	0.6	25.3
Human footprint	19	57.2	20.1

Species data

Geo-referenced data for each of the three species of *Rattus* were obtained from the published literature (primarily from Mostert 2010 and Bastos et al. 2011) and biodiversity databases such as the African Rodentia database (http://projects.diversity.be/afri canrodentia/) and the Global Biodiversity Information Facility (GBIF) (http://www.gbif.org/). Occurrence data for *R. tanezumi* and *R. rattus* were restricted to specimens whose identity was genetically verified and had genetic sequences uploaded and publicly available on GenBank http://www.ncbi.nlm.nih.gov.

Model building

SDM was based on the maximum entropy algorithm that was implemented in MaxEnt modelling package (MaxEnt v. 3.33) that utilises associations between environmental variables and known occurrence records of species to predict potential areas where a given species is likely to occur (Phillips, Anderson, and Schapire 2006). MaxEnt has been shown to perform better than other correlative methods that use presence and background data (Elith et al. 2006). It has been successfully applied to a range of ecological disciplines that include ecology and evolutionary biology, impacts of climatic change (Araújo et al 2004), invasion biology and conservation biology (Peterson and Vieglais 2001; Peterson 2003).

For all SDMs, the algorithm's parameters were set to default with a maximum number of 500 iterations, a regularisation multiplier of 1, convergence threshold of 0.00001, test percentage = 0, and only hinge features were selected. Hinge features, the default setting of MaxEnt (Phillips and Dudik 2008), allow for simpler and more concise approximations of the true response of the species to the environmental variables (Elith et al. 2011), thus preventing over-fitting of the model without significantly increasing the complexity of models and hence improve model performance (Phillips, Anderson, and Schapire 2006). Several different methods have been used to select thresholds of occurrence, and the choice of an appropriate method is dependent on the type of data that are available and the question the study intends to address (Phillips, Anderson, and Schapire 2006; Pearson 2007; Elith et al. 2011). In this study, model output was set to logistic format and an equal training sensitivity and specificity threshold rule of 0.5 was applied.

Background selection

MaxEnt uses the presence and pseudo-absences or background localities to project potential SDMs. The extent of the background is known to influence model performance, where a broad background can cause over-estimates and a constrained background can cause under-estimates (van der Wal et al. 2009; Anderson and Raza 2010). In the current study, the background extent for each species of *Rattus* was limited to areas that had similar climates to known occurrence records from the native and introduced ranges for each respective species. Following Thompson et al. (2011), this was achieved by overlaying the recent Köppen–Geiger climate classification system (Kottek et al. 2006) with a defined species range. The Köppen–Geiger polygons identify areas with similar climates (climate zones) and a given climate zone was included as part of the background if it contained an occurrence record within the respective range of each species of *Rattus* using ArcGIS® v. 10.0 (ESRI 2011). By selecting the entire climatic zone, an intermediate background size was obtained, compensating for areas with few occurrence records (van der Wal et al. 2009; Jiménez-Valverde et al. 2011). The potential SDM for each species was then calibrated with 10 000 pseudo-absence points drawn at random from its defined occurrence range. Ten niche models were then constructed for each species of *Rattus* and in each SDM, all occurrence records were partitioned using the statistical package R (R Core Team 2021) into a calibration set (training set) and a testing set (validation set) using *k*-fold partitioning (Phillips, Anderson, and Schapire 2006). Average model performance was obtained by repeating the process for 10 iterations, and a consensus map was then created as an average of the 10 native range projection maps.

Model evaluation

The accuracy of the SDM was evaluated using the receiver operating characteristic curve (ROC) (Swets 1988; Fielding and Bell 1997). The ROC plots correctly identified presence data at a given locality (sensitivity) against wrongly classified cases (1-specificity) for all possible thresholds and distinguishes between omission (i.e. predicted absence in areas of actual presence) and commission errors (i.e. predicted presence in areas of actual absence) (Fielding and Bell 1997). The resultant area under curve (AUC) gives an indication of the model performance, and the AUC values can range from 0 to 1 (Phillips, Anderson, and Schapire 2006). Following Thuiller et al. (2006), SDMs with AUC values between 0.8 and 0.9 were considered fair, 0.9–0.95 = good, and >0.95 = excellent.

The AUC is not necessarily an appropriate measure for presence-only model evaluation despite its wide use as a measure of model performance (Lobo, Jiménez-Valverde, and Real 2008). We, therefore, used the Continuous Boyce Index (CBI) (Boyce et al. 2002; Hirzel et al. 2006) to further evaluate our SDM outputs. The CBI evaluates the ability of habitat suitability models to predict the presence of a species in a given area. It is continuous, and values may range from −1 to 1, with negative values indicating models that predict worse than random, and positive values indicating models that are consistent with the present distribution in the evaluation dataset.

Variable responses were assessed using the in-built heuristic approach in MaxEnt that assesses the contribution of each variable to model performance in relation to an increase in gain in the model provided by each variable. In addition, a jack-knife analysis was done to determine the environmental variable that increased model performance the most when used in isolation (i.e. the most useful information by itself) and decreased model performance the most when it was omitted (i.e. the most information that was not present in the other variables) (Phillips 2017).

Niche similarity

Niche similarity among SDMs of the three species of *Rattus* from South Africa was estimated using ordination (Broennimann et al. 2012) in the *Ecospat* package in R (Di Cola et al. 2017; R Core Team 2021). Ordinations for quantifying niche overlap have been shown to perform better than other methods that use geographical projections derived from SDMs that are prone to bias associated with geographical dimensions (Broennimann et al. 2012). Niche overlap was quantified using Schoener's index of niche breadth (D). Indices may range from 0 (indicating that SDMs are completely different) to 1 (indicating that niche models are identical). The significance of the D values was then evaluated using null models of niche similarity. *Ecospat* quantifies niche similarity using several ordination techniques, but in this study, we only used principal component analysis (PCA-env) that was shown to consistently out-perform other ordination metrics of niche overlap (Broennimann et al. 2012).

For niche similarity, we tested the hypothesis that SDMs drawn from partially or entirely non-overlapping distribution of *R. tanezumi* and that of *Rattus* congeners in South Africa are more different or similar from one another than expected by random chance. This test was conducted by calibrating the PCA-env with introduced records of *R. tanezumi* but trained on a background randomly drawn from the predicted invasive range of *R. rattus*. The process was repeated by running a PCA-env based on known occurrence records of *R. rattus* and trained on a randomly drawn background from the invasive range of

R. tanezumi. This process was undertaken in either direction to generate 100 pseudo-replicate datasets for pairwise comparisons of the three species. The observed measures of niche similarity (D) were then compared with percentiles of these null distributions. If the observed overlap (D) was greater than 95% of the simulated values, the species occupied environments in their invasive ranges that are more similar to each other than expected by chance.

Results

Rattus tanezumi

The areas that were predicted as suitable for the occurrence of *R. tanezumi* were mainly inland areas in Gauteng and Mpumalanga Provinces, and along the coast in northeast (KwaZulu-Natal Province) and southeast (Eastern Cape Province) regions of the country, and partly in the south (Western Cape Province) (Fig. 1a). The variables that contributed most to model performance were precipitation of driest month (43%), isothermality (27%) and human footprint (19%) (Table 1). The SDM performance was good (AUC = 0.94; CBI = 0.99) (Table 2).

Rattus norvegicus

The areas that were predicted as suitable for the occurrence of *R. novergicus* were in urban areas of most provinces in South Africa, but these were most pronounced in Gauteng, Mpumalanga, KwaZulu-Natal, Eastern Cape and Western Cape Provinces (Fig. 1b). The environmental variables that contributed most to model performance were human footprint (57%) and temperature annual range (11.5%) (Table 1). The SDM performance was excellent (AUC = 0.96; CBI = 1.0) (Table 2).

Rattus rattus

The potential distribution of *R. rattus* was predicted mainly for the coastal areas of the Western Cape, Eastern Cape and KwaZulu-Natal Provinces (Fig. 1c). The interior areas of South Africa included urban areas of Gauteng, Mpumalanga, Limpopo and Free State Provinces. The environmental variables that contributed most to SDM performance were precipitation of coldest quarter (25%), human footprint (20%) and mean temperature of warmest quarter (17%) (Table 1). The SDM performance was fair (AUC = 0.89; CBI = 1.0) (Table 2).

Niche overlap and similarity

The predicted potential distributional range of *R. tanezumi* in South Africa showed significant (P < 0.05) pairwise niche overlaps with the invasive ranges of the other two *Rattus* congeners (Table 3). Niche overlap was most pronounced between *R. tanezumi* and *R. rattus* (D = 0.67), followed by *R. rattus* and *R. norvegicus* (D = 0.65), and the lowest overlap was observed between *R. tanezumi* and *R. norvegicus* (D = 0.50).

Discussion

Predicted distribution of the three Rattus species in South Africa

Three invasive *Rattus* species, *R. norvegicus, R. rattus* and *R. tanezumi*, are known to occur in South Africa but there is disproportionate occurrence data to infer their distribution (Bastos et al.
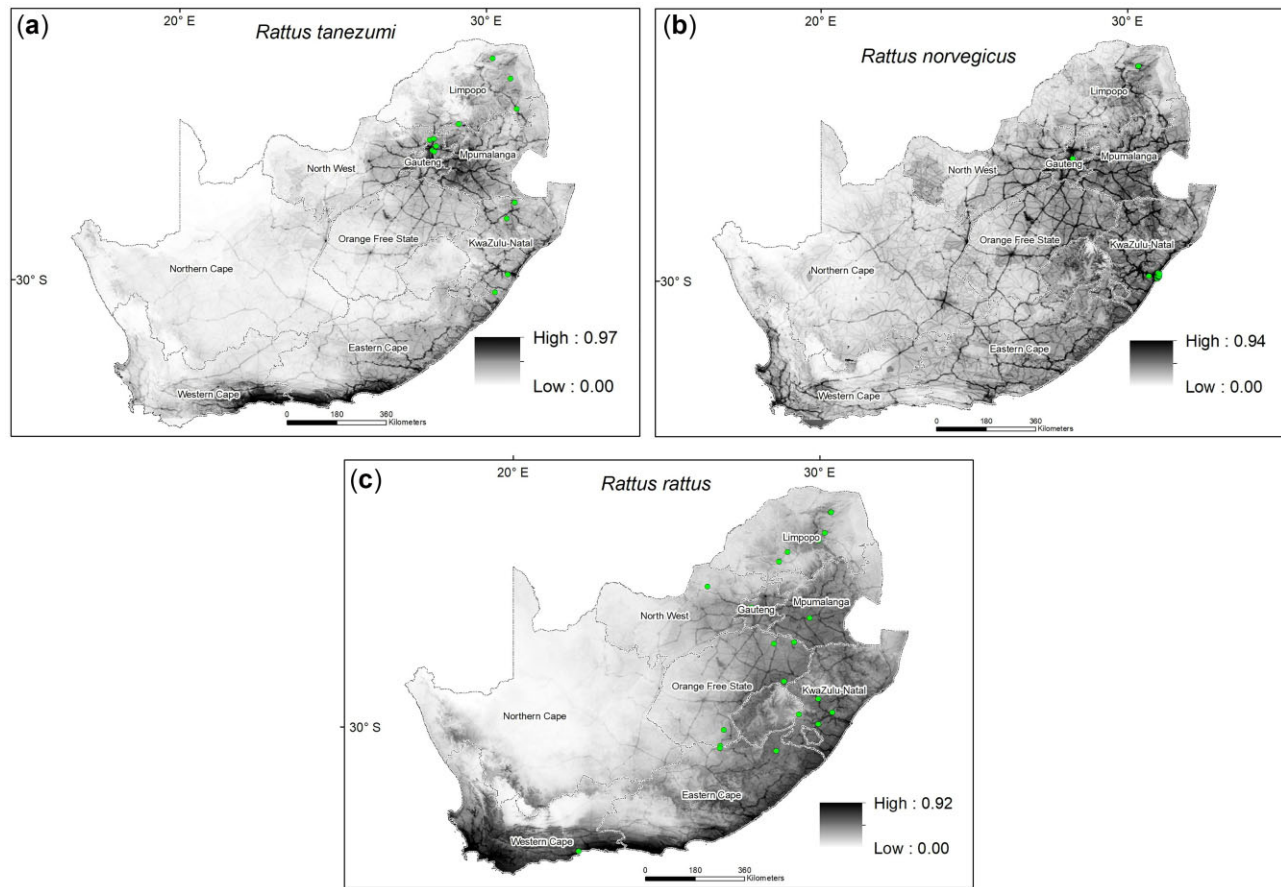
Figure 1: The projected invasive range of (**a**) *R. tanezumi*, (**b**) *R. norvegicus* and (**c**) *R. rattus* in South Africa. Known occurrence records are indicated by circles, and potential distribution is indicated by shaded areas, with darker and lighter colours indicating high and low probabilities of suitable conditions, respectively

Table 2: Average model performance evaluated using the maximum test AUC and the CBI of Predicted (P) and Expected (E) ratios for the invasive synanthropic *R. tanezumi*, *R. rattus* and *R. norvegicus* in South Africa

Species	Test AUC	Boyce index	
		P/E ratio	P-value (Spearman's ρ)
Rattus tanezumi	0.94 ± 0.02	0.99	<0.001
Rattus norvegicus	0.96 ± 0.01	1.00	<0.001
Rattus rattus	0.89 ± 0.00	1.00	<0.001

2011). There is relatively more historical occurrence data for *R. rattus* and *R. norvegicus* that have been used to infer their potential distribution but occurrence records for *R. tanezumi* are minimal and its distribution is largely unknown. This study predicted that *R. tanezumi* is likely to have a broad distributional range that overlaps extensively with that of *R. rattus* and *R. norvegicus* because the establishment and spread of the three species is influenced by similar environmental factors. There was evidence to support this assertion, as all three species were predicted to have a wide distributional range that is largely influenced by proximity to urban areas and a wet and moderate climate.

The predicted distribution of *R. tanezumi* in South Africa shows an invasive potential over most inland urban areas and around the coast. The first attempt to predict the distribution of

R. tanezumi in South Africa was hampered by low sample sizes of occurrence records used to train the species distribution models (Bastos et al. 2011). The low number of occurrence records for *R. tanezumi* was probably due to incomplete sampling in its native range (Bastos et al. 2011). In this study, the number of occurrence records was increased by sourcing records from global biodiversity databases such as the African Rodentia database and the Global Biodiversity Information Facility (GBIF) and from recent studies (Julius 2013; Julius, Schwan, and Chimimba 2018; Julius et al. 2021a, b). In addition, the occurrence data for the two cryptic species, *R. tanezumi* and *R. rattus*, were restricted to specimens whose identity was genetically verified. This enabled models to potentially differentiate the projected invasive ranges of the two species and avoid confounding models that were based on incorrectly identified specimens. The two species are difficult to identify morphologically because of similarities in their external and cranial morphology (Balakirev and Roshnov 2012). However, they can be identified genetically by assessing their diploid numbers (*R. tanezumi*: $2n = 42$; *R. rattus*: $2n = 38$) (Conroy et al. 2013) and mitochondrial DNA data (Robins et al. 2007). In addition, *R. tanezumi* and *R. rattus* are known to hybridise easily making morphological identification difficult in admixed populations (Conroy et al. 2013).

Rattus norvegicus and *R. rattus* were also predicted to occur in most urban areas around the country, except in drier areas. This observation agrees with previous assertions that indicate that the drier part of the country may be unsuitable for their

Table 3: Niche overlap (based on Schoener's index of niche breadth) and niche similarity of projected invasive distributional ranges of synanthropic *R. tanezumi*, *R. rattus* and *R. norvegicus* in South Africa

Species A	Species B	Niche overlap	Niche similarity	
			Invasive range (species A) → background (species B)	Background (species A) → invasive range (species B)
R. tanezumi	*R. rattus*	0.67	0.01	0.01
R. tanezumi	*R. norvegicus*	0.50	0.01	0.02
R. rattus	*R. norvegicus*	0.65	0.01	0.01

establishment (De Graaf 1981; Meester 1986; Skinner and Smithers 1990). For example, *R. norvegicus* is known to prefer wet environments and is usually found near sources of water (Innes 2005; Harper, Dickinson, and Seddon 2005). It also prefers areas affected by anthropogenic disturbances such urban and agricultural landscapes (Traweger et al. 2006), and less likely to occur in natural undisturbed habitats such as forested areas (Innes et al. 2001). *Rattus rattus* on the other hand can occur in urban, peri urban and natural environments that are adjacent to urban areas (Tamayo-Uria et al. 2014). The ability of *R. rattus* to exploit a wider range of habitats makes it among the most widespread and often most abundant *Rattus* species in areas of introduction (Innes 2005; Conroy et al. 2013).

The projected distribution of *R. norvegicus* differs from historical reports that indicated a restricted occurrence along the coast (De Graaf 1981; Skinner and Smithers 1990). Its projected distributional range encompasses inland urban areas including in Gauteng and Limpopo Provinces where its presence has been confirmed. *Rattus norvegicus* may have become established in South Africa after at least two independent introductions (Bastos et al. 2011) and its spread inland may have been through bridgehead invasions that where faciliated by modern and extensive transport networks developed to facilitate the movement of goods and people, as has been observed elsewhere for the dispersal of other *Rattus* species (Aplin et al. 2011). For example, in China, *R. tanezumi* expanded its range from coastal areas where it was initially introduced through shipping to inland areas through improved river and land transport networks (Guo et al. 2019).

Niche overlap among three Rattus species in South Africa

All three species had broad potential distributional ranges that overlapped extensively indicating that they are likely to co-occur in their invasive ranges. The high niche overlap between *R. tanezumi* and *R. rattus* is not surprising because the two species are cryptic and form part of the *R. rattus* species complex and have overlapping native ranges (Aplin et al. 2011). In South Africa, *R. tanezumi* and *R. rattus* were observed to occur in sympatry at several sites (Bastos et al. 2011; Ramatla et al. 2019). Such niche overlap may not only be limited to species of *Rattus* but also with native murid rodents such as species of *Mastomys*, which are also considered to be synanthropic. Local displacement of native species by invasive species may gradually occur in areas where indigenous synanthropic species co-occur with invasive species (Cavia, Cueto, and Suárez 2009; Taylor et al. 2012). For example, *R. rattus* is known to compete with native rodent species for food resources (Gales 1982), and with birds and bats for nesting sites in tree hollows (Threlfall, Law, and Banks 2013). Competition for resources may also be prevalent among

the three *Rattus* species. For example, *R. norvegicus* that has been reported to out-compete and displace *R. rattus* because of its relatively larger body size and aggressive nature (Musser and Carleton 2005; Lack et al. 2012). *Rattus tanezumi* can displace other *Rattus* species through scent-marking, which is strong enough to repulse even the larger and aggressive *R. norvegicus* (Guo et al. 2019).

It is also possible that when they occur in sympatry, the *Rattus* species can co-exist through niche complementarity. For example, in New Zealand, sympatric populations of introduced *R. norvegicus* and *R. rattus* can co-exist in part due to the partitioning of food sources (Harper, Dickinson, and Seddon 2005). In addition, co-existence between *R. rattus* and *R. norvegicus* can be achieved through differences in habitat use—*R. rattus* is an adept climber, often prefers elevated locations such as the upper floors of buildings, roofs and ceilings that are not preferred by *R. norvegicus* (Foster 2010). In contrast, *R tanezumi* can be found both indoors, and in outdoor habitats such as agricultural fields and forests (Stuart, Singleton, and Prescott 2015). In South Africa, the three *Rattus* species occur in sympatry in urban areas, especially in informal settlements where there is a diverse range of available resources such as food and shelter (Bastos et al. 2011). It is possible that the three species are able to co-exist through niche partitioning, but this still needs to be evaluated.

Conservation implications

The SDMs developed in this study highlight that the distribution of the three invasive *Rattus* species may be widespread around the country in contrast to previous estimates of the species distribution that indicated that some of the species might have restricted distribution. The models also show that confirmed occurrences are limited and are mainly localised in urban areas. This highlights the need for long-term monitoring efforts to ground truth results from the SDMs and to generate comprehensive occurrence datasets. Understanding trends in the distribution of species are important if the effective management of interventions are to be monitored and their potential impact is predicted (Zengeya and Wilson 2020). In South Africa, alien species are managed through the National Environmental Management: Biodiversity Act (NEM: BA) (Act 10 of 2004) and the Alien and Invasive Species Regulations of 2014, as recently revised in 2021. The management measures include interventions directed at restricting the importation of high-risk alien species, regulating the movement and utilisation of alien species and interventions aimed at eradicating species that occur in low numbers over limited areas, containing invasions, and reducing the extent and impact of well-established invaders (van Wilgen et al. 2020). The three *Rattus* species are currently not listed in the regulations for the mainland but are listed on South Africa's

offshore islands as species that must be controlled and cannot be traded or otherwise allowed to spread. The evidence base for these regulations is being improved, and processes are underway to compile science-based risk analyses to inform the regulations (see Kumschick, Foxcroft, and Wilson 2020, Kumschick et al. 2020). As part of this process, it has been recommended that the three *Rattus* species should be listed both on the mainland and offshore islands as species that need to be controlled, were possible eradicated on offshore islands (SANBI 2021). The SDMs developed in this study could therefore be used as tools to gain insights into the risk of establishment which can inform decisions on how to manage and control populations of the three *Rattus* species in South Africa.

Acknowledgements

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