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Strengthening ecologically based rodent management in the Philippines using maximum entropy (MaxEnt) predictions

Diane Shiela C. Castillo[1,2] and Motoki Higa[3]

[1]Kuroshio Science Program, Graduate School of Integrated Arts and Sciences, Kochi University, Kochi, Japan; [2]Department of Environmental Science, College of Science, Central Luzon State University, Science City of Muñoz, Philippines and [3]Faculty of Science and Technology, Kochi University, Kochi, Japan

Research Article

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Corresponding author:
Diane Shiela C. Castillo;
Email: dianeshielacastillo1020@gmail.com

Abstract

Rattus species pose a significant threat to the Philippines, causing substantial economic losses in agriculture and posing health risks to humans. While Ecologically Based Rodent Management (EBRM) has been developed to mitigate rodent outbreaks, its implementation is challenging, particularly in the face of climate and land use changes. In this study, we aimed to potentially enhance EBRM strategies by utilizing a high-performing modelling approach, MaxEnt, to predict the habitat suitability for *Rattus* species in the Philippines. This study revealed that forested areas exhibit high suitability for *R. tanezumi, R. exulans,* and *R. everetti*, with a notable degree of similarities in their habitat suitability. Furthermore, the model predicted that *R. argentiventer*, a species with no records in the mainland of Luzon, could potentially find suitable habitats in some areas of these regions, particularly in Central Luzon. Conversely, *R. norvegicus* was predicted to be highly suitable for areas with high-human population density, such as urban cities. The predictive model deepens our understanding of the interactions between *Rattus* species and their environments across the Philippines, which is crucial for identifying high-risk areas that require immediate intervention. These results have the potential to enhance the EBRM approach more effectively on a national scale. The EBRM strategy based on the predictive outcomes of the MaxEnt model is not only crucial for the Philippines but also serve as a guiding framework for other regions facing similar challenges with rodent populations.

Introduction

Rodents belonging to the family Muridae are the largest and one of the most fascinating groups of mammals (Krebs 2014, Heaney 2004, Heaney *et al.* 1998). The *Rattus* is the most diverse genus of rodents, with over 60 currently recognized species worldwide (Musser & Carleton 2005). Most *Rattus* species are restricted to natural habitats within their native ranges, but some species thrive in highly disturbed habitats (e.g., urbanized areas). Thus, many species have become agricultural and urban pests (Stuart *et al.* 2015, Aplin *et al.* 2003) and essential vectors of numerous pathogens that can be transmitted to humans and animals (Keesing & Ostfeld 2021, Meerburg *et al.* 2009). In the Philippines, *Rattus* species are a major pest of pre-harvest crops in the country, causing significant yield loss and financial hardship for smallholder farmers (Wondifraw *et al.* 2021, Brown *et al.* 2008, Singleton 2003). In addition, the country often suffers from rodent disease outbreaks, for instance, and the most significant one leptospirosis (Mendoza & Rivera 2019, Villanueva *et al.* 2014), causing the loss of many human lives in the country. The increased pressure on the food supply and the risk of disease emergence potentially caused by *Rattus* species has attracted more attention and become one of the central research priorities in the Philippines.

To address challenges posed by rodents, a holistic approach called *Ecologically Based Rodent Management (EBRM)* was developed (Singleton 1997). The EBRM is a widely accepted paradigm for rodent pest management that integrates three essential aspects: ecological, taxonomic, and socio-economic studies (Singleton *et al.* 2021). As the title implies, effective rodent management requires understanding rodent species' basic biology, spatial behaviour, and breeding ecology of rodents (Singleton *et al.* 2021, Singleton *et al.* 2007, Singleton 1997). This approach aims to maintain tolerable populations by reducing the availability of food and water, removing nesting/burrowing sites, and creating barriers to limit rodent movement (Singleton *et al.* 2007). EBRM has been implemented in the Philippines (Singleton *et al.* 2021, Brown *et al.* 2017) and various Asian countries, Australia, and eastern Africa (Singleton *et al.* 2010). It has been reported to be effective through coordinated community actions of smallholder farmers in countries like Indonesia, the Philippines, Vietnam, Myanmar, and Lao PDR (Herawati & Purnawan 2019, Brown *et al.* 2008, Palis *et al.* 2008, Brown *et al* 2006).

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The EBRM approach is effective across a variety of agricultural settings (Singleton *et al.* 2021, Brown *et al.* 2020) and more sustainable and environmentally friendly than chemical-induced techniques. However, implementing and monitoring EBRM may present significant challenges (Makundi & Massawe 2011), especially on a large scale. These challenges likely arise from the high adaptability of certain rodent species to climate and environmental changes (Auffray *et al.* 2009). Additionally, Jäkel *et al.* (2017) suggested that while EBRM has proven effective in managing rodent populations, there is now a need to develop models capable of predicting when and where rodent populations might occur. In response to these concerns, integrating modelling techniques for assessing species potential habitat and population dynamics could enhance the management of rodent pests, not just in agricultural contexts but also in varied landscapes experiencing climate and land use changes. Given the complexity and cost associated with understanding the ecological factors influencing rodent populations, developing a predictive model emerges as an essential tool. Such a model may help identify areas requiring immediate intervention and facilitate proactive management efforts.

In the realm of ecological modelling, species distribution models (SDMs) and population dynamics models have gained wide acceptance for their roles in conservation and management. SDMs, especially, are valued for their empirical approach to correlating species observation records with environmental predictors, using statistically or theoretically derived response surfaces (Kuloba *et al.* 2015, Elith *et al.* 2011). Their lower demands for extensive data, both in quality and quantity, render SDMs an efficient and cost-effective choice for enhancing EBRM strategies compared to other modelling tools. Among various SDMs, maximum entropy (MaxEnt) stands out for its consistently high predictive accuracy relative to other modelling approaches (Merow *et al.* 2013). MaxEnt's user-friendly nature (Khan *et al.* 2022), along with its ability to produce reliable results even with limited occurrence records (e.g. Moua *et al.* 2020, Nguyen *et al.* 2019, Papeş & Gaubert 2007, Pearson *et al.* 2007), makes it particularly valuable tool. Furthermore, MaxEnt's ability to model complex ecological relationships (Kaky *et al.* 2020, Elith *et al.* 2006) enhances its utility in rodent ecology, especially in understanding how climate and environmental changes impact rodent populations. MaxEnt has been widely applied to model a diverse array of species globally, particularly for managing pest species (Qin *et al.* 2021, Gutiérrez *et al.* 2016), optimizing vector control efforts (Dicko *et al.* 2014), assessing the potential distribution of invasive pests under climate change (Tang *et al.* 2021), and addressing forest pest concerns (Wei *et al.* 2022).

Extensive field surveys have established the habitats, distributions, and ecological information of some *Rattus* species in the Philippines. These comprehensive details are essential for implementing effective EBRM strategies. Despite existing efforts, there remains an urgent need for detailed studies that apply habitat-based statistical analyses to re-evaluate our understanding of the ecological patterns of rodent species. This critical gap in research represents a significant opportunity for advancing ecological knowledge and management strategies within the national context, an area that has not been explored to date according to our knowledge. Thus, our study is guided by three primary objectives: Firstly, to employ the MaxEnt model using museum records to generate habitat suitability models for selected *Rattus* species and analyse the habitat suitability similarities among these species. Secondly, to identify regions where conditions might be favourable for the *Rattus* species, highlighting potential high-risk areas for possible infestation. Lastly, to offer a cost-effective and practical method for enhancing the EBRM strategy based on the predictive outcomes of the MaxEnt model.

Materials and methods

Study area

The Philippines, an archipelagic Southeast Asian country in the western Pacific Ocean (Figure 1), is a critical study area for rodent research, particularly because rice is fundamental to the nation's cultural heritage (Zapico *et al.* 2020), economic stability (Silva & Ramisch 2018), and food security (Stuecker *et al.* 2018). Recognizing this, the country dedicates considerable resources to studying the effects of rodents on rice crops and the effectiveness of control measures against rodent-borne diseases (e.g., Lorica *et al.* 2020, Jones *et al.* 2017, Meerburg *et al.* 2009).

Species records and environmental data

The Philippines is home to three rodent families within the order Rodentia: Sciuridae (9 species), Hystricidae (1 species), and Muridae (64 species), the latter of which includes *Rattus* species (Heaney *et al.* 2010). Due to limited records with spatial coordinates for many *Rattus* species (fewer than 10 records), this study focuses on five *Rattus* species. Four are considered invasive: the Oriental Asian House Rat (*Rattus tanezumi* Temminck 1844), the Brown Rat (*Rattus norvegicus* Berkenhout 1769), the Polynesian Rat (*Rattus exulans* Peale 1848), and the Rice Field Rat (*Rattus argentiventer* Robinson & Kloss 1916). Additionally, one endemic species, the Philippine Forest Rat (*Rattus everetti* Gunther 1879), is included in the analysis. The former four invasive species are widely distributed and are the main rodent pest species in agricultural, agro-forest, and urban areas (Lorica *et al.* 2022, Syahputri & Priyambodo 2020, Heaney *et al.* 2016). Despite its status as an endemic species, *R. everetti* is also included in this study because it is frequently observed in upland agricultural areas (agro-forestry) and often found coexisting with some invasive *Rattus* species (Stuart *et al.* 2016).

The occurrence records of five *Rattus* sp. were obtained from various reputable sources to ensure a comprehensive data set for species model simulation. The primary source of data was the Global Biodiversity Information Facility (GBIF), widely accepted for biodiversity data. Supplementary records were retrieved from two other trusted sources: the synopsis of the Philippines Mammals (Heaney *et al.* 2010) and the University of the Philippines Los Baños-Museum of Natural History (UPLB-MNH). To ensure the quality and reliability of the data set, extensive data pre-processing and cleaning were conducted using the R package, "CoordinateCleaner ver 3.0" (Zizka *et al.* 2019) within R ver. 4.1.2 (R Core Team 2021). This involved removing records assigned to country or province centroids, open oceans, and locations of biodiversity institutions such as museums, zoos, and universities. Furthermore, records lacking precise coordinates but accompanied by locality descriptions were georeferenced using QGIS ver. 3.22 (QGIS 2021) following the recommendations of Wieczorek *et al.* (2004) to ensure the accuracy of these records. In total, the data set comprised 201 records for *R. everetti*, 170 records for *R. tanezumi*, 157 records for *R. exulans*, 29 records for *R. argentiventer*, and 23 records for *R. norvegicus* were obtained for the species model simulation (see Supplemental Figure S1).

The environmental data that were utilized for this study were 10-meter resolution of 10 categories of land cover map

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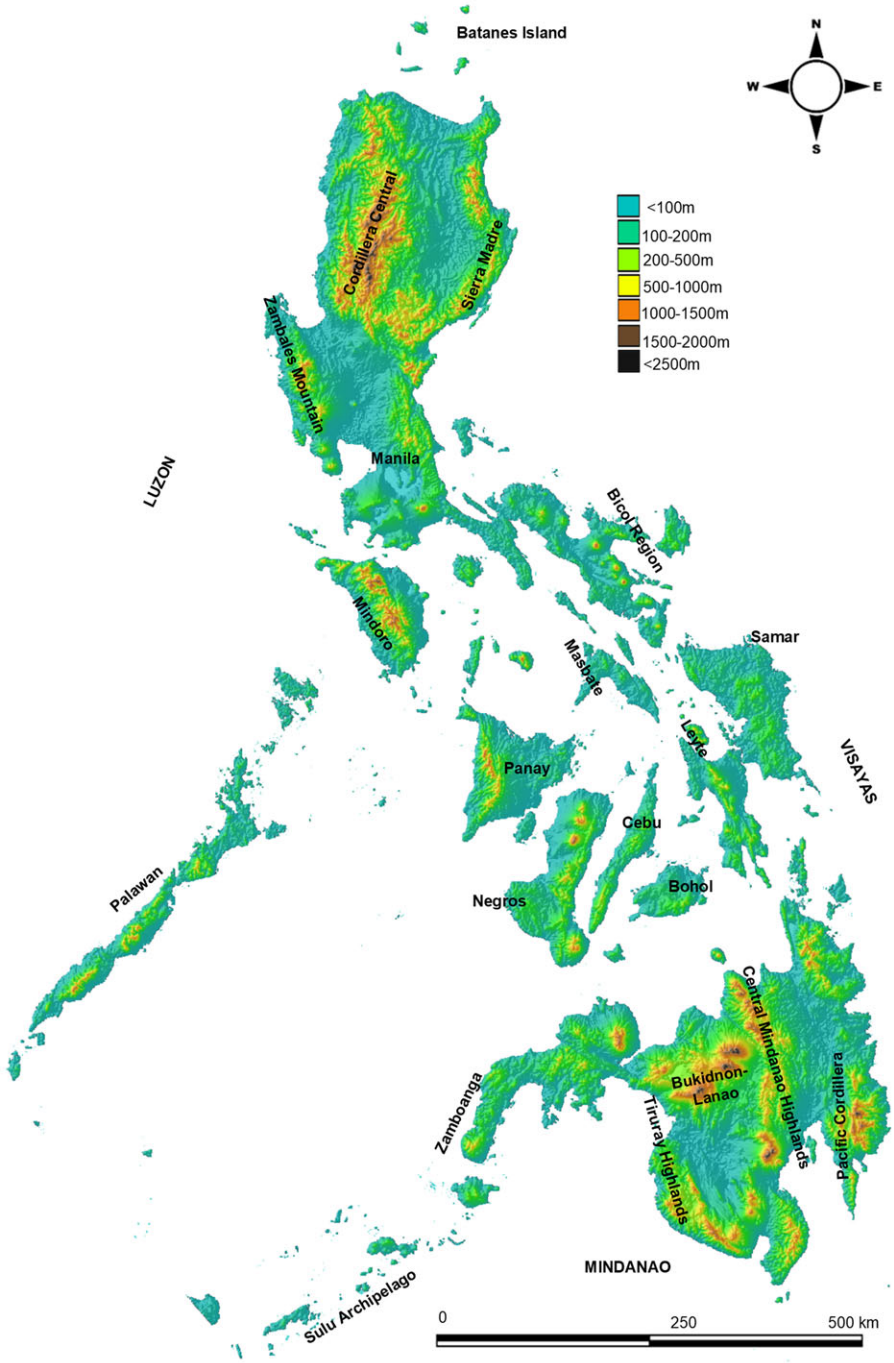


Figure 1. Philippine Physical Map (11°41'52.21' N 122° 37'18.32'E) showing major highlands in the primary groupings of the three islands (Luzon, Visayas, and Mindanao).
Source: Elevation Base Map retrieved from www.worldclim.org and processed in Quantum GIS ver.3.22.

(ESRI 2021); nineteen climatic variables with 30 seconds (~ 1 km^2 spatial resolution) (Fick & Hijmans 2017; retrieved from www.worldclim.org) and ~1 km^2 (1 km × 1 km) resolution of cumulative human pressure on the environment (Venter *et al.* 2018) (see Supplemental Tables S1 and S2). A package "multiColl ver. 2.0" (Salmerón *et al.* 2021) was used to check the cross-correlation of the thirty environmental variable predictors to ensure incorrect inferences and predictions will be avoided. A cut-off threshold was used to reduce the influence of highly correlated variables. The selection of environmental variables considered the following criteria: pairwise correlation coefficient |r| of >0.7; Condition Number (CN) of >30; Determination of Correlation Matrix (D) closer to 1 affirms no collinearity; and variance inflation factor (VIF) of >10 (see Dormann *et al.* 2013). These environmental data, including the species records, were processed in GRASS GIS to aggregate all data in ~1 km × 1 km spatial resolution.

Model development

The occurrence records of *Rattus* species may not be collected uniformly across their distribution range due to variations in data collection methods employed by different individual researchers. This selective sampling can result in an uneven distribution of

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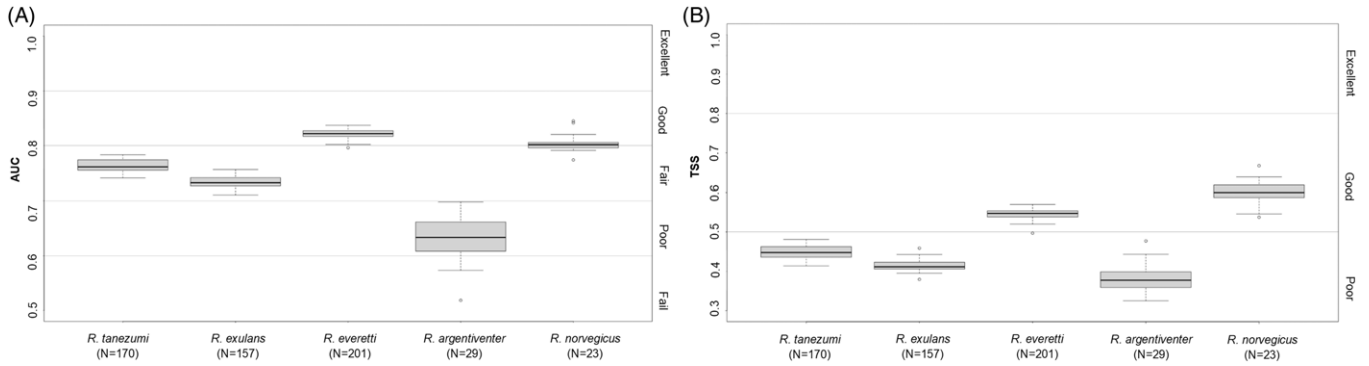


Figure 2. MaxEnt model performance evaluation for five *Rattus* sp. The figure indicates the area under the curve (AUC) (A) and True Skills Statistics (TSS) (B) evaluation for each *Rattus* species. The left y-axis of the figures denotes the range of AUC and TSS values of model metrics, while the right y-axis indicates the interpretation of the model metric values.

records across the country. To correct spatial sampling bias, we generated Gaussian Kernel Density map of occurrence records (Elith *et al.* 2010), as we had no information on the inherent bias of the data sets. This density map was used as bias file in MaxEnt to allocate 10,000 background sampling points across the study area. This method is commonly used to smooth out data point clusters for reducing sampling bias (Liu *et al.* 2018, Fourcade *et al.* 2014). MaxEnt employs a logistic regression algorithm to analyse the correlation between environmental variables and the occurrence (Merow *et al.* 2016, Elith *et al.* 2011, Phillips *et al.* 2006) of *Rattus* species. This analysis was further enhanced by employing the package "MIAmaxent ver.1.2" (Vollering *et al.* 2019), which aided in selecting important environmental variable predictors for each *Rattus* species. This package provides tools for user-controlled transformation of explanatory variables, selection of variables by nested model comparison and flexible model evaluation. This follows principles based on the maximum-likelihood interpretation of maximum entropy modelling (Halvorsen *et al.* 2015), and uses infinitely weighted logistic regression for model fitting (Fithian & Hastie 2013). This method ensures simpler yet effective models with reduced overfitting risk, focusing on variables that significantly enhance predictive accuracy for each *Rattus* species (Vollering *et al.* 2019).

This study used the MaxEnt modelling approach, specifically employing the "FLEXSDM ver. 1.3.0" package (Velazco *et al.* 2022), to build a predictive model for *Rattus* species. This method involved partitioning the data set for threefold cross-validation to maximize the efficiency of the data set for training and validation purposes. To further evaluate the model's robustness, 100 separate runs of each *Rattus* species model were conducted. The outcomes of these runs were then averaged together to create a single predictive map. This map represents the average predictive metric outcome across all 100 iterations, providing a more reliable measure of the model's performance. A sensitivity of 95% (Pearson *et al.* 2004) was used as the threshold dividing potential distribution areas and non-distribution areas. These potential distribution area maps were overlaid on the land cover map to identify regions where conditions might be favourable for the *Rattus* species, highlighting potential high-risk areas for possible infestation, particularly for invasive species.

The model's accuracy was assessed using two key metrics: the area under the curve (AUC) and True Skill Statistics (TSS). A value greater than 0.5 for the AUC metric suggests that the model's predictions are better than chance (Liu *et al.* 2018). As for the TSS metric, a value below 0.5 indicates poor model performance, while a value above 0.8 is considered excellent (Pramanik *et al.* 2018). Furthermore, we utilized Schoener's D metric to quantify habitat suitability similarities among *Rattus* species, ranging from 0 (no similarity) to 1 (complete similarity) (Schoener 1968).

Results

Model performance and environmental factors influencing Rattus *species*

Rattus tanezumi

The SDM performance for *R. tanezumi* ($N = 170$) was fair (AUC = 0.77 ± 0.01; TSS = 0.45 ± 0.02) (Figure 2). The model predicts that *R. tanezumi* is highly suitable in mountainous regions (forest areas) of the main Luzon island, including Mindoro and Palawan, as well as in Central and Western Visayas, Northern and Southern Mindanao (Figure 3-A). The key environmental variables influencing the habitat suitability of *R. tanezumi* as predicted by the model were mean annual temperature (BIO1), mean diurnal temperature range (BIO2), temperature seasonality (BIO4), precipitation of the wettest quarter (BIO16), precipitation of the driest quarter (BIO17), forest (LULC2), agricultural crops (LULC5), flood vegetation (LULC6), built-up/residential areas (LULC7), and cumulative human pressure on the environment (HFP) (Table 1). Among the *Rattus* species, *R. tanezumi* demonstrates a high degree of similarity in habitat suitability with *R. exulans* (Figure 4). The response pattern of *R. tanezumi* to the environmental variables is detailed in Supplemental Figure S2.

Rattus exulans

The SDM performance for *R. exulans* ($N = 157$) was fair (AUC = 0.73 ± 0.01; TSS = 0.41 ± 0.02) (Figure 2). This species and *R. tanezumi* exhibited similar environmental variables (Supplemental Figures S2 and S3), demonstrating a high degree of similarity in habitat suitability between these species when the data were collected (Figure 4). The environmental variables include mean annual temperature (BIO1), mean diurnal temperature range (BIO2), temperature seasonality (BIO4), precipitation of the wettest quarter (BIO16), precipitation of the driest quarter (BIO17), forest (LULC2), agricultural crops (LULC5), flood vegetation (LULC6), built-up/residential areas (LULC7), and cumulative human pressure on the environment (HFP) (Table 1). The response pattern of *R. exulans* to the environmental variables is detailed in Supplemental Figure S3.

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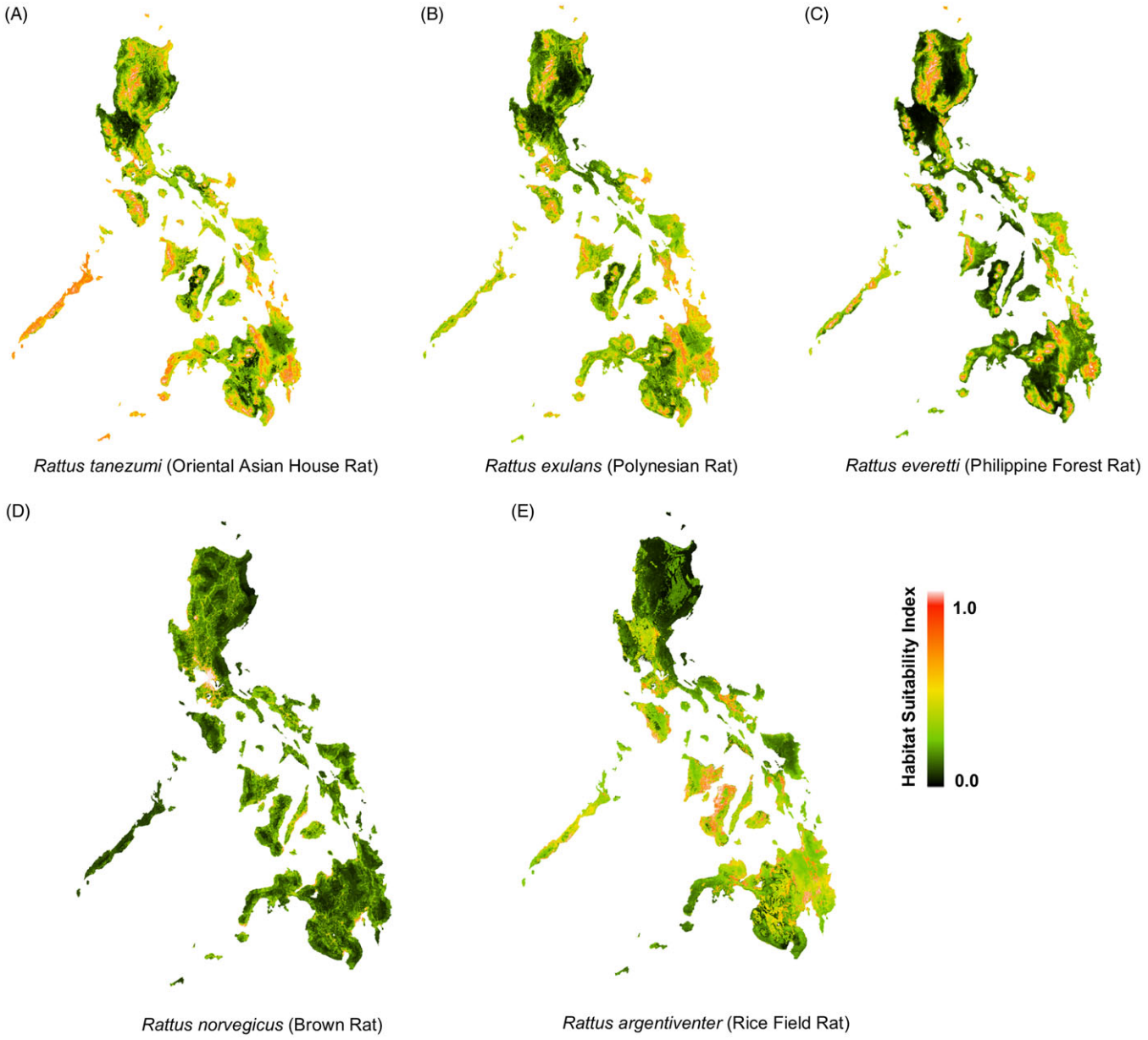


Figure 3. Predicted habitat suitability for five *Rattus* species in the Philippines.

Rattus everetti

The SDM performance for *R. everetti* ($N = 201$), the only endemic species in this study, was good (AUC = 0.82 ± 0.00; TSS = 0.54 ± 0.01) (Figure 2). The model predicts that the elevated and mountainous regions (forest areas) of Luzon, Visayas, and Mindanao are highly suitable habitats for this species (Figure 3-C). Conversely, the model predicted that lowland agricultural areas, primarily in Luzon and a few regions in Visayas and Mindanao, especially those characterized as prime agricultural lands around main urban areas and high population density areas, are unsuitable for *R. everetti* (Figure 3-C). The environmental variables influencing the habitat suitability of this species were mean annual temperature (BIO1), mean diurnal temperature range (BIO2), temperature seasonality (BIO4), precipitation of the driest quarter (BIO17), forest (LULC2), agricultural crops (LULC5), and cumulative human pressure on the environment (HFP) (Table 1). The *R. everetti* also demonstrates moderate similarity in habitat suitability with both *R. tanezumi* and *R. exulans* (Figure 4). The response pattern of *R. everetti* to the environmental variables is detailed in Supplemental Figure S4.

Rattus norvegicus

The SDM performance for *R. norvegicus* ($N = 23$) was fair (AUC = 0.79 ± 0.02; TSS = 0.58 ± 0.02) (Figure 2). *R. norvegicus* is predicted to be highly suitable in highly urbanized areas (e.g., Greater Metro Manila) in the Philippines (Figure 3-D). The environmental variables influencing the distribution of this species were agricultural crops (LULC5), built-up/residential areas (LULC7), forest area (LULC2), and cumulative human pressure on the environment (HFP) (Table 1). Compared to prior species, *R. norvegicus* exhibits a low degree of similarity in habitat suitability with the other *Rattus* species (Figure 4). The response pattern of *R. norvegicus* to the environmental variables is detailed in Supplemental Figure S5.

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Table 1. Important environmental variables most likely influence each *Rattus* species distribution and their endemicity and habitat preferences

Species	Environmental variables	Endemicity (IUCN 2022)	Habitat preference	Example references on recorded habitat preferences of *Rattus* species
Rattus everreti	BIO1, BIO2, BIO4, BIO17, LULC2, LULC5, HFP	Native/ Endemic	Primary forest, lowland montane, mossy forest, disturbed forest, lowland forest, agro-forest	(Heaney *et al*. 2016, Stuart *et al*. 2015, Stuart *et al*. 2012, Balete *et al*. 2009, Salibay & Luyon 2008, Ong & Rickart 2008, Rickart *et al*. 1993)
Rattus tanezumi	BIO1, BIO2, BIO4, BIO16, BIO17, LULC2, LULC5, LULC6, LULC7, HFP	Invasive	Cropland (low and upland), second-growth forest, lowland forest, montane forest, residential areas, and grassland/ shrub	(Reginaldo *et al*. 2021, Castillo & Paller 2018, Stuart *et al*. 2015, 2016, Morand *et al*. 2015, Rickart *et al*. 2011, Salibay & Luyon 2008, Ong & Rickart 2008)
Rattus exulans	BIO1, BIO2, BIO4, BIO16, BIO17, LULC2, LULC5, LULC6, LULC7, HFP	Invasive	Cropland (low and upland), second-growth forest, montane forest, residential, agro-forest	(Reginaldo *et al*. 2021, Morand *et al*. 2015, Shiels *et al*. 2014, Rickart *et al*. 2011; Ong & Rickart 2008, Rickart *et al*. 1993)
Rattus norvegicus	LULC5, LULC7, LULC2, HFP	Invasive	Mainly in cities, occasionally cropland, low forest elevations	(Salibay & Luyon 2008, Russell & McClelland 2022, Byers *et al*. 2019, Castillo & Paller 2018, Morand *et al*. 2015, Aplin *et al*. 2011)
Rattus argentiventer	BIO2, BIO4, BIO17, LULC2, LULC5, HFP	Invasive	Cropland, open grassland, and swampy grassland, seldom in high elevational areas of forest	(Cosson *et al*. 2014, Htwe *et al*. 2012, Singleton *et al*. 2010, Tristiani *et al*. 2003)

Note: Description of the abbreviated final environmental variables are as follows: BIO1-mean annual temperature; BIO2-mean diurnal temperature range; BIO4-temperature seasonality; BIO16-precipitation of the wettest quarter; BIO17-precipitation of the driest quarter; LULC2-forest trees; LULC5-crops; LULC6-flood vegetation (mixed with grass/shrub/trees/bare ground); LULC7-built up/residential areas; HFP-human footprint.

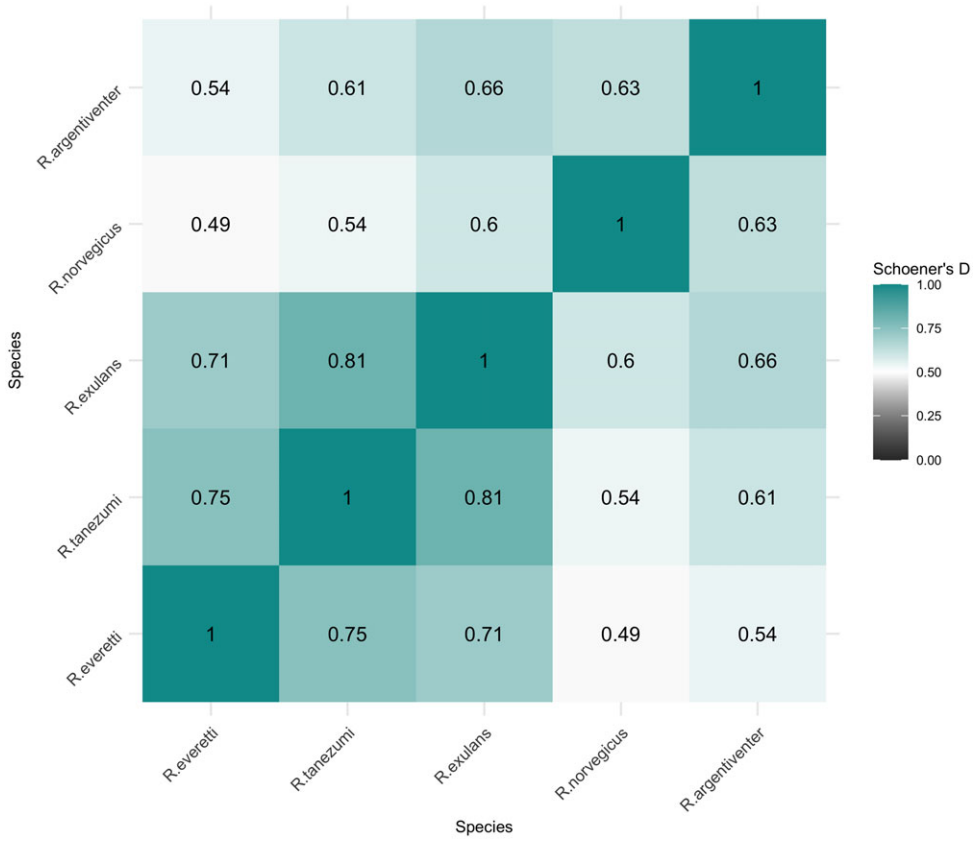


Figure 4. Habitat suitability similarity among *Rattus* species as determined by Schoener's D metric.

Rattus argentiventer

The SDM performance for *R. argentiventer* ($N = 29$) was poor (AUC = 0.63 ± 0.04; TSS = 0.39 ± 0.04) (Figure 2). The model predicts that *R. argentiventer* is likely suitable in most lowland areas in a few regions of Luzon island, including Palawan and Mindoro, Western Visayas, and several regions in Mindanao island (Figure 3-E). The environmental variables influencing the habitat suitability of this species were mean diurnal temperature range (BIO2), temperature seasonality (BIO4), precipitation of the driest quarter (BIO17), forest (LULC2), agricultural crops (LULC5), and cumulative human pressure on the environment (HFP) (Table 1). Similar with *R. norvegicus*, the *R. argentiventer*

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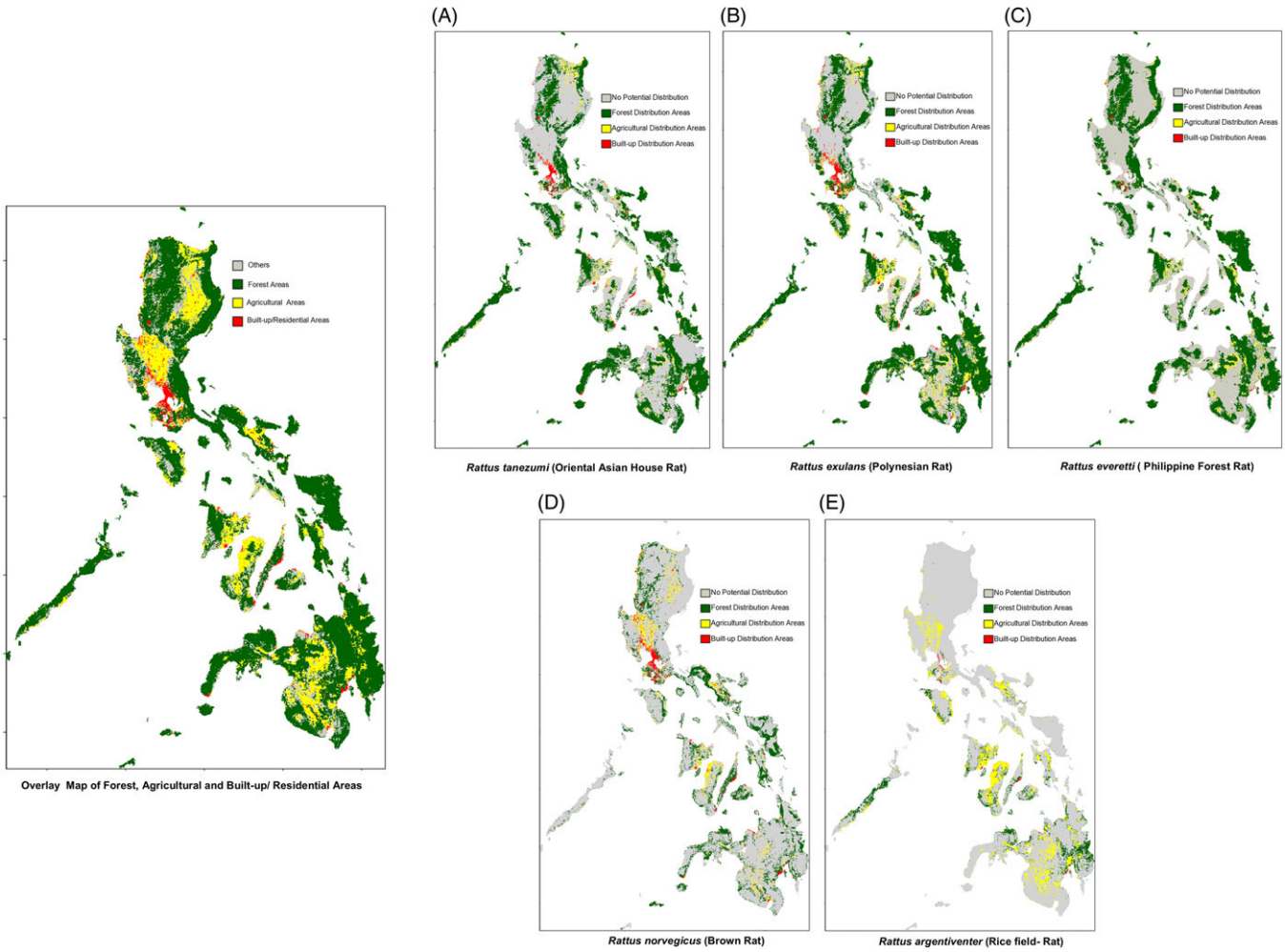


Figure 5. Land cover map and potential distribution maps of *Rattus* species. The distributional areas across different land cover types highlight the potential risk areas that may be infested by invasive species (*R. tanezumi, R. exulans, R. norvegicus,* and *R. argentiventer*), while also indicating areas that may be more favourable for native species (*R. everetti*). *Note*: The land cover map is derived from ESRI 2021 global-scale data and may exhibit discrepancies in land cover details at micro or finer scales.

exhibits a low degree of similarity in habitat suitability with the other *Rattus* species (Figure 4). The response pattern of *R. argentiventer* to the environmental variables is detailed in Supplemental Figure S6.

Potential infestation areas of Rattus *species at macro-scale level*

Figure 5-A indicates extensive forested regions across multiple islands are potentially at high risk for *R. tanezumi* infestation. Also, the species seems more likely to increase in numbers within agricultural areas of lower density compared to densely cultivated fields. Additionally, *R. tanezumi* may spread into residential and built-up areas, showing its distribution capacity in densely urbanized environments. Meanwhile, Figure 5-B indicates that *R. exulans* will likely to distribute in forested areas across various islands. Compared to *R. tanezumi*, *R.exulans* may be more likely to distribute in agricultural settings, especially in Mindanao, certain Visayan islands, and urbanized settings. Conversely, *R. everetti* may predominantly occupies extensive forest regions of the study area. The species also shows a tendency to expand in smaller-scale agricultural areas, but is not expected to spread into large, intensively farmed agricultural zones. Additionally, *R. everetti* may potentially distribute in less disturbed human environments within built-up areas (Figure 5-C). Meanwhile, Figure 5-D demonstrates that built-up/residential environments, particularly in highly urbanized areas, are at greater risk for the distribution of the *R. norvegicus'* population. Further, this species is also potentially put at risk of infestation in prime agricultural areas. This species also potentially proliferates lowland forest areas or edges of forest area. On the other hand, *R. argentiventer* exhibits potential for infestation across diverse agricultural environments, notably showing potential distribution in Central Luzon, a region currently lacking records of this species. It is also likely to proliferate along the edges of lowland forests but is not expected to pose a risk to denser forest areas. Additionally, *R. argentiventer* may potentially infest built-up/residential environments (Figure 5-E).

Discussion

The application of SDM, specifically utilizing the MaxEnt model, has significantly enhanced our understanding of habitat suitability for five *Rattus* species on a macro-scale, which may strengthen EBRM strategies. In this study, we developed and applied a MaxEnt model, utilizing museum records to assess the potential of predictive approach-based EBRM strategies. Our analysis provided

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detailed information on the habitat requirements and overlap areas at a national scale, which generally aligned with knowledge from detailed field surveys. In addition, we identified potential distribution areas for these species, which may help identify high-risk areas for infestation. These results suggest that the MaxEnt model's predictive approach enables a cost-effective method for reinforcing EBRM strategies, potentially facilitating the timely and effective management of rodent populations. The subsequent discussion provides a detailed examination of how this predictive modelling approach could enhance EBRM strategies based on the findings presented.

Predicted habitat suitability and similarity of five Rattus *species*

In this study, the model predicted that *R. tanezumi* and *R. exulans*, two invasive *Rattus* species, likely to find highly suitable habitats in mountainous regions (i.e., forest area) (see Figures 3-A, B), suggesting a broad distributional range. Building on insights from various studies in the Philippines, *R. exulans* and *R. tanezumi* have been observed in secondary growth forests, lowland forests (Stuart *et al.* 2016, 2015, Aplin *et al.* 2011, Ong & Rickart 2008), and even montane forests (Balete *et al.* 2009). Specifically, *R. exulans* has been recorded at elevations up to 1,925 meters (m) (Rickart *et al.* 2011), while *R. tanezumi*'s range extends from 1,495 m to 1,800 m (Rickart *et al.* 2011, Heaney *et al.* 1998). Moreover, these two *Rattus* species are recognized as principal pests affecting various agricultural crops (both lowland and upland) and some human settlements in the Philippines, as consistently documented by both historical and recent studies (e.g., Reginaldo *et al.* 2021, Stuart *et al.* 2016, 2015, 2012, Ong & Rickart 2008, Duque *et al.* 2005, Heaney *et al.* 1998, Fall 1977). However, the model underestimated their potential distribution across a broader range of agricultural areas, particularly in most parts of lowland agricultural settings (Figures 5-A, B). In the case of *R. tanezumi*, the presence and breeding biology of this species in agricultural settings are closely tied to crop phenology, specifically the developmental stages of rice crops (Stuart *et al.* 2015, Htwe *et al.* 2012). Possibly, relying solely on land cover and climatic data may not adequately capture this essential ecological driver. Additionally, the limited number of occurrence records (Stockwell & Peterson 2002) from museum collections available for this study may not adequately represent the full range this species could inhabit. This highlights the need to incorporate diverse, ecologically relevant variables and occurrence data more closely related to their distributions (Williams *et al.* 2012).

Contrary to invasive species, the model accurately identifies *R. everetti*, an endemic forest specialist, as unsuitable for lowland agricultural areas while indicating its high suitability across a wide range of forest habitats (see Figure 3-C). The model's predictions corroborate findings from several studies, which have recorded this species' preference for forest habitats and its typical absence from densely cultivated lowland agricultural areas (Heaney *et al.* 2016, Stuart *et al.* 2015). *R. everetti* has been documented thriving in a variety of forest areas up to a range of 1,605 to 1,690 meters (Rickart *et al.* 2011, Balete *et al.* 2009). Alongside the two invasive species, this study demonstrates that *R. everetti* overlaps in habitat with *R. tanezumi* and *R. exulans*, suggesting shared habitat preferences (see Figure 4). The observed moderate habitat overlap among the three species, as indicated by our findings, likely occurs in elevated mountainous or forested regions, predominantly within montane forests. This inference is based on the elevation range at which these species have been documented. In the Philippines, montane forests are generally found at elevations ranging from 900 up to 1600 m, with some areas extending up to 2,300 m on other islands (The Field Museum c. 2024) with varying temperatures across the regions. The model predictions, aligning with the species' preference for cooler areas (see Supplemental Figures 2 to 4). The *R. everetti's* tolerance for cooler temperatures aligns to its forest habitat specialization. Conversely, *R. tanezumi* and *R. exulans*' can adapt well across climates, thriving in both tropical (Aplin *et al.* 2011) and temperate environments (Motokawa *et al.* 2022, Ricardo *et al.* 2020), exhibiting their broad temperature tolerance. The climatic conditions that characterized by cooler temperatures and increased rainfall, may significantly impact plant community diversity and leads to more complex forest structures of tropical regions, such as Philippines. The habitat conditions of these areas may be advantageous for many *Rattus* species such as these three species, offering them improved shelter, diverse food sources, and perhaps a microclimate suited to their needs, as noted by Rickart *et al.* (2011) and Heaney (2008).

Given the habitat suitability among these three species does not indicate complete similarity or overlap (see Figure 4), it becomes apparent that there are underlying reasons for this distinction. For example, *R. tanezumi* (invasive species) tends to exhibit specific microhabitat preferences in the presence of *R. everetti* (native species) (Stuart *et al.* 2016). In the absence of *R. everetti*, *R. tanezumi* utilizes a broader range of habitats, as it no longer needs to avoid areas dominated by the competitively superior *R. everetti*. As Stuart *et al.* (2016) suggested, this can be more closely associated with the significant impact of competitive pressure, such as aggression and territorial behaviour, exerted by native species on the habitat selection and resource use of invasive species. This interference competition may also be observed between *R. exulans* and *R. everetti*. Contrarily, some studies suggest that the coexistence of these three *Rattus* species could harm native rodent populations. Human-induced habitat alterations create highly disturbed environments (Salibay & Luyon 2008, Heaney *et al.* 2006, Heaney *et al.* 1998, Rickart 1993), which negatively impact and displace native species while inadvertently promoting the survival and proliferation of invasive pests (Rickart *et al.* 2011, Ong & Rickart 2008, Rickart *et al.* 2007). Considering these, it has been suggested that reducing habitat disturbances could enhance native rodent populations and effectively manage invasive *Rattus* species (Stuart *et al.* 2016, Banks *et al.* 2012).

On the other hand, the other two invasive *Rattus* species, *R. norvegicus* and *R. argentiventer*, which have fewer records in this study, are more likely predicted by the model to show preferences for lowland areas (i.e., urban areas and prime agricultural lands), as illustrated in Figure 3-D and E. This is further supported by Figure 4, which demonstrates significant dissimilarities in habitat suitability compared to the previously mentioned three species. Specifically, the *R. norvegicus*, is predicted to be highly suitable for urban areas, showing low suitability in denser agricultural areas and forested regions (see Figure 3-D). This species is known to adapt well to living alongside humans and is often found in dwellings and other buildings, especially in the main cities (Salibay & Claveria 2006). Thus, this species become a significant public health concern in populated areas (McGarry *et al.* 2015, Hoque & Sanchez 2008). Furthermore, several studies have observed that these species can thrive in disturbed low-forest areas and adapt to higher elevations, especially in regions influenced by farming and agroforestry (Salibay & Luyon 2008, Heaney *et al.* 1999, Gratz 1990, Sanchez 1985). Given this, the evidence suggests that these

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species, which may exhibit adaptability to environments beyond urban areas, could also coexist with other *Rattus* species (e.g., Castillo & Paller 2018, Hoque & Sanchez 2008). However, our model likely did not fully capture this, possibly due to limited occurrence records, which might have hindered the model's ability to accurately represent the extensive habitat range these species can occupy (Stockwell & Peterson 2002).

Meanwhile, *R. argentiventer* which is also consider agricultural crop pest and predominantly found in the lowland agricultural areas (Aplin *et al.* 2003, Heaney *et al.* 1998) of some islands in the Philippines such as Mindanao, Visayas, and Mindoro (Htwe *et al.* 2012, Heaney *et al.* 1999, Sumangil 1990, Sanchez 1985). Among the *Rattus* species, *R. argentiventer* indicates a poor model performance (see Figure 1), mainly due to low occurrence records. Furthermore, as of the available data, *R. argentiventer* has not been confirmed in Northern and Central Luzon (Htwe *et al.* 2012, Duque *et al.* 2008, Stuart *et al.* 2008, Miller *et al.* 2008, Ong & Rickart 2008). The lack of documented occurrences in these regions may have also hindered the model's performance. However, despite the absence of records of this species into these regions, the model suggests that *R. argentiventer* may find suitable habitat in some areas within this region. The reasons for the absence of records for this species in these regions remain unclear, to the best of the author's knowledge. From an ecological perspective, the limited spread of this species across significant regions of Luzon could be due to dispersal limitations, geographical barriers and historical ecological changes. However, the most plausible primary reason appears to the relatively shorter timeframe to establish and spread compared to other non-native *Rattus* species. This temporal disadvantage may likely position *R. argentiventer* at a competitive disadvantage, especially against species like *R. tanezumi*, which is the predominant agricultural rice pest in Central and Northern Luzon (Htwe *et al.* 2012, Duque *et al.* 2008). This discrepancy raises questions about the absence of records in Central and Northern Luzon, which requires further research to ascertain whether it is attributable to the ecological factors mentioned or simply a lack of detection. Understanding this difference is crucial for improving the model's performance for *R. argentiventer*, as described in prior studies by Vaclavik & Meentemeyer (2009), Meentemeyer *et al.* (2008), McPherson & Jetz (2007).

Optimizing EBRM in the Philippines through the integration of MaxEnt modelling

EBRM is designed to offer science-based solutions by enhancing our understanding of rodent diversity, behaviour, ecology, and population dynamics (Singleton *et al.* 2021). The concept of integrating predictive modelling, such as MaxEnt, which provides habitat-based statistical outcomes, can substantially enhance EBRM efforts, as exhibited by several studies across various species and taxa (e.g., Kriticos 2012, Hauser & McCarthy 2009). Through this approach, EBRM can be augmented with data-driven information, providing local communities with actionable knowledge to innovate and improve rodent management practices, ultimately reducing economic losses and addressing rodent population challenges more effectively. By leveraging environmental data and known occurrences, our findings provide a detailed macro-ecological information of selected *Rattus* species. In addition, this study identifies potential high-risk areas as illustrated in Figure 5, requiring targeted management efforts, aligning with the core objectives of EBRM.

Integrating a macro-scale habitat suitability modelling into the EBRM framework may significantly enhances the approach beyond its traditional, localized scope. For example, this approach enables agricultural sectors to strategically plan and identify areas across large geographical scales that are at high risk of potential rodent infestations, providing crucial information needed for focused intervention efforts. This valuable information can help local government units in agriculture and biosecurity develop an efficient action plan within a reasonable timeframe and budget. By directing resources and research efforts to the area's most in need or require immediate actions. The strategic insights provided by our study require regular updates of models with the latest environmental data and rodent occurrence records. This enables timely adjustments in EBRM strategies, allowing for proactive measures to address potential risks before they escalate into widespread infestations. Such an approach will not only enhance rodent management strategies in the Philippines but also serve as a guiding framework for other countries facing similar challenges with rodent populations.

Limitations and usage notes for future practical implementation

Our study is subject to several limitations that should be taken into account. In our study, we addressed the sampling bias in occurrence data by employing a widely used method: generating a density map for a bias file in MaxEnt modelling, similar to the approach in Liu *et al.* (2018), which enhanced model accuracy. However, this method has potential drawbacks. Smoothing occurrence distributions may unintentionally overestimate the likelihood of species presence in areas with few occurrences, suggesting higher habitat suitability than might be realistically expected (Kramer-Schadt *et al.* 2013). Thus, while this strategy is helpful, it requires careful consideration to avoid overgeneralizing habitat suitability estimates. Fourcade *et al.* (2014) highlight that offering a universal solution to sampling bias is challenging due to an incomplete understanding of the bias's extent and nature within data sets. Therefore, systematic data collection should be employed wherever possible as an effective means to counteract sampling bias. This approach enhances the reliability of model predictions by ensuring a uniform distribution of sampling efforts, thus eliminating the need for complex bias correction methods during model development.

The Philippines is home to an exceptional diversity of non-volant mammals, particularly within the murine rodents ("rats and mice") group, one of the largest in mammalian diversity. However, a major limitation of our study is the sparse availability of geographical occurrence data for many of these species. This limitation alone could potentially restrict the model's capacity to fully capture the comprehensive habitat preferences of these species. According to Proosdij *et al.* (2016), constructing a reliable model requires a minimum of 14 occurrence records for narrowly distributed species and 25 for widespread species. In our analysis, *R. everetti,* considered a narrowly ranging species (forest specialist), is represented with 201 records, sufficiently surpassing the threshold for reliable model predictions. Meanwhile, to more accurately define the four *Rattus* invasive species' complete habitat range, we suggest acquiring additional unique occurrence data beyond what was utilized in this study. Despite its limitations, our study presents important findings that complement and build upon existing literature on the ecological preferences of the modelled species. Our study provides a thorough understanding, supported by habitat-based statistical analysis, potentially opening avenues for further reassessment of established ecological information about these species.

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Geolocation records from various archival data sources offer a more comprehensive range of habitats, conditions, and temporal spans than primary data from a single researcher or team. This extensive data set enhances modelling accuracy and robustness but presents challenges in quality, consistency, and biases, requiring thorough preprocessing and validation. Conducting a thorough data validation process, mitigating bias, and integrating ecologically important variables are crucial to avoid misleading outcomes. With these considerations, researchers can leverage archival data sources for pre-modelling to identify priority areas, validate findings through field surveys, and refine models with post-modelling adjustments. This iterative approach will improve EBRM by updating methods with current species and environmental data, resulting in more effective rodent management strategies during climate and environmental changes.

For future field survey, we emphasize the significance of ongoing data collection that prioritizes both quantity and quality, aiming to comprehensively represent the diverse environments inhabited by rodent species of interest. Efforts should be made to standardize data collection methods as much as possible to ensure the full range of environmental heterogeneity within the region is captured, thereby minimizing sampling bias.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467424000208

Data availability. The occurrence data of *Rattus* species were obtained and derived from the Global Biodiversity Information Facility (GBIF) https://www.gbif.org (last accessed 5 December 2022), the Field Museum's Philippine Mammals website https://www.fieldmuseum.org/philippine_mammals/ (last accessed 3 December 2022), and the Museum of Natural History at the University of the Philippines Los Baños (UPLB-MNH). The environmental variables employed in this study are readily accessible, and the public domain resources can be found in the methodology section of this manuscript. The codes used for this study are available upon reasonable request; further inquiries can be directed to the corresponding author.

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Authors contributions. Castillo DSC and Higa M were responsible for designing the model, analysing the results, and contributing to the manuscript's writing.

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