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HABITAT SUITABILITY AND NICHE INTERACTION BETWEEN THE INVASIVE SNAIL *ACHATINA FULICA* AND ITS BIOCONTROL FLATWORM *PLATYDEMUS MANOKWARI* IN SOUTHEAST ASIA

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ABSTRACT

Bioinvasions are increasingly disrupting community structures worldwide, especially as the climate remains unstable. In invaded areas, biocontrol agents are often introduced to help manage the spread of invasive species. However, these agents can proliferate and threaten non-target organisms without thorough evaluation. We assessed the niche dynamics between invasive *Achatina fulica* (Giant African Snail) and its biocontrol agent, the *Platydemus manokwari* (New Guinea Flatworm), in Southeast Asia. Species occurrence and environmental data were used to model the habitat suitability of both species in the present and future climate scenarios using ecological niche modeling with the MaxEnt algorithm. These models predicted 25.9% and 42.0% of the current conditions as suitable and 73.8% and 57.8% as unsuitable for *A. fulica* and P. manokwari, respectively. There was a predicted steady increase in suitable areas and a gradual decrease in *A. fulica's* unsuitable areas as the carbon emissions are predicted to increase. Moderate to high niche overlap of 61.2% to 83.4% was expected between the species under different climate scenarios. Predicting the suitable areas for invasive species and their niche interaction with other species, especially in the context of climate change, will aid in identifying vulnerable areas for conservation and potential outbreaks of infectious diseases.

Keywords:
climate change, niche expansion, niche overlap, ecological niche modeling, MaxEnt.

INTRODUCTION

Biological invasions are threatening the biodiversity of ecological communities all over the world. Invasive species continue to endanger the survival of numerous populations as their effects cascade through the ecosystem. Hence, it is essential to control these biological invasions to prevent biodiversity loss. Strategies have been implemented to regulate the invasive species' populations through chemical, mechanical, and biological methods. Mechanical control involves the physical collection of the target species for eventual disposal. While this method is effective for small-scale applications, it requires a large workforce, making it expensive. Meanwhile, chemical control uses chemicals to remove target species, harming the surrounding organisms and the environment (Weidlich et al., 2020).

Among the strategies, the biological method is the most sustainable way (Clewley et al., 2012). Classical biological control (hereafter referred to as biocontrol) involves natural enemies to regulate the population of invasive species. As the selected biocontrol agent exists in the same environment as its target species, its niche may expand or contract, demonstrating the competitive exclusion principle. Using biocontrol agents that feed exclusively on their target species will reduce the probability of disturbing other organisms in the vicinity. In contrast, predators introduced to infested areas without prior evaluation of their host specificity typically eradicate native species (Gerlach et al., 2021). Such is the case with the Euglandina rosea (Rosy wolf snail) and *Platydemus manokwari* (New Guinea flatworm) in controlling the global population of the giant African snail (*Achatina fulica*). The presence of these animals led to the drastic reduction of the native snail population in Japan and Hawaii, making it imperative to assess potential biocontrol agents before their release to invaded areas.

Laboratory and field experiments are typically used to evaluate the interaction between species. However, laboratory conditions may not simulate the environment in the natural setting. Field experiments provide this advantage but can unintentionally release potentially invasive species instead. A more recent approach is the use of ecological niche modeling (ENM) to determine the niche interaction between two species by considering their distribution and the set of environmental conditions they need for optimal survival and reproduction (Valencia-Rodríguez et al., 2021). The advent of ENM has made it more convenient to investigate invasive species' niche dynamics and their respective target hosts. However, studies investigating the niche interaction between biocontrol agents and their target invasive species are still limited.

The niche concept has long been a struggle for researchers to define due to its multifaceted nature, as interpreted by previous authors, such as Grinel, Elton, and Hutchinson (Sales et al., 2021). In their work, Sales et al. (2021) dissected this concept in terms of key components, including but not limited to the species' relationship with the environment, the presence of competition, and the scope of niche in research. Habitat suitability modeling studies utilize species distribution under specific environmental conditions to predict habitable areas at a given time. Recently, these studies involve a wide range of relevant ecological issues, such as the conservation of endemic and endangered species (Paul & Samant, 2024), the invasion risk of invasive species (Ahn et al., 2023), and the effect of climate change on their distribution (Mothes et al., 2020). When the needs of two or more species overlap, their niche will potentially influence the other, resulting in habitat shifts (Chen et al., 2024).

Achatina fulica, or the Giant African Snail, is a terrestrial mollusk native to East Africa. They are hermaphroditic gastropods that produce approximately 1,200 eggs annually. It was eventually introduced to the Southeast Asian region through intentional and accidental introductions. Presently, *A. fulica* continues to feed on a wide variety of vegetation. This characteristic is detrimental to residential areas with ornamental plants, particularly agricultural farms (Ramdwar et al., 2018). *Platydemus manokwari*, on the other hand, are raptorial flatworms introduced to *A. fulica's* invaded areas as biocontrol agents. Initial research considered these flatworms effective, but there was no long-term evaluation of their environmental impact (Muniappan et al., 1986). The overwhelming evidence of *P. manokwari*'s negative impacts on the native fauna is highly substantial in the literature (Muniappan et al., 1986; Gerlach et al., 2021). In their review, Gerlach et al. (2021) strongly asserted terminating any further introductions of *P. manokwari* to control *A. fulica*.

Aside from threatening biodiversity, ***A. fulica*** and *P. manokwari* are also hosts to parasitic nematodes that carry potential diseases to humans. Studies from the Philippines, Thailand, Hawaii, and the United States found the rat lungworms Angiostrongylus cantonensis and A. malaysiensis present in these two species (Hollingsworth et al., 2013; Chaisiri et al., 2019). Eosinophilic meningitis, the primary disease associated with the Angiostrongylus genus, could be lethal to humans as it can cause neurological defects and even death. With the ongoing climate crisis, determining possible invasion areas by these species could be unpredictable. This study aims to assess the niche interaction between the invasive snail *A. fulica* and its biocontrol agent *P. manokwari* in the Southeast Asian region in the current and future climate scenarios. Specifically, this study aims to (a) assess the current habitat suitability of both species in Southeast Asia, (b) compare the current and future habitat suitability for both species and (c) evaluate the niche interaction between the two species in all climate scenarios using niche overlap and niche dynamics analysis.

MATERIALS AND METHODS

A correlative ecological niche modeling approach was used to predict the habitat suitability and niche of *A. fulica* and *P. manokwari* in the Southeast Asian region under current and future environmental conditions.

Study Species

In this study, the species of interest are the invasive Giant African snail (*A. fulica*) and the invasive biocontrol agent, which is the New Guinea flatworm (*P. manokwari*). *A. fulica* is a terrestrial mollusk of the Achatinidae family with varying patterns of yellow to brownish striations around its shell. Due to their broad environmental tolerance, *A. fulica* snails are now widespread pests in agricultural lands; they consume crops such as grains, rice crops, cabbages, and even other snails. To control the *A. fulica* invasion, *P. manokwari* was introduced in *A. fulica*'s invaded areas. *P. manokwari* is a flatworm belonging to the family Geoplanidae characterized by its dark brown to black coloration, a light brown band running along its body, and a pale underbelly.

Study Site

This study analyzed the occurrence of the two species in Southeast Asia (11°S–28°N and 92–141°E) as shown in Figure 1. Southeast Asia comprises eleven countries in the mainland and island zones, including Thailand, Malaysia, Cambodia, Myanmar, Brunei, Timor-Leste, Indonesia, Singapore, Laos, Vietnam, and the Philippines. The climate is tropical, with average temperatures above 25°C all year round; Asian monsoons bring significant rainfall to these tropical areas. Southeast Asia, known for its biodiversity hotspots, faces severe threats to its ecosystems despite being home to several of them.

Occurrence and Environmental Data

The occurrence data for *A. fulica* and *P. manokwari* were downloaded from online biodiversity databases, particularly the GBIF (Global Biodiversity Information Facility at https://www.gbif.org) and iNaturalist (https://www.inaturalist.org/). Criteria on the type of data, basis of observation, and geographic location were filtered out before downloading. Only presence data from Southeast Asian countries gathered through human observation, preserved specimens, and species were downloaded from GBIF. Likewise, only verifiable and research-grade data were downloaded from iNaturalist. Data from published studies involving the occurrence of the two species in Southeast Asian countries were also included, such as from the works of Chaisiri et al. (2019), Huang et al. (2019), and Muniappan et al. (1986). The occurrence records were georeferenced using QGIS 3.24.2 (QGIS Development Team, 2009). The raw data now includes 3984 *A. fulica* and 199 *P. manokwari* occurrence points.

The species occurrence data were processed before modeling using R 4.2.0 (R Core Team, 2020). Spatial filtering removed data points found outside the study area to ensure that the remaining points were within the geographic extent (Minimum Longitude: 92.208; Minimum Latitude: 12.192; Maximum Longitude 141.000; Maximum Latitude: 28.542). The duplicate coordinates were then filtered out using the R package CoordinateCleaner. Spatial thinning, using the spThin package, was performed to reduce sampling bias while retaining the highest number of substantial data points. After cleaning the data, 1386 and 124 occurrence points remained for *A. fulica* and *P. manokwari*, respectively (Figure 1).

The environmental variables in the study consist of 19 bioclimatic and 10 soil variables, which were also used in other related studies (Banerjee et al., 2020; Feng et al., 2021). The bioclimatic variables were acquired from WorldClim ver 2.1 with a spatial resolution of 30-arc seconds (~ 1 km2) taken from 1970 to 2000 (Fick & Hijmans, 2017). These are derived from monthly measurements of temperature and rainfall alongside their derivations in terms of annual trends, seasonality, and extreme conditions. Meanwhile, the soil data sets were downloaded from ISRIC (International Soil Reference and Information Center) SoilGrids (https://www.isric.org/explore/soilgrids). The soil variables are described in Table 1. The soil parameters are important since they influence the biology of the study species, as both are land dwellers.

The environmental variables were then cropped to the Southeast Asian extent using the raster package in R. The resolution and extent of the species occurrence and environmental variables should be the same to avoid any discrepancy. The autocorrelation between the environmental variables was also prevented using Pearson's correlation coefficient. Highly correlated variables below the threshold were assessed; only one among two highly correlated variables (> 0.75) was retained for modeling based on their ecological significance to the species. After analyses, 10 environmental variables were retained for niche modeling (Table 1).

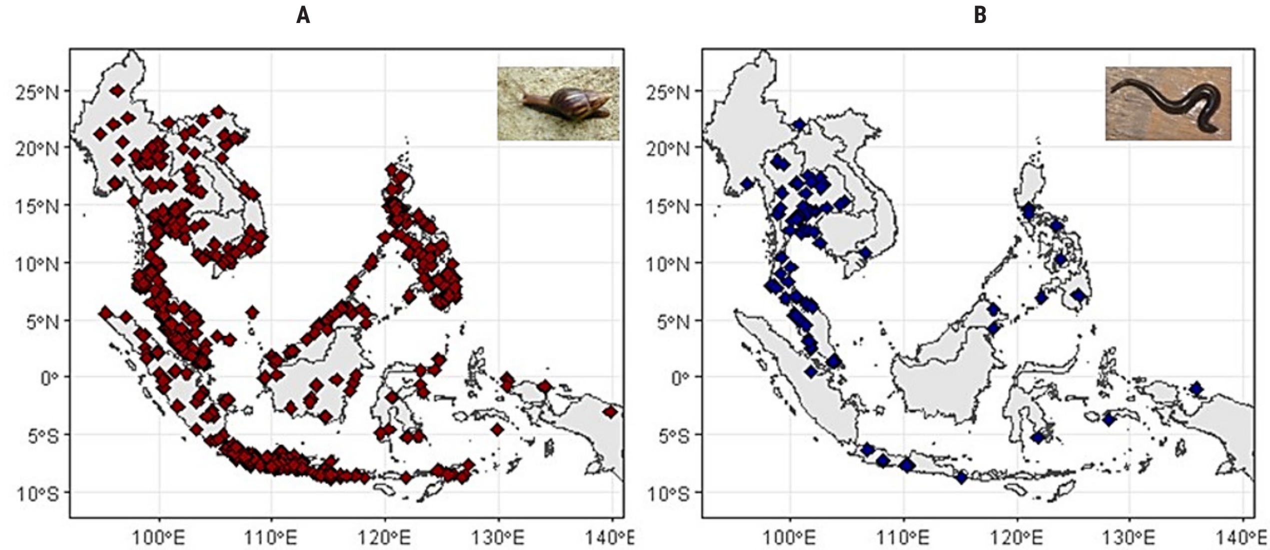

Figure 1. Occurrence data of (A) *Achatina fulica* and (B) *Platydemus manokwari* in Southeast Asia. Photo source of the two species:
https://indiabiodiversity.org/species/show/237254;
https://commons.wikimedia.org/wiki/File:Peerj-297-fig-1_Platydemus_manokwari.png#filelinks)

Table 1. List of environmental variables used in the model development for *Achatina fulica* and *Platydemus manokwari*.

Variable code	Variable	Units	Source
bio1*	Annual mean temperature	°C	Wordclim ver 2.1 (Fick and Hijmans, 2017)
bio2*	Mean diurnal range	°C	
bio3	Isothermality	°C	
bio4	Temperature seasonality	°C	
bio5	Maximum temperature of warmest month	°C	
bio6	Maximum temperature of coldest month	°C	
bio7	Temperature annual range	°C	
bio8	Mean temperature of wettest quarter	°C	
bio9	Mean temperature of driest quarter	°C	
bio10	Mean temperature of warmest quarter	°C	
bio11	Mean temperature of coldest quarter	°C	
bio12*	Annual precipitation	mm	
bio13	Precipitation of wettest month		
bio14	Precipitation of driest month	mm	
bio15	Precipitation seasonality	mm	
bio16	Precipitation of wettest quarter	mm	
bio17	Precipitation of driest quarter	mm	
bio18*	Precipitation of warmest quarter	mm	
bio19*	Precipitation of coldest quarter	mm	
bdod*	Bulk density of the fine earth fraction	kg / dm^3	ISRIC SoilsGrid (Poggio et al., 2021)
cfvo*	Volumetric fraction of coarse segments	cm^3 / dm^3	
nitrogen	Total nitrogen (N)	g / kg	
ocd*	Organic carbon density	kg / m^3	
phh2o*	pH of water in soil		
sand	Sand (>0.05 mm) in fine earth	%	
silt	Silt (0.002 - 0.05 mm) in fine earth	kg / m^3	
ocs	Organic carbon stocks	kg / m^3	
soc*	Soil organic carbon in fine Earth	g*kg^-1	

*Variables used in the final models to produce habitat suitability and niche interaction results

Modeling the Current Distribution of *A. fulica* and *P. manokwari*

The Maximum Entropy (MaxEnt) algorithm was used to model the habitat suitability of *A. fulica* and *P. manokwari*. MaxEnt is widely used to model species distribution, considering several predictor variables and a wide range of species occurrence data points. However, it is susceptible to sampling bias. The background points were estimated using the RasterStack object of the selected environmental variables and species occurrence data to account for sampling bias. Separate bias files were created for *A. fulica* and *P. manokwari* using the MASS package's two-dimensional kernel density estimation. The bias files in .asc format, alongside the environmental variables and species occurrence data, were inputted into the MaxEnt software version 3.4.4 (http://biodiversityinformatics.amnh.org/open_source/maxent/). To improve predictive accuracy, the parameters were set according to the results from the ENMevaluate function of the ENMeval package. This function considers the species occurrence and the stack of the 10 selected environmental layers using the "randomkfold" cross-validation method. The parameter settings with the lowest delta AICc (delta AICc = 0) were selected, particularly involving the linear, quadratic, hinge, product, and threshold features with a regularization parameter of 0.5. The maximum number of background points was set to 10,000 as more than 50,000 potential background points for Southeast Asia. The occurrence data were randomly divided into two groups, with 75% allocated for training the data and 25% for testing the models using the bootstrapping method with ten replicates per model. Each environmental variable's percentage contribution and relative importance were assessed using the jackknife test available in the MaxEnt software. The rest of the parameters were set to default. Model accuracy is determined through the area under the receiver operating characteristic curve score (AUC ROC), with a value closer to 1 being the most accurate (Shabani et al., 2018).

Predicting the Current and Future Habitat Suitability

The species distribution models using the current environmental conditions were projected to future climate scenarios for 2070. The future bioclimatic variables with a 30-second spatial resolution were downloaded from CMIP5 (Coupled Model Intercomparison Project Phase 5) using the Beijing Climate System Model (BCC-CSM) as the general circulation model (GCM). The soil variables in the current condition were retained due to the unavailability of future simulations, assuming the soil conditions do not change in the future. The future climate scenarios were based on four Representative Concentration Pathways (RCPs) set by the Intergovernmental Panel on Climate Change (IPCC), which are the RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 (van Vuuren et al., 2011). RCPs are projections that take into account current data on energy, land use, and greenhouse gas emissions; the higher the RCP level, the higher the simulated emissions values. According to Table 2, the study site was classified as either unsuitable or suitable based on the maximum test sensitivity plus specificity logistic threshold of the models. The present and future habitat suitability for each species were mapped using the QGIS 3.20 software (QGIS Development Team, 2009).

Niche Overlap and Statistical Analysis

The niche overlap between *A. fulica* and *P. manokwari* in the current and future climate scenarios was determined using the PCA-env technique adapted from Broennimann et al. (2012). This technique considers the density of species occurrences while accounting for the 10 selected environmental variables and the available background points. A hundred replicates of niche overlap over the density distributions of both species were measured and then visualized using histograms. Niche overlap indices used in this study were the Schoener D and Hellinger I indices, wherein values closer to 0 signify no overlap, while 1 represents identical niche models. Niche similarity and niche equivalency were used to determine if there was a statistical difference between the niches of the two species. Niche similarity analyzes whether the two interest niches have higher similarity than is expected by chance. In contrast, niche equivalency determines how constant the niche overlap is over randomized species occurrence points. All niche overlap analyses were then analyzed using the ecospat package in R ver. 4.1.1 (Warren et al., 2021).

RESULTS

Model Evaluation and Environmental Variables

The AUC ROC score for *A. fulica* and *P. manokwari* was 0.78 ± 0.01 and 0.76 ± 0.05, respectively, indicating a moderate model accuracy (Shabani et al., 2018). After modeling, the response curves of environmental variables with a percent contribution of more than five percent were produced. Table 2 shows the highest contributing variables for *A. fulica*, which includes phh2o (34%), bio2 (15.4%), cfvo (12.8%), bdod (11.7%), and soc (10.2%). Additionally, it shows that bio2 was the highest contributing variable to the *P. manokwari* model with a 39.9% contribution, followed by phh2o (31.9%), bio1 (9.2%), and bio18 (6.8%). The probability of habitat suitability for both species in different variables is shown in Figures 2 and 3.

Table 2. Environmental variables for the present habitat suitability model of *A. fulica* and *P. manokwari*

Variable	*A. fulica*		*P. manokwari*	
	Percent contribution	Permutation importance	Percent contribution	Permutation importance
pH of water in soil	34	27.4	31.9	31.9
Mean diurnal range	15.4	5	39.9	11.3
Volumetric fraction of coarse segments	12.8	19	1	2.3
Bulk density of the fine earth fraction	11.7	16.6	3.1	5.3
Soil organic carbon in fine earth	10.2	12.3	1.7	2.8
Annual mean temperature	4.2	2.1	9.2	21.3
Precipitation of coldest quarter	4.2	5.3	2	8.8
Organic carbon density	4.2	5.9	1	0.6
Precipitation of warmest quarter	2.7	5.4	6.8	1.2
Annual precipitation	0.6	1.1	3.5	14.5

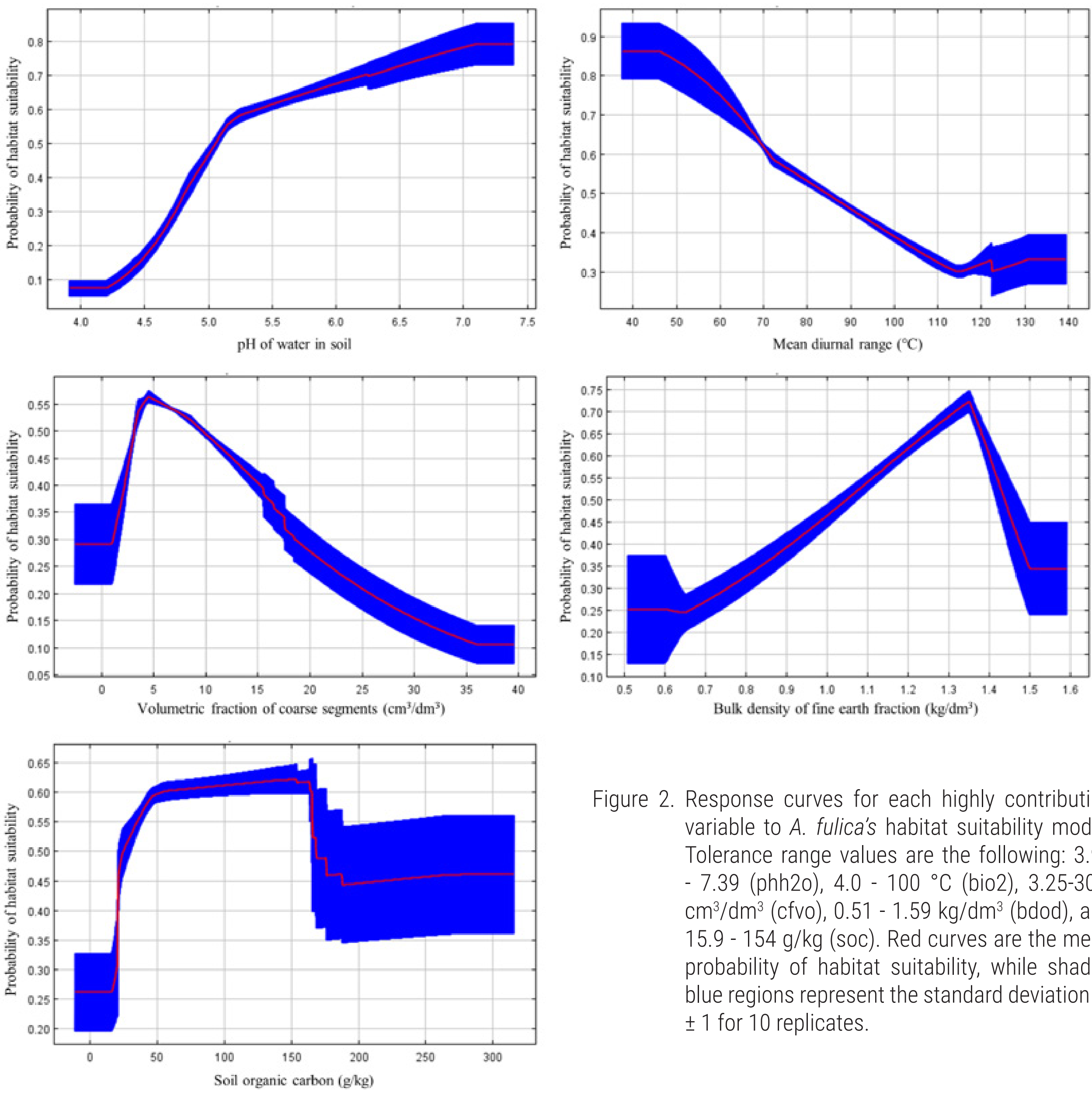

Figure 2. Response curves for each highly contributing variable to *A. fulica's* habitat suitability model. Tolerance range values are the following: 3.91 - 7.39 (phh2o), 4.0 - 100 °C (bio2), 3.25-30.8 cm^3/dm^3 (cfvo), 0.51 - 1.59 kg/dm^3 (bdod), and 15.9 - 154 g/kg (soc). Red curves are the mean probability of habitat suitability, while shaded blue regions represent the standard deviation of ± 1 for 10 replicates.

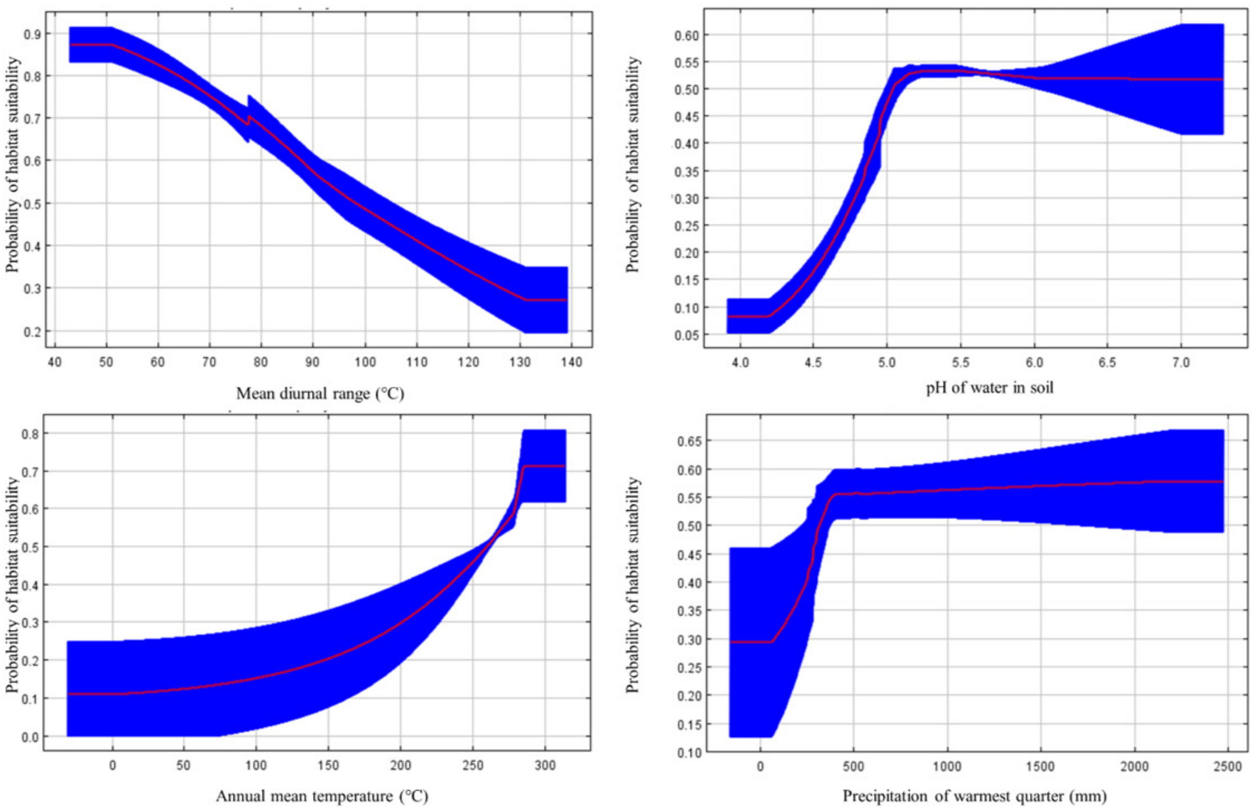

Figure 3. Response curves for each highly contributing variable to the habitat suitability model of *P. manokwari*. Tolerance range values are the following: 4.5 - 10 °C (bio2), 3.9 - 7.-0 (phh2o), 3 - 31 °C (bio1), 500 - 2500 mm (bio18). Red curves are the mean probability of habitat suitability, while shaded blue regions represent the standard deviation of ± 1 for 10 replicates.

Present Habitat Suitability

The models generated using the environmental variables in Table 2 predicted the presently suitable habitats for *A. fulica* and *P. manokwari* (Figure 4). The predicted geographical extent of suitable habitats in Southeast Asia in km2 is shown in Figure 5. Areas unsuitable for *A. fulica* were predicted to cover the majority of the region at approximately 73.8%, while only 25.9% are suitable. Predicted suitable areas include the Vietnam coasts, Myanmar, Lao, and Brunei, and a few portions of Indonesia and the Philippines. Similarly, 57.8% of the region was predicted to be unsuitable for *P. manokwari*, and only 42.0% was found suitable. Some places are commonly suitable for both species but *P. manokwari* occupies a larger geographical extent (Figure 4).

Future Habitat Suitability

The niche models generated from the present environmental conditions were used to predict the future habitat suitability for *A. fulica* and *P. manokwari*. The steady increase of suitable areas with increasing RCPs yields a gradual decrease in unsuitable areas for *A. fulica* snails (Figure 6). Particularly, there is an increase in suitable habitats of 8.5%, 17.5%, 17.5%, and 21.3% for RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5, respectively. On the other hand, the extent of suitable and unsuitable areas for *P. manokwari* was predicted to be relatively stable at RCPs 4.5, 6.0, and 8.5 compared to that of *A. fulica*. Only in RCP 2.6 was the proportion of suitable to the unsuitable area predicted at 1:3 or approximately 24.9% and 74.9%, respectively (Figure 7). Figure 8 shows the projected habitat suitability maps of both *A. fulica* and *P. manokwari* in the present and future climate conditions.

Niche Overlap and Dynamics

Moderate to high niche overlap was observed between *A. fulica* and *P. manokwari*, ranging from 61.2% to 83.4% (Table 3). Schoener's D value had little to no change in the present conditions relative to the future climate scenarios. In terms of equivalence, a significant difference between the invasive *A. fulica* and biocontrol agent *P. manokwari* was only observable in RCP 2.6. Furthermore, the niches of both species were predicted to be more similar than expected only in future climate scenarios. Under predicted current conditions, the niches were neither equivalent nor similar.

Niche dynamics were evaluated by determining the niche stability, expansion, and unfilling between the invasive species and the biocontrol agent to assess their niche interaction (Table 4). Niche stability pertains to the areas occupied by both *A. fulica* and *P. manokwari*. On the other hand, niche expansion and niche unfilling refer to areas inhabited exclusively by *A.*

fulica or *P. manokwari*, respectively. These measures of niche dynamics show one species' influence on the other's niche. The niche interaction between the two species was predicted to be relatively constant in all future climate scenarios, with no significant expansion of *A. fulica*. However, the niche unfilling by *P. manokwari* was considered significant, albeit small, in the present ($p = 0.009$) and future climate conditions ($p = 0.009$, $p = 0.020$, $p = 0.010$, $= 0.010$ for RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 respectively).

Table 3. Niche overlap indices between *A. fulica* and *P. manokwari* in present and future climate conditions.

Indices	Climate Scenarios				
	Present	**RCP 2.6**	**RCP 4.5**	**RCP 6.0**	**RCP 8.5**
Overlap (D)	61.2 %	61.6%	61.8%	63.1%	63.0%
Equivalence (p-value)	0.07	0.02*	0.25	0.06	0.12
Similarity (p-value)	0.05	0.01*	0.02*	0.01*	0.02*
Overlap (I)	83.1%	83.2%	83.4%	83.1%	83.4%
p-value	0.08	0.02*	0.15	0.09	0.08

** statistically significant (p-value < 0.05)*

Table 4. Niche overlap dynamics between *A. fulica* and *P. manokwari* in present and future climate conditions.

Indices	Climate Scenarios				
	Present	**RCP 2.6**	**RCP 4.5**	**RCP 6.0**	**RCP 8.5**
Expansion	0.68%	1.20%	1.30%	0.50%	0.74%
Stability	99.3%	98.8%	98.7%	99.5%	99.3%
Unfilling	5.00%*	4.85%*	3.18%*	5.61%*	4.68%*

**** statistically significant (p-value < 0.05)***

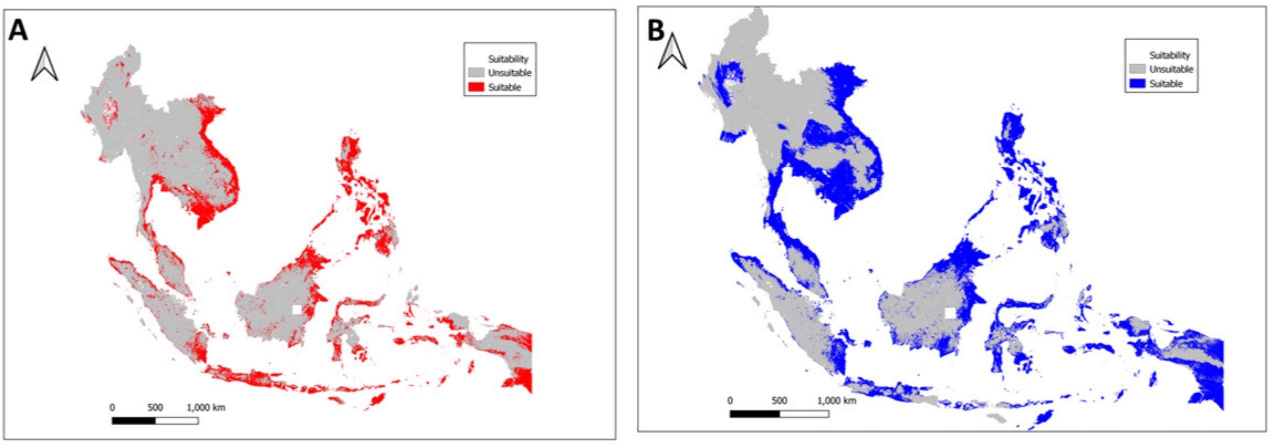

Figure 4. Present habitat suitability for *A. fulica* (A) and *P. manokwari* (B).

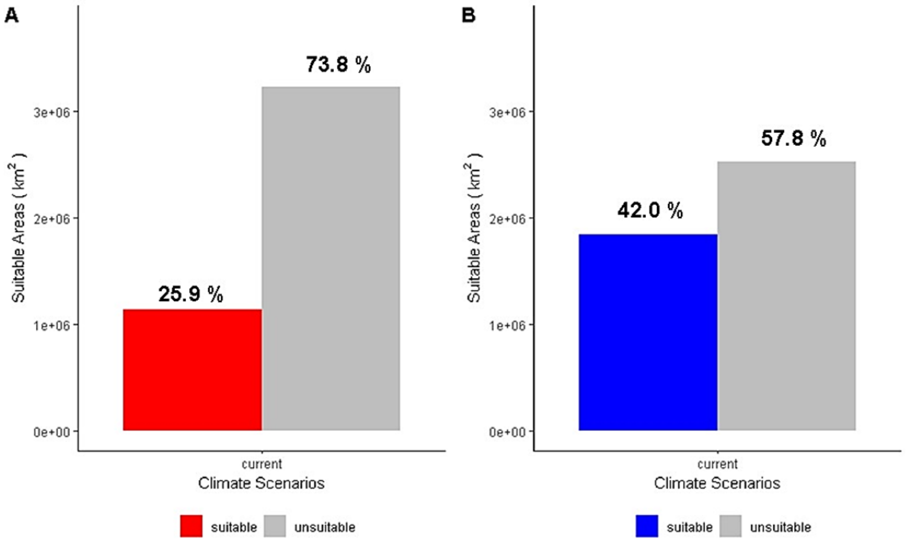

Figure 5. Areas of present habitat suitability for *A. fulica* (A) and *P. manokwari* (B) in km² relative to the whole of Southeast Asia.

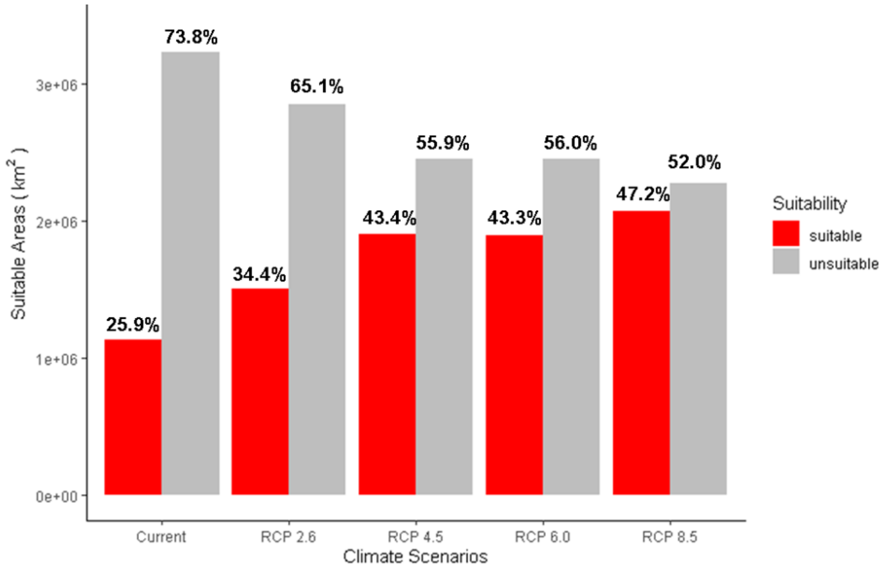

Figure 6. Areas of habitat suitability (km²) of *A. fulica* in present and future climate scenarios (2070).

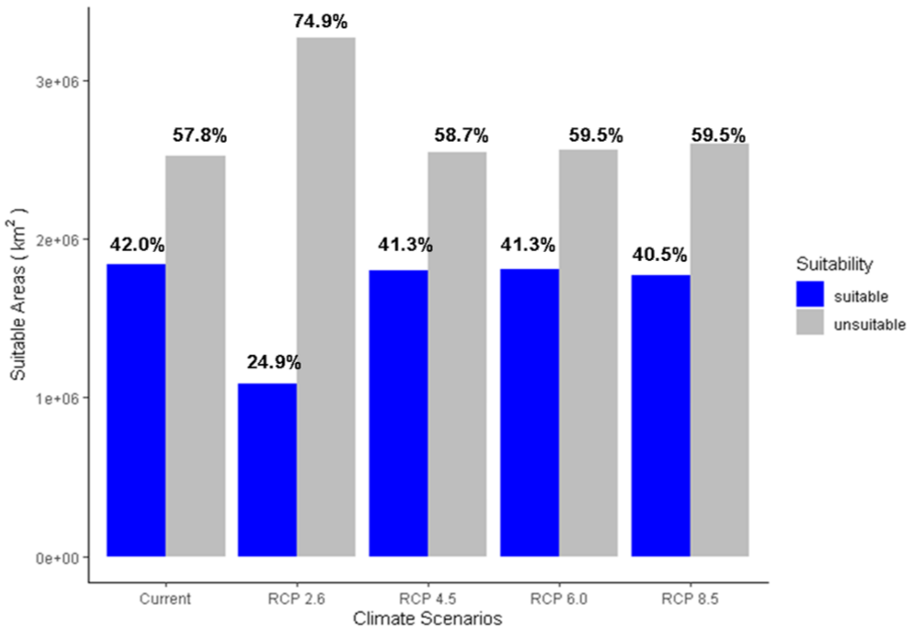

Figure 7. Areas of habitat suitability (km²) of *P. manokwari* in present and future climate scenarios (2070).

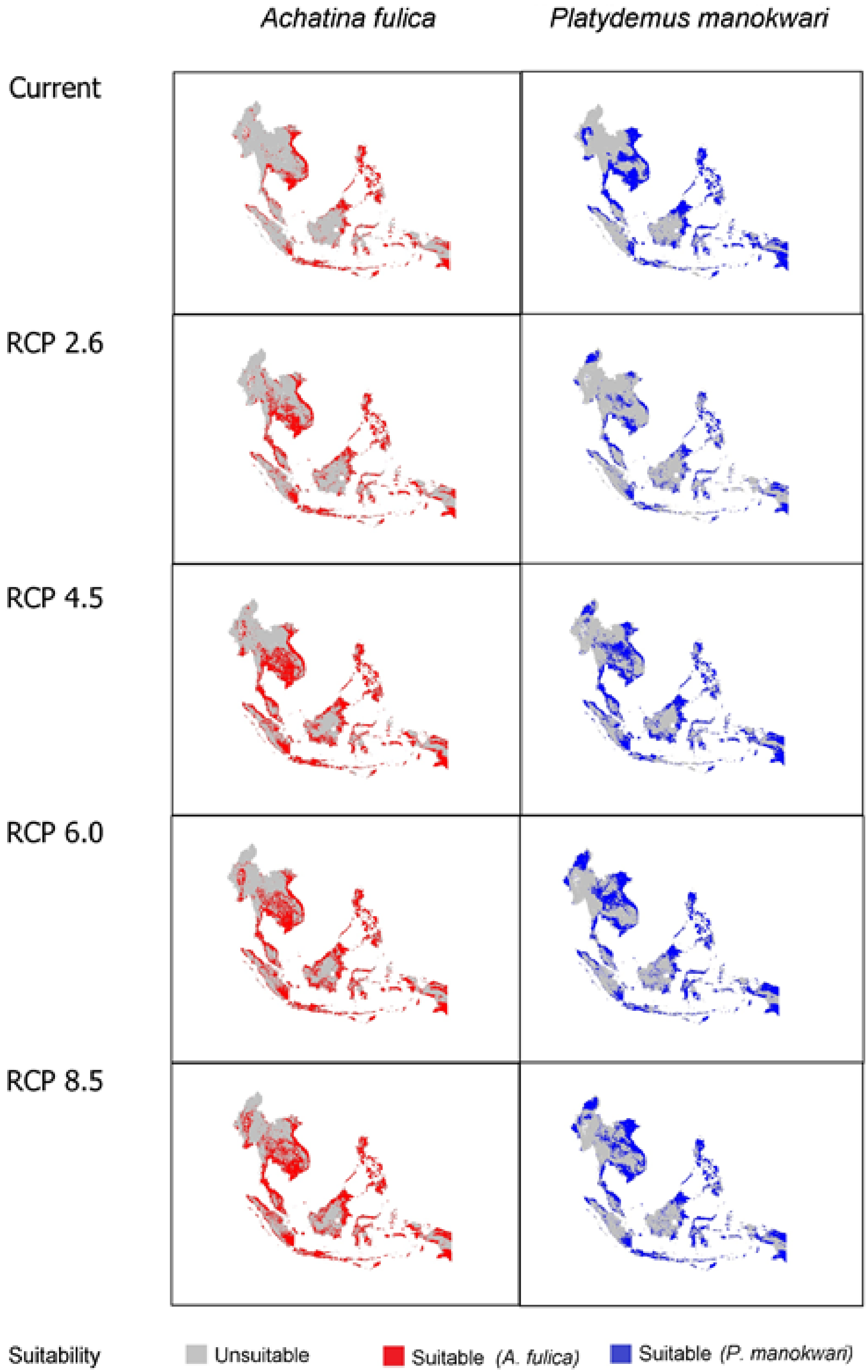

Figure 8. Present and future habitat suitability maps of *A. fulica* and *P. manokwari* in the Southeast Asian region for 2070 in four Representative Common Pathways (RCP) scenarios.

DISCUSSION

Present Suitability

Determining which areas are suitable for a particular species requires consideration of the species' biology, tolerance range, and interaction with other organisms. *A. fulica* and *P. manokwari* are both soil-dwelling organisms that feed on plants and small invertebrates, respectively. Despite the similarity in their environment, these species have different top environmental factors associated with their suitable habitats. *A. fulica's* suitable habitat is primarily associated with soil factors, while *P. manokwari* is associated mainly with climatic ones. Factors such as the volumetric fraction of coarse segments, bulk density of the fine earth fraction, and soil organic carbon are specifically relevant to *A. fulica*. At the same time, the distribution of *P. manokwari* is affected by the annual mean temperature and precipitation of the warmest quarter. Similar findings were also found in the literature, such as how Idohou and Codjia (2013) found the soil type as the main determinant for *A. fulica's* distribution and Gerlach's (2019) findings on the impact of temperature and humidity on *P. manokwari*'s activity.

One possible reason is the presence of *A. fulica's* protective shell, which allows it to conserve moisture in its body. On the other hand, *P. manokwari*'s body is more exposed, making it more sensitive to severe climate changes. However, the differential effect of both climatic and soil variables on these species is poorly documented, making it difficult to ascertain this claim. Soil data is currently not widely used in modeling and experiments alike, especially in studying flatworms. On the other hand, temperature and humidity influence both *A. fulica* and *P. manokwari*'s distribution. For instance, Sarma et al. (2015) found that the temperature mainly influences *A. fulica's* invasion risk. Although they could not account for the soil variables, their results were consistent with the previous studies (Albuquerque et al., 2009; Sharma & Dickens, 2018). *P. manokwari* flatworms, on the other hand, are more susceptible to severe temperature changes than *A. fulica* snails. As shown in Figure 3, *P. manokwari* can only survive temperatures from 25°C to 30°C most of the time, which is consistent with Gerlach's (2019) findings of 24°C to 30°C while *A. fulica* can survive 28°C to 45°C (Sharma & Dickens, 2018).

Aside from the previously mentioned variables, the pH of water in the soil and the mean diurnal range are common in *A. fulica's* and *P. manokwari's* habitat suitability models. Soil acidity influences the bioavailability of nutrients such as nitrogen and phosphorus. Both species generally prefer slightly acidic soils with pH values ranging from 5.0 to 7.0 at 50% probability (Figures 2 and 3). Constant rainfall can lead to high soil acidity, which could explain the currently predicted occurrence of these species in Southeast Asia (Silva et al., 2022), as shown in Figure 6. Rainfall, in turn, directly affects the air's humidity. When rainfall occurs for a long time, the water vapor in the air will increase, which also elevates the moisture content in the soil. *A. fulica's* body size and weight during development increase with increasing humidity (Albuquerque et al., 2009). Similarly, the *P. manokwari* relies on its surroundings' moisture for locomotion (Gerlach, 2019). Preference for areas with high humidity and a specific temperature range could imply that areas with low precipitation and too extreme temperatures have a low risk of invasion.

The mean diurnal range (MDR) is the difference between the highest and lowest temperatures on a single day. This variable is an essential climate change indicator because it correlates with other factors, such as local warming (Libanda et al., 2019). Over the years, there has been a downward trend of MDR, suggesting an unequal increase between the daily maximum and minimum temperatures (Braganza et al., 2004). *A. fulica* and *P. manokwari* are nocturnal organisms; hence, changes in nighttime temperature could disrupt their activity. However, little to no evidence support the relationship between mean diurnal range and nocturnality. In this study, the MDR at the highest logistic probability is 4.0 °C and 4.3 °C for *A. fulica* and *P. manokwari*, respectively (Figures 2 and 3). Reduction in MDR has been observed in the majority of Southeast Asia at approximately 1°C to 2 °C (Hamed et al., 2022). The author noted that the MDR varies in spatial and temporal aspects, highlighting the need to investigate this variable and its effects in localized regions.

In this study, *A. fulica* has lower suitability than *P. manokwari* despite having higher species occurrence data (Figure 5). Other factors could have shaped its distribution aside from the variables applied here, such as the exposure of these snails to anthropogenic activities and possible predation. On the other hand, *P. manokwari* lives in less conspicuous areas, possibly reducing its vulnerability. While the maps can help pinpoint which areas need regular surveillance, further experimental studies are necessary to confirm the findings, specifically on the species' tolerance range. In addition, future research could investigate the dispersal patterns of *A. fulica* and *P. manokwari*. Understanding their movement will help determine the geographic range of the biocontrol agent *P. manokwari* in relation to the invasive *A. fulica* and its spread. The study suggests that drastic changes in the soil and bioclimatic variables could shift species distribution, making it crucial to investigate these dynamics in the context of climate change.

Future Suitability

The suitable areas for *A. fulica* snails were predicted to expand with increasing greenhouse gas concentrations in the year 2070 (Figure 6), implying that these snails may continue to proliferate in the future. Their resistance to extreme temperatures is attributed to their behavioral adaptation. In exceedingly low temperatures, they undergo the process of aestivation, while in arid conditions, these snails hibernate. Their tendency to enter a state of dormancy could help them thrive in the future, regardless of the temperature. These findings, however, were contradicted by Ananthram et al.'s (2022) study. Through niche conservatism, the authors predicted that *A. fulica* would retain its niche in the SSP2 and SSP5 climate scenarios from 2061 to 2080. Unlike RCPs, SSPs (Shared Socioeconomic Pathways) take into account the possible course of action based on different policies toward climate change in their scenarios, providing a more holistic approach Riahi et al. (2017).

The niche of the biocontrol flatworm *P. manokwari* is expected to be maintained in 2070 for RCP 4.5, RCP 6.0, and RCP 8.5. However, for RCP 2.6, a niche contraction is expected to occur. The absence of a trend with increasing RCPs nor the lack of considerable difference between present and future climate scenarios is not expected. A laboratory experiment by Sugiura (2009) found that a temperature of less than 17.1°C limited *P. manokwari*'s feeding activity toward its prey. These findings imply that *P. manokwari*'s invasion risk could increase with elevated temperatures due to climate change. The conflicting results could be due to the varying methods used, specifically the mechanistic nature of Sugiura's (2009) study compared to the correlational approach in this study.

The overall positive response of *A. fulica* and *P. manokwari* to worsening climate scenarios imply their persistence in Southeast Asia, indicating potential future invasions. This finding suggests that biological interactions might be more advantageous for invasive species than their native prey, as higher temperatures could significantly diminish native prey populations. Biodiversity decline poses a negative forecast for the recovery of ecosystems, especially with climate change. While this study projected the average conditions tolerable for these species, future studies could delve into their physiology to validate these findings (Peterson et al., 2015). However, the results may differ depending on whether experiments are conducted in the field or in laboratory settings. Nevertheless, recent literature supports Sugiura's (2009) conclusion on *P. manokwari's* niche expansion. *P. manokwari* is now reported outside New Guinea, such as in Hong Kong, Europe, Japan, and even the French West Indies (Hu et al., 2019; Justine et al., 2021, 2014). Most of these areas have temperate to semi-temperate climates, which is disparate from the humid and tropical characteristics of New Guinea. These studies substantiate the capacity of these flatworms to thrive in new locations.

In Southeast Asia alone, the suitable areas for both *A. fulica* and *P. manokwari* are changing. Presently, *A. fulica* is predicted to thrive in the eastern coasts of the Indo-China peninsula, the central Philippines, and some portions of Brunei and Indonesia. In 2070, however, these areas are expected to change under different climate scenarios. For instance, the suitable areas are expected to shift to the eastern parts of the Indo-China peninsula in RCP 2.6, whereas, in RCP 4.5, movement is predicted towards the northern region. *P. manokwari*'s suitability exhibits these similar dynamics. Some scenarios show a shift toward the northern areas, while others show a shift toward the central area. Hence, there is no single direction in terms of niche shift. While evaluating each species' response to climate change is essential, it is equally important to determine how their interactions could change in the future.

Niche Overlap and Dynamics

The stable interaction between *A. fulica* and *P. manokwari* across time and climate scenarios in Southeast Asia demonstrates the similarity of their niche. The findings of this study imply that these species will continue to coexist in the future, but *P. manokwari* could begin to occupy spaces not occupied by the invasive snail, where they could consume native snail species. Niche unfilling can occur due to several reasons, including differences in environmental tolerance, availability of food, and competition for space. While invasive land snails and flatworms occupy areas with similar environmental conditions, they have different food preferences. *A. fulica* snails consume vegetation and other decaying materials, whereas *P. manokwari* flatworms consume snails, isopods, and other invertebrates. Due to their generalist behavior, *P. manokwari* can survive even without their target invasive species.

One of the early introductions of *P. manokwari* as a biocontrol agent for the invasive *A. fulica* snails was in 1986 for Muniappan et al. (1986) field experiment. The authors deliberately introduced the flatworm in the coconut fields of Bugsuk Islands, Philippines, and found a drastic decrease in *A. fulica* snail populations, implying that the flatworms were effective. However, the authors did not monitor the possible interactions of flatworms with other species in that area. In support of this, Kaneda et al. (1992) determined the suitable conditions for producing more flatworms to regulate the snail population. Later studies would then find that these flatworms also consume native land snails, as observed in the Osagawara Islands, Japan – marking them as another invasive species (Sugiura, 2010). Despite initial claims of being an effective biocontrol agent for *A. fulica*, *P. manokwari* is now classified as one of the world's most invasive species. In their review, Gerlach et al. (2021) highlight these flatworm species as ineffective, urging the community to terminate their introduction to new areas.

To be effective biocontrol agents, biocontrol candidates must establish their populations in the same environmental conditions as their target invasive species. One aspect to consider is the biocontrol agent's role as a consumer. For example, in their native ecosystems, *A. fulica* functions as a primary consumer and detritivore, aiding in the cycle of nutrients, while *P. manokwari* acts as a secondary consumer. These species could still maintain their ecological roles when introduced to new areas, potentially disrupting established biological interactions. When the local and introduced species have the same functional role in one community, competition could arise threatening the fitness of the involved species. It is important to emphasize that biocontrol agents are also introduced, which means they are subject to the same constraints as invasive species. In this study, the niche overlap and dynamics were evaluated based only on the species occurrence data. Future researchers could investigate biological interactions such as inter- and intra-specific competition at a finer scale using stable isotopes (Rosengren & Magnell, 2024).

Future Directions

This study mainly focuses on the interaction of organisms on a macroecological scale. To support the findings of this study, future research could explore the mechanistic aspect of the species' relationship by evaluating the biological and physicochemical parameters to a finer extent. Moreover, since anthropogenic activities highly influence dispersal and species distribution, their impact on niche shift could be further investigated. Future researchers can also model the interaction between invasive species and their potential hosts at different trophic levels to fully characterize the invasion risk. In soil communities, *A. fulica* snails are primary consumers, while *P. manokwari* flatworms are notorious predators. Both species are intermediate hosts of Angiostrongylus cantonensis. Investigating the impact on both lower and higher trophic levels will aid in an integrative understanding of the role of these species in biodiversity loss.

Future research on niche dynamics should focus on identifying the specific direction of the niche shift by evaluating changes in the centroid of the population density. Through this method, conservation efforts can pinpoint specific places for control. While biocontrol through the introduction of natural enemies in invaded areas is promising, it carries risks, such as the potential extinction of native species. Inducing the local extinction of these invasive species could complement effective biological control strategies (Sharma & Dickens, 2018; Gerlach, 2019). For instance, determining the species' tolerance limits to temperature and humidity could simulate a hostile environment, reducing their probability of survival and aiding in their control without introducing potential invasive species.

CONCLUSIONS

The suitable habitats for the invasive *A. fulica* snails in the Southeast Asian region are predicted to expand in 2070. On the other hand, the ratio of suitable to unsuitable areas for *P. manokwari* will remain the same, except in RCP 2.6. The acidity of water in the soil (phh2o) and the mean diurnal range (bio2) are the two common variables affecting both species. Bioclimatic factors such as temperature and precipitation are found to mainly influence *P. manokwari's* distribution, while soil variables primarily affect *A. fulica*. Furthermore, the niche overlap between the two species is predicted to be stable in the future. However, there may be areas suitable only for *P. manokwari* and not for *A. fulica*. This could lead to *P. manokwari* flatworms preying on native snail species. Therefore, despite their similar niches, *P. manokwari* flatworms may not be an appropriate biocontrol agent in the long term. It is critical to assess the compatibility of a biocontrol candidate not only with the target species but also with other species within the community. Understanding how the niches of these species contract or expand will help determine areas vulnerable to biodiversity loss and potential outbreaks of infectious diseases, particularly in regions where these species serve as hosts for parasitic nematodes.

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