

Research Article

Establishment potential across South Korea for two gecko species, *Gekko japonicus* and *G. swinhonis*, adapted to different climates

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Abstract

The introduction of exotic species and the associated impacts are increasing worldwide due to the development and increase in transportation and international trade. As new populations of the non-native *Gekko japonicus* and *G. swinhonis* have recently been discovered in South Korea, this study was conducted to investigate the distribution of these species, evaluate the establishment potential of non-native populations and infer their routes of introduction. The study comprised targeted field surveys around the major international ports, generation of ecological niche models (ENMs), based on the known distributions and comparison of the ecological niches of the two species. The results suggest that *G. japonicus* and *G. swinhonis* are primarily distributed in the humid subtropical climate (Cfa) and the monsoon-influenced hot-summer humid continental climate (Dwa), respectively. According to the ENMs predicted across South Korea, suitable habitats for *G. japonicus* were located along the western and southern coasts of the country, whereas those for *G. swinhonis* were predicted along the western coastal regions and several major cities inland. These distributional patterns may be attributed to adaptations of the two gecko congeners to distinct climatic conditions leading to divergent ecological niches. Considering the known distributions of the two species in South Korea, the most likely routes of introduction are accidental translocations through international trade and the inland populations most likely originated from human-mediated dispersals along the major rivers. This study highlights the need to implement quarantine procedures for international cargo arriving in South Korea. Additional field surveys are further recommended to focus on urban areas adjacent to international ports and major rivers to curtail further introductions of non-native geckos.

Key words: Ecological niche models, Köppen-Geiger climate classification, MaxEnt, niche comparisons, non-native gecko

Introduction

The global increase in introduced species is correlated with the development and increase in international trade, transportation and the exotic pet industry (Hulme 2009; Gippet and Bertelsmeier 2021). Introduced species can cause severe ecological damage to the native ecosystems through predation pressure and interspecific



Academic editor: Helen Sofaer

Received: 2 January 2024

Accepted: 6 April 2024

Published: 2 May 2024

Citation: Park I-K, Shin Y, Baek H-J, Kim J, Kim D-I, Seok M, Oh Y, Park D (2024) Establishment potential across South Korea for two gecko species, *Gekko japonicus* and *G. swinhonis*, adapted to different climates. NeoBiota 93: 39–62. <https://doi.org/10.3897/neobiota.93.118085>

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competition (Dueñas et al. 2021; Cox et al. 2022). Dueñas et al. (2021) reported that 304 introduced species had a negative impact on 40% of known terrestrial vertebrate species. Introduced species can also cause economic damage; Cuthbert et al. (2022) reported that 60 of the worst invasive species cause an annual median economic loss of 43 million dollars globally. Despite this, the potential negative impacts of numerous introduced species remain unassessed (Dueñas et al. 2021; Cuthbert et al. 2022).

Identifying the characteristics of the native habitat of introduced species, the establishment potential within the introduced range and evaluation of potential habitats may provide crucial baseline information for the management and prevention of damage caused by introduced species (Rödder et al. 2009; Rodríguez-Rey et al. 2019). The climatic conditions of the introduced areas are a key factor in the establishment of introduced species (Menéndez et al. 2007; Simončič et al. 2019). Therefore, understanding the climate of the native habitat of invasive species provides essential information for predicting the establishment potential in the introduced ecosystem. In this context, ecological niche models (ENMs) provide a convenient, yet powerful methodological framework to predict the spread of various invasive species, based on their habitat characteristics and, further, provide valuable insights into establishing effective management strategies and preventing potential damage from invasive species (Smolik et al. 2010; Bellard et al. 2018; Agarwal et al. 2021). In fact, ENMs have been applied to assess the invasion trends of introduced species (Petrosyan et al. 2023; Tietz et al. 2023).

Geckos make up a considerable portion of the globally documented introduced species (Weterings and Vetter 2018; Agarwal et al. 2021). Several species of geckos possess characteristics that make them especially well-suited for human-mediated translocations, such as high demand in the pet trade (Valdez 2021) and the ability to be transported as accidental stowaways (Mouane et al. 2021). Successfully established populations of exotic geckos can have negative impacts on the native ecosystem through direct competition for prey with native species (Cole et al. 2005), predation of small native invertebrates (Hoskin 2011) and spread of diseases (Casey et al. 2015). These negative consequences are exemplified by the introduction of *Hemidactylus frenatus* to Australia, which led to the extirpation of some native gecko species (Newbery and Jones 2007; Hoskin 2011).

South Korea has reported the presence of three gecko species that are presumed to be non-native – the Schlegel's Japanese gecko (*Gekko japonicus*), the Peking gecko (*G. swinhonis*) and the Common house gecko (*H. frenatus*) (Stejneger 1907; Kim et al. 2020a; Kwon et al. 2023). In South Korea, *G. japonicus* was first reported from Busan in 1885 (Stejneger 1907) and has been further recorded along the southern coastal regions of the country (Kim et al. 2017; Kim et al. 2020a). Based on previous studies on genetic diversity, the Korean *G. japonicus* populations most likely originated from Japan through past human-mediated dispersal events (Kim et al. 2020b). *Gekko swinhonis* is an endemic species in China, which was first reported from Incheon, South Korea in 2021, as an accidental stowaway (Kwon et al. 2023). Meanwhile, *H. frenatus* has only been documented from scattered individual observations with no confirmed population (Kwon et al. 2023). Despite the increasing reports of gecko populations in the country, no assessment or management efforts have been made compared to other invasive species that are more conspicuous than geckos, such as freshwater turtles (Baek et al. 2023) and

the American bullfrog (*Lithobates catesbeianus*; Park et al. 2022a). Considering the globally increasing ecological and economic damages caused by non-native geckos (Newbery and Jones 2007; Hoskin 2011), appropriate management strategies supported by ecological information are vital for the geckos introduced into South Korea.

Since the original reporting of the populations of *G. japonicus* and *G. swinhonis* from South Korea, new populations have been discovered in the north-western coastal regions of the country. This study aims to evaluate the establishment potential and suitable habitats of the two species through ENMs, based on the projection of current environmental conditions and infer the most likely routes of introduction. The study further aimed to gain insights into the patterns of partial range overlap between the two species given the environmental conditions of South Korea. In conclusion, we expect to provide key information for the effective management of introduced geckos in South Korea.

Materials and methods

Field surveys and location data

We selected seven ports located on the west coast of South Korea as study sites (namely, Gyeongin, Incheon, Pyeongtack-Dangjin, Daesan, Janghang, Gunsan and Mokpo Ports) amongst the 14 international ports managed by the Korean Government. We targeted these ports considering the recent observations of non-native geckos primarily near the Incheon Port located in the northwest coastal region of South Korea (Fig. 1). Between April 2022 and October 2023, we conducted field surveys within a 10 km radius of each selected port and surveyed each site five times in a team of two people. Additionally, we surveyed a specific area in Seoul, where a Korean herpetologist reported that geckos had been newly observed.

We additionally collected georeferenced location data of *G. japonicus* and *G. swinhonis* across the distributional range of the two gecko species, including South Korea, Japan and China, from the published literature (Wada 2003; Yan et al. 2010; Kim et al. 2020a, b; Kwon et al. 2023) and iNaturalist Research-Grade observations (<https://www.inaturalist.org/>) [Accessed on 16 November 2023]. Each iNaturalist observation was quality-checked by examining the associated photographs and coordinate accuracy. We also compared the iNaturalist coordinates to the published distribution records and verified that the selected iNaturalist observations did not deviate considerably from the known ranges of the two species. Thus, data on 985 locations for *G. japonicus* and 64 locations for *G. swinhonis* were obtained. We used only one coordinate within a 10 km radius of each location data to reduce the spatial autocorrelation and bias of location data (Boone and Krohn 1999; Anderson and Raza 2010). This resulted in 309 location data for *G. japonicus* and 51 location data for *G. swinhonis* used in downstream analyses (Table 1). These occurrence datasets include occurrence points from both native (China) and non-native (South Korea) ranges of the two species. The inclusion of non-native occurrence points was deemed appropriate as these compose only a minor portion of the entire dataset ($n = 9$ for *G. japonicus* and $n = 1$ for *G. swinhonis*) and, thus, unlikely to produce spurious predictions. Nevertheless, we repeated the modelling steps without including occurrence points from South Korea (see below).

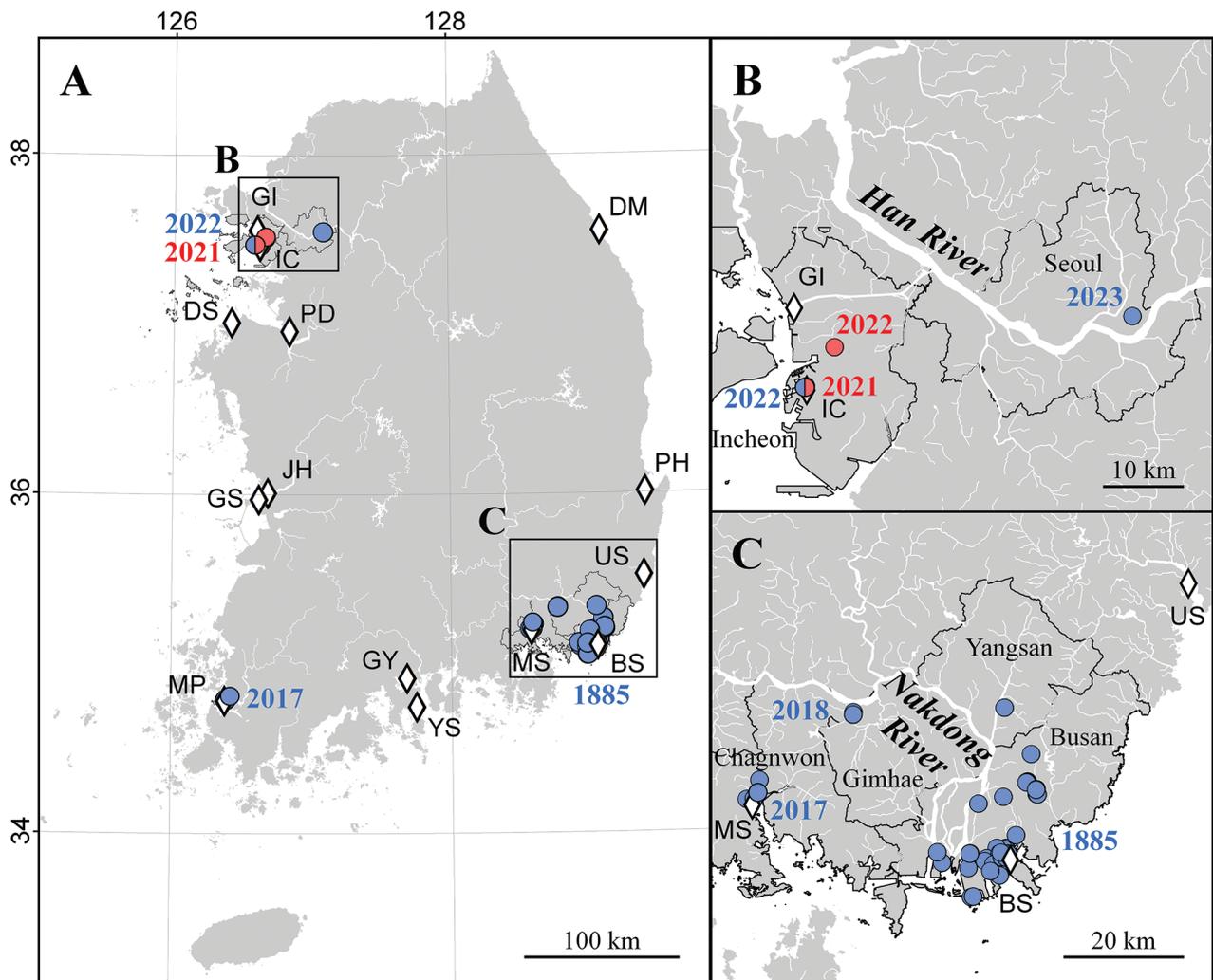


Figure 1. The distributions of *Gekko japonicus* (blue dots) and *G. swinhonis* (pink dots) in South Korea, along with the locations of 14 major international ports (white diamonds). It is to be noted that the gecko populations are generally distributed near international ports or major rivers. The number written next to each population indicates the year of the first observation **A** the overall distributions of gecko populations in South Korea **B** recently discovered gecko populations in the north-western part of South Korea. **C** In the southern part of South Korea, most *G. japonicus* are distributed near international ports or large rivers. The abbreviated port names are as follows – GI = Gyeongin Port, IC = Incheon Port, PD = Pyeongtaek and Dangin Port, DS = Daesan Port, JH = Janghang Port, GS = Gunsan Port, MP = Mokpo Port, GY = Gwangyang Port, YS = Yeosu Port, MS = Masan Port, BS = Busan Port, US = Ulsan Port, PH = Pohang Port, DM = Donghae and Mukho Port.

Table 1. The number of location data used in this study and the calculated area of suitable habitats for *Gekko japonicus* and *G. swinhonis*. Future area refers to the projected habitable areas of both gecko species in the 2050s.

Country	<i>Gekko japonicus</i>			<i>Gekko swinhonis</i>		
	Location data (selection/all)	Habitable area (km ²)	Future area (km ²)	Location data (selection/all)	Habitable area (km ²)	Future area (km ²)
South Korea	9/48	47,248	45,244	1/3	4,607	1,337
China	125/158	1,091,066	1,018,180	50/61	958,322	776,935
Japan	175/779	321,566	273,308	N/A	9,653	6,879
Total	309/985	1,470,179	1,347,463	51/64	977,952	788,572

Environmental data

We used six environmental variables to generate ENMs for *G. japonicus* and *G. swinhonis* across the extent of their known geographic distributions (Fig. 2; Table 2). Three climatic variables, annual mean temperature, temperature seasonality and annual precipitation, were selected based on a published gecko study (Buckland et al. 2014; Kim et al. 2020a). We also used the distance to urban areas and the distance to forests considering that both gecko species inhabit urban areas adjacent to forests (Kim et al. 2019; Park et al. 2019; Sun et al. 2019). Lastly, altitude was used as a topographic variable, based on previous studies suggesting that both gecko species are mainly distributed in low-elevation urban areas rather than high-elevation mountainous areas (Yan et al. 2010; Kim et al. 2020a). The raster layers for climate and altitude data were obtained from WorldClim 2.1 (<https://www.worldclim.org/>) (Fick and Hijmans 2017). The layers for the distance to forests and urban areas were produced based on the digital land cover map (Copernicus Global Land Service; <https://land.copernicus.eu>). All the raster layers used for ENMs were ~ 1 km spatial resolution. Additionally, we obtained the Köppen-Geiger climate classification map from Gloh2o (<https://www.gloh2o.org/>) (Beck et al. 2023) to further investigate the relationships between the geographic distributions of the two gecko species within the climatic zones in Northeast Asia.

Ecological niche models

We generated ENMs using the maximum entropy (MaxEnt) algorithm, implemented in the R package *SDMtune* (Vignali et al. 2020). MaxEnt is a machine-learning method that has been extensively applied to ecological studies (Phillips et al. 2006; Elith et al. 2011; Heikkinen et al. 2012). This method has also been applied to diverse East Asian squamates (Shin et al. 2021; Park et al. 2023), as well as introduced gecko species (Buckland et al. 2014; Weterings and Vetter 2018; Kim et al. 2020a, b). The following modelling steps were conducted separately for each species. First, we randomly sampled 10,000 background points across the entire study area using the “randomPoints” function of the *dismo* package (Hijmans et al. 2022). Next, we generated 4-fold spatial blocks using the *ENMeval* package version 2.0 (Kass et al. 2021) to generate a default model. We then used this default model to test model

Table 2. Mean values of the six environmental variables used for ecological niche models and their permutation importance and percent contribution in the output models. The value indicates the mean value ± standard deviation (range). The abbreviated variable names are as follows: AMT = annual mean temperature, TS = temperature seasonality, AP = annual precipitation, ALT = altitude, DTU = distance to urban areas, DTF = distance to forests.

Variable	<i>Gekko japonicus</i>			<i>Gekko swinhonis</i>		
	Value	Permutation importance	Percent contribution	Value	Permutation Importance	Percent contribution
AMT (°C)	15.3 ± 1.8 (5.0-21.2)	16.3	9.6	12.8 ± 2.0 (7.0-15.8)	20.5	2.5
TS (°C)	8.2 ± 0.6 (6.1-10.5)	46.9	13.5	10.4 ± 0.9 (8.3-12.0)	2.2	4.4
AP (mm)	1,510.4 ± 349.8 (726.0-2,356.0)	10.5	33.8	640.5 ± 153.2 (435.0-1,231.0)	45.4	18.4
ALT (m)	186.6 ± 303.1 (0-2,367.0)	11.4	4.7	194.3 ± 277.7 (4.0-1,127.0)	4.3	4.5
DTU (km)	2.9 ± 6.4 (0-56.0)	14.4	38.3	2.2 ± 4.8 (0-27.0)	20.3	62.9
DTF (km)	4.4 ± 8.3 (0-59.4)	0.5	0.1	16.9 ± 22.1 (0-103.3)	7.3	7.4

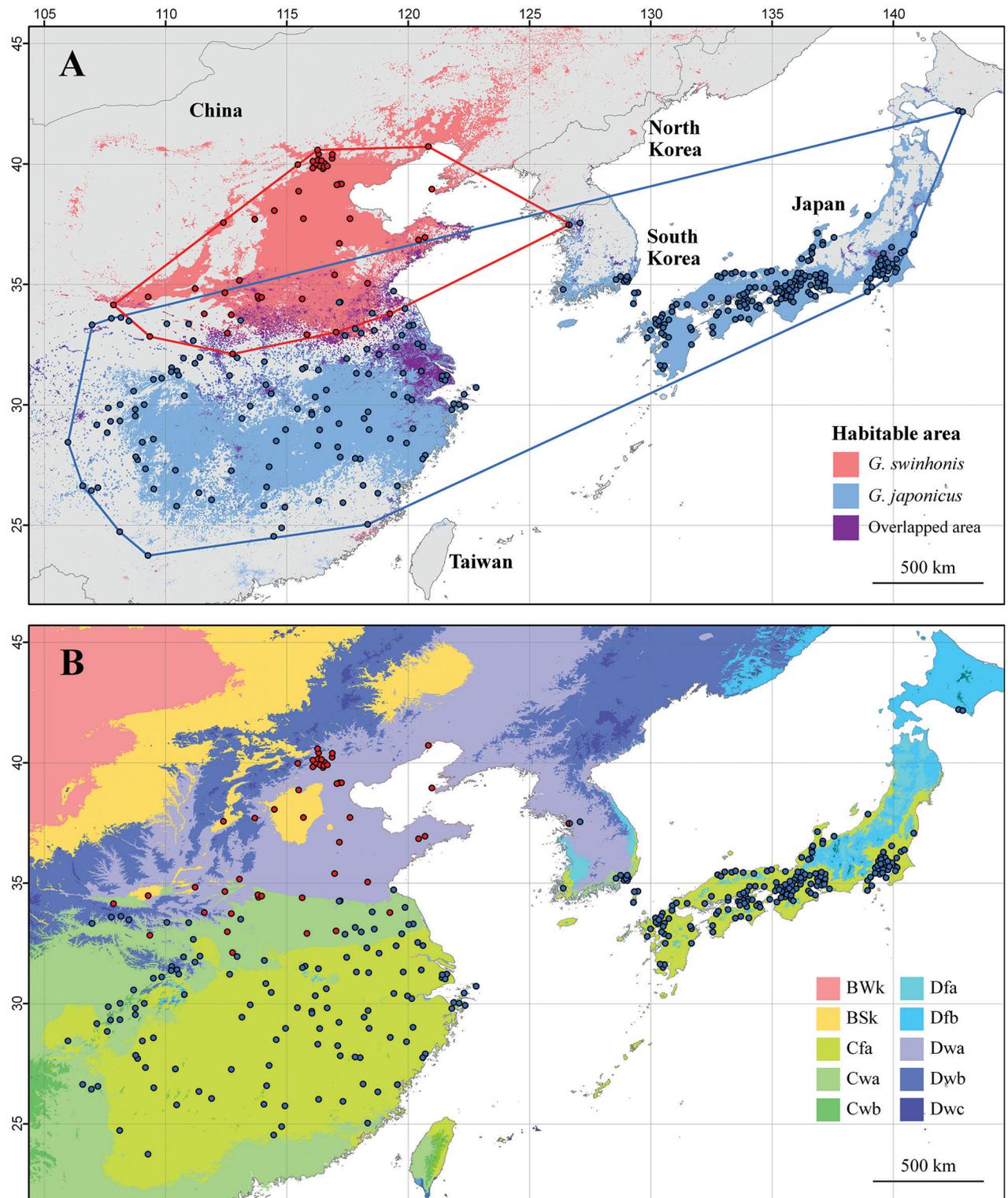


Figure 2. The geographic distribution and predicted suitable habitats for *Gekko japonicus* and *G. swinhonis* in Northeast Asia **A** the suitable habitats were estimated using the MaxEnt ecological niche models. The minimum convex polygon for each species denotes the general extent of the species range **B** the occurrence points of the two gecko species are plotted on the Köppen climate classification map in Northeast Asia. Blue and red points indicate *G. japonicus* and *G. swinhonis*, respectively. The abbreviated Köppen-Geiger climate classifications are as follows – BWk: Cold desert climate, BSk: Cold semi-arid climate, Cfa: Humid subtropical climate, Cwa: Monsoon, Cwb: Subtropical highland climate, Dfa: Hot-summer humid continental climate, Dfb: Warm-summer humid continental climate, Dwa: Monsoon-influenced hot-summer humid continental climate, Dwb: Monsoon-influenced warm-summer humid continental climate, Dwc: Monsoon-influenced extremely cold subarctic climate.

hyperparameters with 13 feature combinations (L, Q, H, P, LQ, LP, QH, QP, HP, LQH, LQP, LQHP and LQHPT; where L = linear, Q = quadratic, H = hinge, P = product, T = threshold) and regularisation values ranging from 0.5 to 5 with a 0.5 increment, using the “gridSearch” function of the *SDMtune* package.

Therefore, we evaluated a total of 130 candidate models per species using spatial block cross-validation and calculated the area under the receiver operating characteristic curve (AUC) from the training (AUC_{TRAIN}) and testing data (AUC_{TEST}), respectively. To select a model with a low degree of overfitting and high predictive performance, we retained the optimal hyperparameter combinations for each species, based on the highest AUC_{TEST} and the lowest AUC_{DIFF} ($AUC_{\text{TRAIN}} - AUC_{\text{TEST}}$) (Warren and Seifert 2011). Based on these filtering criteria, the final ENM for *G. japonicus* was generated with an H feature and a regularisation value of 5 and the final ENM for *G. swinhonis* was generated using LQHPT features combined with a regularisation value of 5. In addition, we also calculated the true skill statistic (TSS) values, based on the sensitivity and specificity of the selected ENM (Allouche et al. 2006), as an additional measure of predictive performance. All the model outputs were in the complementary log-log transformation (cloglog) format (Phillips et al. 2017) and the final model for each species was projected to the geographic area of the study extent. Furthermore, we assessed variable importance, based on permutation importance and percent contribution computed with the “varImp” function of the *SDMtune* package and generated response curves for the input variables (Fig. 3). To define the suitable habitat for both gecko species,

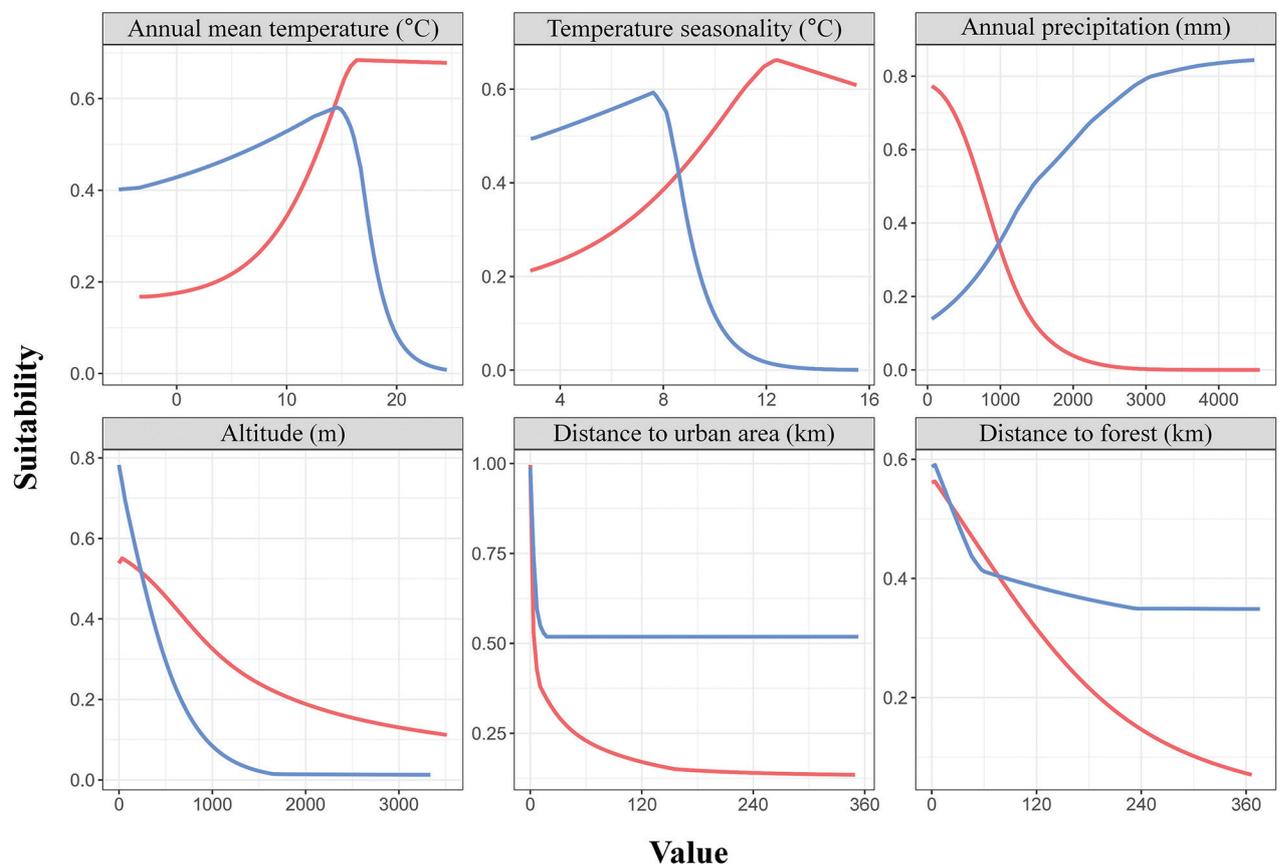


Figure 3. The MaxEnt response curves for six environmental variables, based on the 309 occurrence points for *Gekko japonicus* (blue) and 51 occurrence points for *G. swinhonis* (red).

we converted the predicted continuous habitat suitability output to the presence/absence binary map, using a threshold that maximised the sum of model sensitivity and specificity (maxSSS). This threshold has been widely applied as the most robust amongst the MaxEnt threshold values (Liu et al. 2013). For both species, the current ENMs were repeated without occurrence points from South Korea.

Additionally, we projected the current habitat suitability models onto the climate conditions of the 2050s (climatic averages between 2041 and 2060) to assess the potential for range expansions of *G. japonicus* and *G. swinhonis* in South Korea under future climate change. We used climatic variables simulated in the HadGEM3-GC31 climate model under the Shared Socioeconomic Pathways scenario 2-4.5 (SSP245), provided by the 6th IPCC Assessment Report (IPCC 2022). The SSP245 represents an intermediate climate warming forecast amongst the several projected future climate scenarios (O'Neill et al. 2013) and the HadGEM3-GC31 model is effective in simulating climate distribution (Abbas et al. 2022). This future model was also downloaded from WorldClim 2.1 (<https://www.worldclim.org/>). We maintained the non-climatic variables used in ENMs constant in our future projections. To assess the extrapolation risk associated with temporal projections, we computed the multivariate environmental similarity surface (MESS) using the *dismo* package (Elith et al. 2010; Hijmans et al. 2022). All the output prediction rasters followed the WGS 84 coordinate reference system and were visualised and processed in ArcMap v.10.8.2 (ESRI, Redlands, CA).

Niche comparison

Considering both *G. japonicus* and *G. swinhonis* populations have been recorded in South Korea (Fig. 1), we compared the habitat niches of the two species to gain further insights into the patterns of co-occurrence. First, we extracted raster values for the six environmental variables from the location data of each species and conducted the Kolmogorov-Smirnov test to verify normality. This was followed by t-tests to compare the values of six environmental variables in the habitats of the two species. Second, we conducted the niche identity and the symmetric background tests to quantitatively compare the ecological niches of the two species given habitat availability. The niche identity test compares the observed values of niche overlap to the null distribution of overlap values calculated from randomised pseudo-replicates to test whether the two species occupy identical niches (Warren et al. 2008; Broennimann et al. 2012). The randomisation test for the niche identity test was implemented by first pooling the location data of a species pair and randomising species identity. The pseudo-replicate data was then randomly sampled from this pool of location data, retaining the original number of occurrence points for each species. A statistically significant test result leads to the rejection of the null hypothesis. The symmetric background test compares the observed niche overlap values to the null distribution of niche overlap calculated from the broad environmental background occupied by the two species being compared (Warren et al. 2008; Broennimann et al. 2012). Therefore, the pseudo-replicate samples for the background test were generated using random sampling points within the defined range of each species, rather than sampling from a pool of randomised location data. Significantly higher overlap values indicate higher niche similarity than expected from the null distribution, whereas significantly lower overlap values may indicate niche divergence. We used Schoener's *D* (Schoener 1968) and Warren's *I* (Warren et al. 2008) as in-

dices of niche overlap. These two indices quantify the degree of niche similarity or dissimilarity for a species pair. The values of both indices range from 0 to 1, where values closer to 0 indicate low niche overlap and values closer to 1 indicate high niche overlap (Warren et al. 2008).

We conducted the niche identity and symmetric background tests in ecological space (Broennimann et al. 2012). We first conducted a principal components analysis of environmental variables (PCA-env; Broennimann et al. 2012) across the entire study area using the “*raster.pca*” function from the R package *ENMTools* (Warren et al. 2021). Here, the same set of environmental variables were used to generate the ENMs, where the first two axes of principal components (PCs) were used to define the two-dimensional environmental space. Next, we generated minimum convex polygons (MCPs), based on the occurrence points of *G. japonicus* and *G. swinhonis* to define the geographic range of each species (Fig. 2A). We used this range to extract the PC scores from all grid cells masked by the MCP to define the environmental background within the range of each species. PC scores were extracted from the occurrence points to define the environmental space occupied by each species. This environmental space was divided into a grid of 1,000 × 1,000 cells to produce the occurrence density grid for each species. We then conducted 1,000 replicates of niche identity and symmetric background tests to assess statistical significance, using the functions “*enmtools.ecospat.id*” and “*enmtools.ecospat.bg*”, respectively, in the *ENMTools* package (Warren et al. 2021). The t-test was conducted using SPSS v. 24 (IBM Corp., Armonk, NY, USA) and all the modelling and associated analyses were conducted in R v.4.2.2 (R Core Team 2022).

Results

Field surveys

Through field surveys, we found new populations of *G. japonicus* in Incheon (37.4686°N, 126.6231°E) on 28 April 2022 and in Seoul (37.5493°N, 127.0865°E) on 22 May 2023. We noted that the population of *G. japonicus* in Incheon was found at the same site where the population of *G. swinhonis* was initially observed in South Korea in 2021 (Kwon et al. 2023). In addition, we found a new *G. swinhonis* population in Incheon (37.5134°N, 126.6632°E) on 18 July 2023, approximately 6 km away from the initially discovered population of *G. swinhonis* (Fig. 1).

Ecological niche models

The full details of our ENMs according to the ODMAP framework of Zurrell et al. (2020) is available in Suppl. material 1. Based on the evaluation metrics used in the study, the ecological niche models for both *G. japonicus* ($AUC_{TEST} = 0.818$; $TSS = 0.574$; $AUC_{DIFF} = 0.096$) and *G. swinhonis* ($AUC_{TEST} = 0.941$; $TSS = 0.805$; $AUC_{DIFF} = 0.019$) predicted well and had a low level of overfitting. The threshold values for *G. japonicus* and *G. swinhonis* were 0.217 and 0.334, respectively and the threshold binary maps for both species showed that ENM predictions under current environmental conditions generally match their known geographic distributions (Fig. 2A). Accordingly, the potential distribution of *G. japonicus* covered a broader area of 1,470,179 km² across South Korea, China and Japan (Fig. 2; Table 1). In South Korea, narrow strips of suitable habitats for *G. japonicus* were identi-

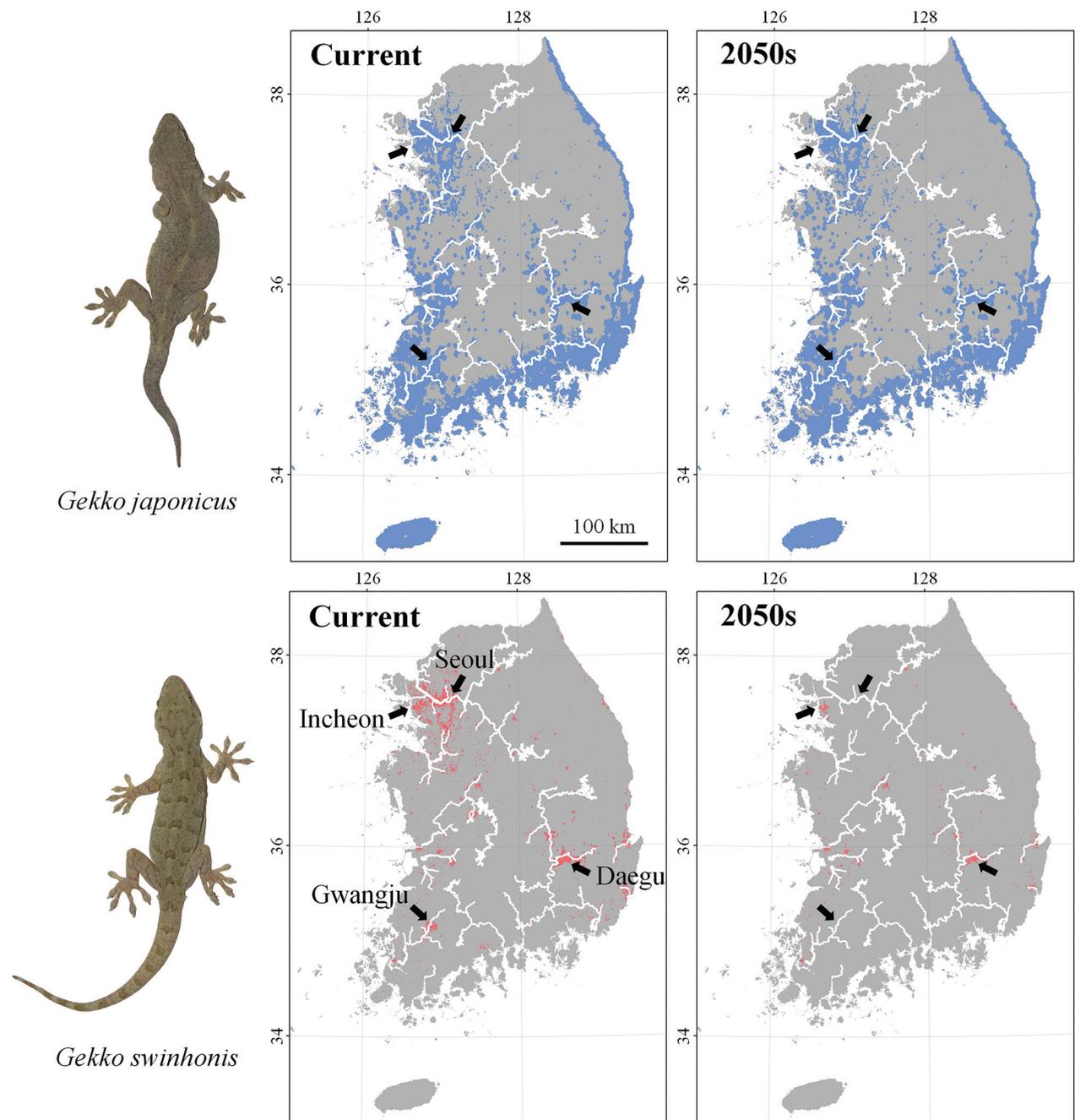


Figure 4. Predicted habitable areas of *Gekko japonicus* (blue) and *G. swinhonis* (red) within South Korea. The black arrows indicate major suitable habitats of *G. swinhonis*.

fied along the eastern, southern and western coasts and several patches were, additionally, predicted along the major riverways and urban areas (Fig. 4). On the other hand, the ENM of *G. swinhonis* predicted a total habitable area of 977,952 km² across South Korea, China and Japan (Fig. 2A; Table 1). The predicted area of optimal environment for *G. swinhonis* in South Korea was primarily located in the metropolitan cities adjacent to coasts and/or major rivers, such as Incheon, Seoul and Daegu (Fig. 4). For the predictions of ENMs, calibrated without occurrence points from South Korea, the extent of suitable habitat was smaller. However, most of the decrease was within the native ranges of the two species in China. While the habitable area also decreased in South Korea when occurrence points from this

country were excluded, most of the habitable areas predicted by the ENMs calibrated with a full set of occurrence points were still predicted to be habitable for both species. The predictions of ENMs, calibrated without the occurrence points from South Korea, are available in Suppl. material 2.

In terms of variable importance, based on permutation importance, the most important variable for *G. japonicus* was determined to be temperature seasonality, followed by annual mean temperature, distance to urban area, altitude, annual precipitation and distance to forests. On the other hand, the most important variable for *G. swinhonis* was found to be annual precipitation, followed by annual mean temperature, distance to urban area, distance to forests, altitude and temperature seasonality (Table 2). Based on the response curves, the predicted habitat suitability of the two species was observed to generally follow a decreasing trend with increasing altitude, the distance to urban area and the distance to forest. The two species also demonstrated a notable difference in their response to the annual precipitation, where the predicted habitat suitability of *G. japonicus* increased with increasing annual precipitation, while the habitat suitability of *G. swinhonis* decreased with increasing annual precipitation.

Projections of ENMs in the 2050s predicted the overall decrease of suitable habitats for both *G. japonicus* and *G. swinhonis* (8% decrease and 19% decrease, respectively; Table 1; Appendix 1). Focusing on South Korea, the future range for *G. japonicus* showed a minor decrease (4% decrease) compared to the current predicted range, while the future range of *G. swinhonis* showed a considerable decrease (71% decrease; Table 1). The predicted range decrease of *G. swinhonis* was found to be most noticeable in the north-western coastal and urban areas, including Seoul and Gwangju (Fig. 4). The MESS results suggested a low extrapolation risk over the study area for both species (Appendix 2).

Niche comparison

Comparing the six environmental variables used in this study, the distribution of *G. japonicus* was found to be significantly associated with higher annual mean temperature ($t = 9.019$, $df = 358$, $P < 0.001$), lower temperature seasonality ($t = -22.360$, $df = 358$, $P < 0.001$), higher annual precipitation ($t = 17.469$, $df = 358$, $P < 0.001$) and closer distance to the urban area ($t = -9.084$, $df = 358$, $P < 0.001$) than *G. swinhonis*. There was no significant difference observed in the altitude and distance to forests between the two species ($P_s > 0.05$) (Fig. 5). Based on the Köppen-Geiger climate classification, a majority of the populations of *G. japonicus* were observed to be distributed in the humid subtropical climate (Cfa), whereas *G. swinhonis* was highly associated with the monsoon-influenced hot-summer humid continental climate (Dwa) (Fig. 2B). The area of Cfa presents an average monthly temperature ranging from 0 °C to 22 °C with no significant difference in precipitation between seasons (Kottek et al. 2006). The area of Dwa has an average monthly temperature ranging from -3 °C to 22 °C with at least a tenfold difference in precipitation between the driest and the wettest months (Kottek et al. 2006).

In terms of the niche comparison in environmental space, the first three principal components (PCs) explained 90.0% of the total variance in the environmental variables, whereof PC1 and PC2 explained 59.5% and 16.2%, respectively (Fig. 6A). Based on the environmental space defined by the first two PCs, the observed niche overlap between *G. japonicus* and *G. swinhonis* was found to be low (Schoen-

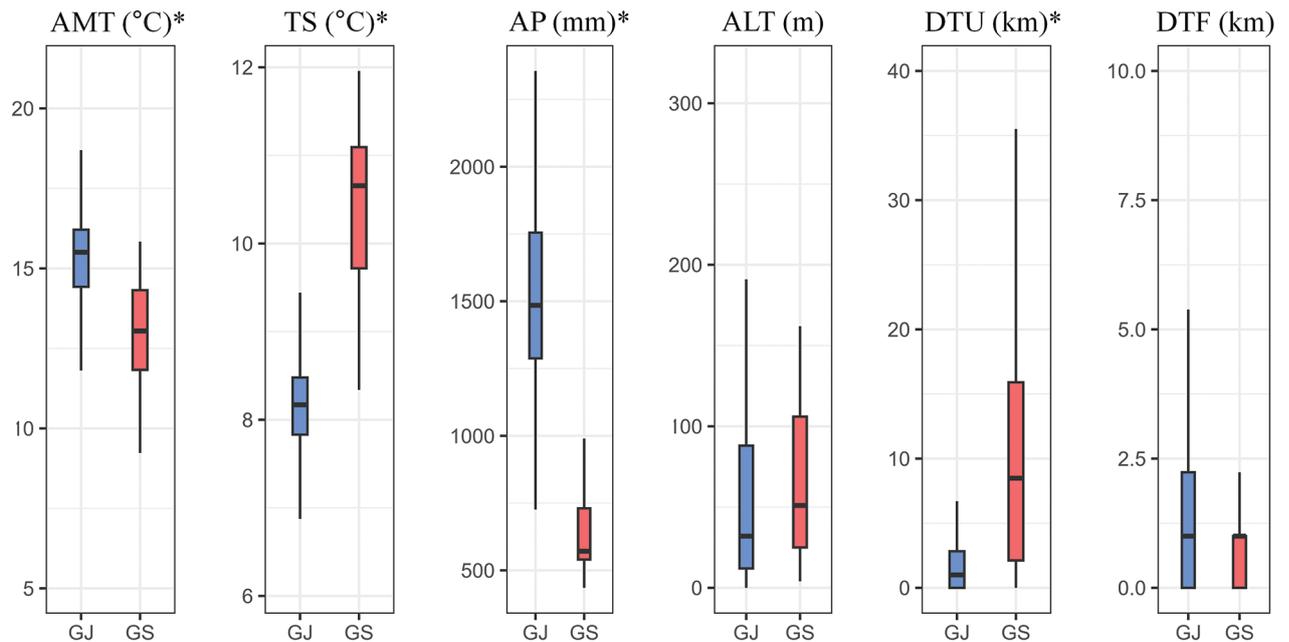


Figure 5. Comparisons of six environmental variables between *Gekko japonicus* (GJ; blue) and *G. swinhonis* (GS; red), based on t-tests. The asterisks indicate the variables that were significantly different between the two species ($P < 0.05$). The abbreviated variable names are as follows: AMT = annual mean temperature, TS = temperature seasonality, AP = annual precipitation, ALT = altitude, DTU = distance to urban areas, DTF = distance to forests.

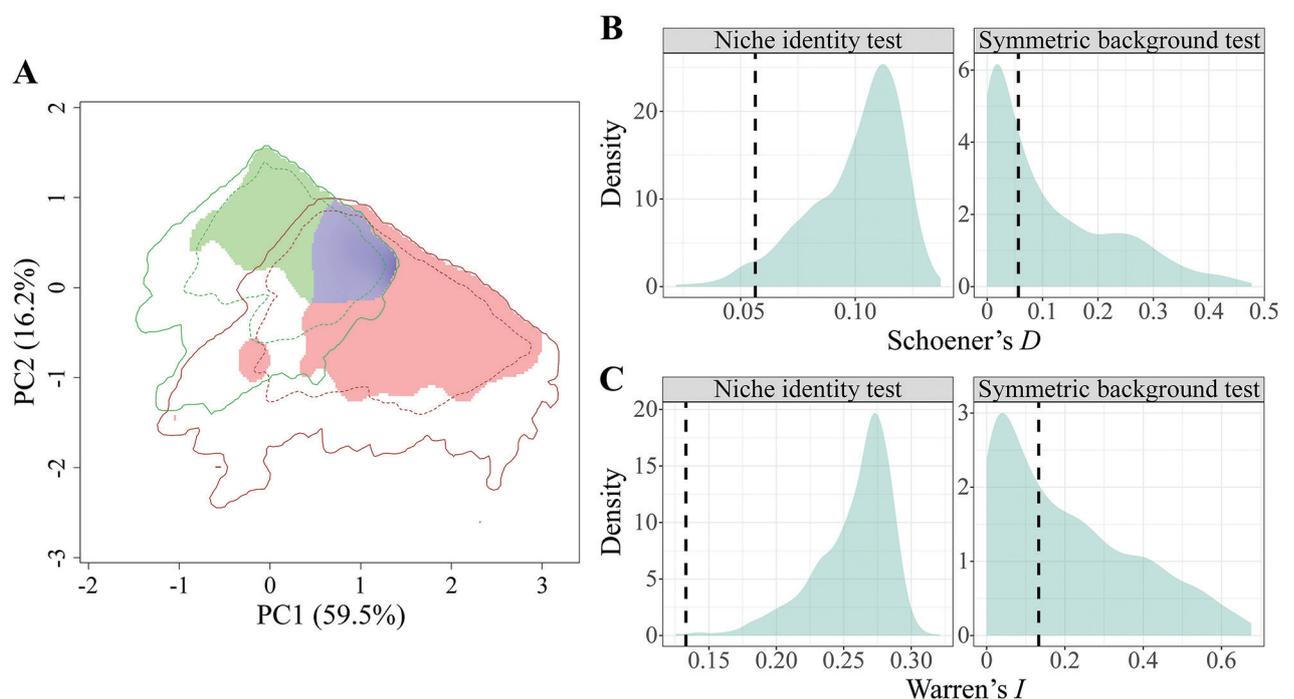


Figure 6. The analyses of niche overlap between the two gecko species **A** the quantified niche overlap (purple) between *G. japonicus* (red) and *G. swinhonis* (green) in the two-dimensional environmental space defined by six environmental variables. Solid contour and dashed lines each indicate the 100% and 50% range of the environmental space. The results of the niche identity test and symmetric background tests are based on Schoener's D **B** and Warren's I values **C**. The empirical niche overlap values (vertical dashed lines) were 0.06, based on Schoener's D and 0.13, based on Warren's I . The statistically significant niche identity test suggests non-identical niches for *G. japonicus* and *G. swinhonis*. On the other hand, the non-significant symmetric background test suggests that the observed niche difference between the two gecko species may be explained by the underlying environmental differences across the ranges of the two species.

er's $D = 0.06$; Warren's $I = 0.13$) (Fig. 6B, C). The observed values of D and I were significantly lower than expected from a random distribution ($P_D = 0.040$; $P_I = 0.003$), rejecting the null hypothesis of no niche identity. On the other hand, the results of the symmetric background test suggested that the observed niche overlap is not significantly lower than expected from the underlying environmental differences ($P_D = 0.46$; $P_I = 0.45$). These results suggest that the low niche overlap between the two gecko species may be primarily attributed to distinct environmental conditions occurring in the geographic ranges of the two species.

Discussion

Habitat suitability of geckos in South Korea

The ENMs in this study demonstrated that the suitable habitats for *G. japonicus* are primarily located along the south-western coastal regions of South Korea, south-eastern China and the south-central coasts of Japan. This distribution pattern is largely consistent with the extent of Cfa in Northeast Asia, as per the Köppen-Geiger climate classification. Based on previous studies on the genetic diversity of *G. japonicus*, it is presumed that the Japanese populations originated from China through overseas translocations about 3,000 years ago, after which some of them spread to South Korea (Kim et al. 2020b; Chiba et al. 2022). Based on the distribution of climatic zones, it is unlikely that they dispersed through northern China and North Korea to South Korea. The populations of *G. japonicus* have only been reported along the southern coastal region of South Korea, including Busan and Mokpo Cities in previous studies (Kim et al. 2019, 2020a). Unlike the northern region, which has the typical continental climate, the southern coastal regions of South Korea exhibit highly suitable conditions of low-temperature seasonality and high annual mean temperature for *G. japonicus*. The ENMs additionally predicted suitable habitats of *G. japonicus* in the north-western coastal regions of the country within the Dwa climatic zone. The field surveys of this study uncovered new populations of *G. japonicus* in Incheon and Seoul, consistent with the ENM results. This may be primarily explained by the adaptation of *G. japonicus* to urban environments because the populations are located out of the best suitable climatic zone of Cfa for the species.

The successful establishment of geckos, adapted to urban areas in different climatic zones from their native range, could be caused by the following factors. First, the underdeveloped claws of geckos are inappropriate for digging holes for brumation, resulting in their not being able to adapt well to habitats with low winter temperatures (Weterings and Vetter 2018; Kim et al. 2020a). However, geckos can utilise urban buildings as microhabitats due to their adhesive toepads and the urban heat island effect and heating systems in buildings may allow them to establish even in areas with otherwise lower temperatures than their original habitats (Wessels et al. 2018). Furthermore, large cities (e.g. Incheon and Seoul) close to international ports are particularly well-suited for the establishment of populations of *G. japonicus* considering they provide highly suitable habitats immediately adjacent to major routes of introduction. Considering new populations of *G. japonicus* were discovered significantly distant from its existing distribution range in South Korea, additional field surveys are required to assess the population size at these locations and to find additional populations. The future projection models presented no significant change in the present habitable area of *G. japonicus* in South Korea in the 2050s. The distri-

bution of *G. japonicus* in the country is currently limited near several international ports. However, the habitable areas are relatively wide along the south and west coastal areas. Considering these situations, populations of *G. japonicus* would be further established in additional habitable areas, including nearby urban areas and even natural ecosystems in the near future if there are opportunities for dispersal. Continuous efforts are, therefore, suggested to prevent the spread of *G. japonicus*.

Based on the ENM predictions, suitable habitats for *G. swinhonis* were mostly located in north-eastern China, with limited predicted habitats in both South Korea and Japan. According to the Köppen-Geiger climate classification, the geographic distribution of *G. swinhonis* largely coincided with the Dwa climatic zone. This climatic zone extends to most of the Korean Peninsula, except coastal areas, as well as north-eastern China and does not include Japan. The most contributed climatic variables for the distribution of *G. swinhonis* were the annual precipitation and the annual mean temperature. *Gekko swinhonis* was distributed in areas with relatively low annual precipitation of 641 mm; the lower the precipitation, the higher the habitat suitability. In addition, compared to *G. japonicus*, *G. swinhonis* has adapted to a lower temperature and severe temperature change, at an annual mean temperature of 12.8 °C and temperature seasonality above 12 °C. *Gekko swinhonis* is known to be able to tolerate temperature fluctuations and maintain thermoregulatory abilities under such conditions (Meng and Zhang 2000). The Dwa climate zone in South Korea is widespread in the north-western coastal and inland regions. However, the ENM for *G. swinhonis* predicted the habitable areas are limited only to cities adjacent to major rivers such as the Han and Nakdong Rivers, barring the north-western region. This could be explained by the elevational distribution of this species. As per the results of this study, *G. swinhonis* is primarily observed in lowlands with altitudes below 200 m above sea level across the geographic range in China, while the central and eastern areas of South Korea are mainly composed of mountainous areas with high altitudes (Park et al. 2023). On the other hand, the north-western coastal regions, including Incheon and Seoul, are within the Dwa climate zone, generally have low altitudes and are connected to eastern China through active overseas trade through major international ports. Therefore, the northwest coastal areas are particularly well-suited for the introduction and establishment of *G. swinhonis* populations (Kim et al. 2018; Sun et al. 2019). According to the ENM projected for the climatic conditions of the near future (2050s), the suitable habitats of *G. swinhonis* in South Korea are expected to decrease significantly by 29% from the current suitable habitats. In particular, a significant decrease is projected in the currently highly suitable habitats in the north-western coastal area, including Seoul. This is most likely due to the transition of climatic zones in southern areas following climate change (Park et al. 2022b), thereby rendering these areas unsuitable for *G. swinhonis*. Nevertheless, as *G. swinhonis* is well-adapted to urban areas (Meng and Zhang 2000; Sun et al. 2019), it could persist in South Korea through changes in microhabitat use that can effectively buffer the effects of climate change.

Niche difference between the two gecko species

Our results demonstrate that *G. japonicus* and *G. swinhonis* have adapted to different climatic environments. Firstly, *G. japonicus* prefers warmer and more humid climatic conditions than *G. swinhonis*, as per the ENMs. For example, there is a significant

difference in the average annual precipitation between the ranges of the two gecko species. While the habitat of *G. japonicus* receives an average annual precipitation of approximately 1,510 mm, the average annual precipitation within the range of *G. swinhonis* is approximately 640 mm. The main criterion for classifying Cfa and Dwa, where *G. japonicus* and *G. swinhonis* are primarily distributed, respectively, is also precipitation (Kottek et al. 2006; Beck et al. 2023). In addition, according to the response curve, the habitat suitability of *G. japonicus* increased as the annual precipitation increased, while the suitability of *G. swinhonis* tended to increase with the decrease in annual precipitation. Second, *G. swinhonis* appears to better tolerate seasonal temperature fluctuations and lower annual mean temperature than *G. japonicus*. In terms of the distribution of two species within China, *G. japonicus* occurs across south-eastern China with a mild temperate climate and *G. swinhonis* inhabits north-eastern China which has a continental (cold) climate. Looking at the response curves, the habitat suitability of *G. japonicus* drops sharply at a temperature seasonality below 8 °C, unlike *G. swinhonis*, which appears to tolerate greater temperature fluctuations in its habitats. Consistent with the environmental differences in their native distribution areas, the results of niche identity and the symmetric background tests suggested that the low degree of niche overlap between the two species may be caused by different climatic conditions in their habitats. Such climatic heterogeneity across the landscape is one of the major drivers of speciation in closely-related reptile species (Hua and Wiens 2013; Jezkova and Wiens 2018). *Gekko japonicus* and *G. swinhonis* have adapted to different climatic zones, despite their close phylogenetic relationships (Kim et al. 2016; Xia et al. 2022), morphological similarities (Rösler et al. 2011; Kwon et al. 2023) and similar microhabitat use (Kim et al. 2018; Sun et al. 2019).

Based on the actual occurrences, predicted suitable habitats and estimated niche differences, the co-occurrence of *G. japonicus* and *G. swinhonis* in South Korea may be best explained by the two species occupying patches of suitable habitats within narrowly overlapping ecological niches. Since the north-western coastal regions, including Incheon and Seoul, are within the Dwa climatic zone, it is likely to be more habitable for *G. swinhonis* than *G. japonicus*. Nevertheless, this area still falls within the range of *G. japonicus* defined by MCP, which is further supported by the ENM results and the presence of newly-detected populations. It is also likely that this area may represent the distribution edge of both *G. japonicus* and *G. swinhonis*. The northern part of the distribution range of *G. japonicus* and the southern part of the distribution range of *G. swinhonis* are in contact across their native ranges in China. This co-occurrence may be further attributed to the adaptation of these species to urban residential microhabitats. Various shelters in urban areas could allow two gecko species to find their suitable habitats even though they have adapted to different climate zones. For example, *G. japonicus* shares habitats with *G. tawaensis* and hybridisation occurs within some areas of Japan (Toda et al. 2003, 2006) because of its non-territorial characteristics (Park et al. 2019).

Origins and routes of introductions

The continued discovery of new gecko populations possibly indicates ongoing introductions of non-native geckos into South Korea. Directly detecting the introduction of geckos *in situ* is generally difficult due to their small size, cryptic colouration and nocturnal ecology. Considering the genetic and geographic patterns of population distributions in South Korea (Kim et al. 2020b; Kwon et al. 2023), the origins of

these non-native individuals are most consistent with the introduction of stowaways in cargo ships. Geckos have spread to timbers and cargoes through international trade due to their high stealth and adhesive pads (Rödder et al. 2008; Bomford et al. 2009; Hoskin 2011). Considering most of the gecko populations in South Korea have been found near international ports, such as Incheon, Mokpo, Masan and Busan Ports (Lee et al. 2004; Kim et al. 2020b), overseas trade by ships could be a primary route for introduction into South Korea. On the other hand, Gimhae, Yangsan and Seoul are located relatively far inland from the international ports. While their distance to international ports may be viewed as puzzling, these inland locations are all situated along the major rivers of South Korea (the Han and Nakdong Rivers) that drain to the seas leading to several international ports. It is noted that the Han and Nakdong Rivers were the major routes of inland trade and transportation until the mid-1900s, before the development of extensive road networks. This may represent an additional mode of dispersal of non-native geckos through inland water transportation along with land transportation (Bauer and Baker 2008; Hoskin 2011). Further population genetic studies as well as fine-scale spatial analyses are encouraged to shed light on the detailed history of the establishment of geckos in South Korea.

Conclusion

Our results demonstrated that *G. japonicus* and *G. swinhonis* have adapted to distinct climatic zones in their habitats and have divergent ecological niches, despite their morphological similarities and close phylogenetic relationships. Nevertheless, their microhabitats in urban areas that provide shelter even under unsuitable climates and similar introduction routes, allow co-occurrence in South Korea. The current distributions of introduced geckos in South Korea are likely explained by multiple overseas introduction events mediated by international trade, followed by the successful establishment of populations in suitable habitats immediately adjacent to the points of introduction. Furthermore, given that numerous non-native reptile species inhabit novel niches within their introduced range (Li et al. 2014; Wiens et al. 2019) and that MaxEnt tends to underestimate the adaptive capacity of various introduced reptile species (Fieldsend et al. 2021; Claunch et al. 2023; Shin et al. 2024), our ENMs are likely to be underestimating the true establishment potential of these species. This is especially likely as we kept the non-climatic variables constant during the model transfer to future climatic conditions. As such, further anthropogenic activities and urbanisation, combined with acclimatisation or adaptation to local environmental conditions, may open up favourable habitats and enable these geckos to colonise far greater of South Korea than what our ENMs predicted. Therefore, we suggest the establishment and implementation of rigorous quarantine protocols for international cargo arriving in South Korea, especially at the major trading ports located in the western and southern coastal regions, to prevent further introduction of non-native geckos. In addition, targeted field surveys in urban areas near international ports and major rivers should be conducted at regular intervals to uncover additional introduced gecko populations that have gone undetected.

Acknowledgements

We thank Hyerim Kwon and Min-Woo Park for their help in the field and data management.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was funded by grants from the National Institute of Ecology and the Ministry of Environment of Korea (grant numbers NIE-C-2024-09 and NIE-A-2024-08).

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Il-Kook Park: Conceptualisation, Formal analysis, Investigation, Visualisation, Writing – Original draft; Yucheol Shin: Methodology, Software, Formal analysis, Writing – Original draft; Hae-Jun Baek: Writing – Review and Editing, Resources, Project administration, Funding Acquisition; Jongsun Kim: Investigation, Validation, Data Curation, Writing – Review and Editing, Validation; Dae-In Kim: Investigation, Writing – Review and Editing; Minjeong Seok: Investigation, Writing – Review and Editing; Yaechan Oh: Investigation, Writing – Review and Editing; Daesik Park: Conceptualisation, Validation, Resources, Supervision, Writing – Review and Editing

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Data availability

The full R codes for the MaxEnt ENMs and niche analyses can be found in the GitHub repository of Yucheol Shin (<https://github.com/yucheols/Gekko>).

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Appendix 1

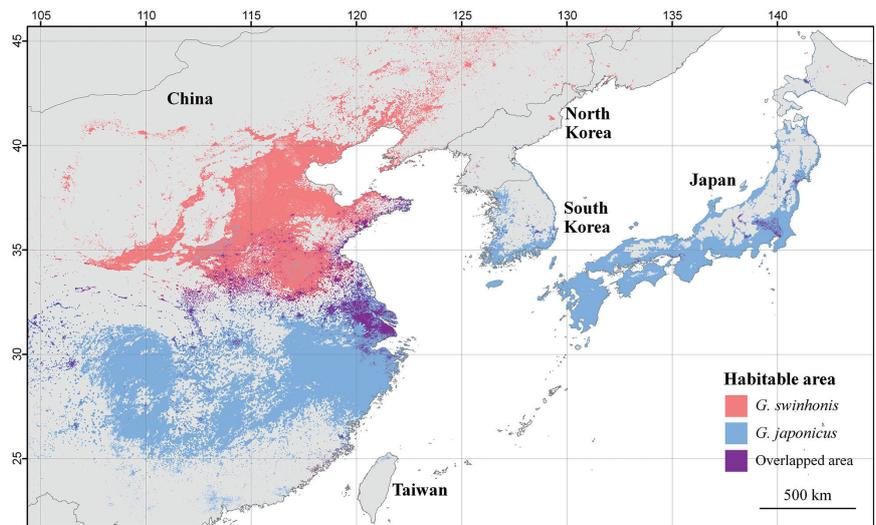


Figure A1. Predicted habitable areas of the two gecko species in the 2050s, based on the SSP245 scenario.

Appendix 2

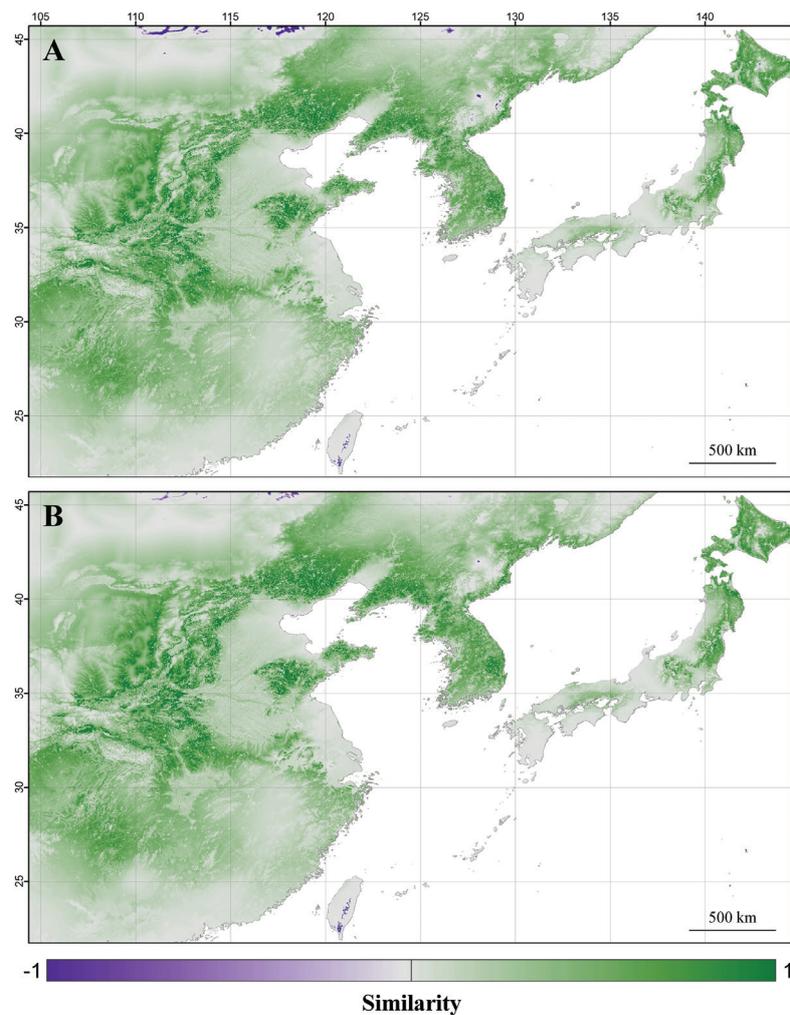


Figure A2. Multivariate environmental similarity surfaces (MESS) for the ecological niche model projections of A *G. japonicus* and B *G. swinhonis*.

Supplementary material 1

The ODMAP niche modelling report protocol

Authors: Il-Kook Park, Yucheol Shin, Hae-Jun Baek, Jongsun Kim, Dae-In Kim, Minjeong Seok, Yaechan Oh, Daesik Park

Data type: docx

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Link: <https://doi.org/10.3897/neobiota.93.118085.suppl1>

Supplementary material 2

Predictions for models calibrated without occurrence points from South Korea

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