Species Distribution Modeling Provides New Insights into Different Spatial Distribution Patterns among Native and Alien Freshwater Turtles in Japan

Authors: Kagayama, Shawichi, Ogano, Daiichi, Taniguchi, Mari, Mine, Kanako, Ueno, Shintaro, et al.

Source: Current Herpetology, 39(2) : 147-159

Published By: The Herpetological Society of Japan

URL: https://doi.org/10.5358/hsj.39.147

Current Herpetology 39(2): 147–159, August 2020
© 2020 by The Herpetological Society of Japan
doi 10.5358/hsj.39.147

Species Distribution Modeling Provides New Insights into Different Spatial Distribution Patterns among Native and Alien Freshwater Turtles in Japan

Shawichi KAGAYAMA[1]*, Daiichi OGANO[2], Mari TANIGUCHI[3],
Kanako MINE[3], Shintaro UENO[3], Hiroo TAKAHASHI[4],
Naoki KAMEZAKI[5], and Masami HASEGAWA[6]

[1]*Department of Biology, Graduate School of Science, Toho University, Miyama 2–2–1, Funabashi, Chiba 274–8510, JAPAN*
[2]*Chiba Wildlife Research Society, Semata 962–40, Ichihara, Chiba 290–0151, JAPAN*
[3]*Nature Recovery Co., Ltd., Nishidaidori 1–1–5–504, Nagata, Kobe, Hyogo 653–0844, JAPAN*
[4]*Japan Wildlife Research Center, Kotoubashi 3–3–7, Sumida, Tokyo 130–8606, JAPAN*
[5]*Department of Biosphere-Geosphere Science, Faculty of Biosphere-Geosphere Science, Okayama University of Science, Ridai-cho 1–1, Kita, Okayama, Okayama 700–0005, JAPAN*
[6]*Department of Biology, Faculty of Science, Toho University, Miyama 2–2–1, Funabashi, Chiba 274–8510, JAPAN*

Abstract: The endemic Japanese freshwater turtle *Mauremys japonica* is the most common turtle in foothill areas, whereas it is usually absent or scarce in lowland environments in Japan. In contrast, another turtle, Reeves' pond turtle (*M. reevesii*), usually inhabits lowland areas. Explanation of this pattern based on habitat segregation between *M. japonica* and *M. reevesii* remains controversial because several studies have emphasized that *M. reevesii* is not indigenous but rather introduced from mainland China and the Korean Peninsula. The newly proposed hypothesis is that *M. reevesii* and the recently introduced red-eared slider (*Trachemys scripta elegans*) have excluded *M. japonica* from certain suitable habitats in lowland areas. In this study, to test whether *M. japonica* originally had a broad distribution range covering the habitats currently occupied exclusively by *M. reevesii* and *T. s. elegans*, we applied species distribution modeling using MaxEnt and ENMTools to estimate the suitable habitats and ecological niches of *M. japonica*, *M. reevesii*, and *T. s. elegans*, respectively, and examined these similarities. The models showed that *M. japonica* had the largest suitable habitat range, from flatlands to foothill areas, compared to that of alien species; however, almost the entire habitat area of the native turtle and that of the aliens overlapped. Moreover, these turtles possessed significantly high niche similarity. These results are consistent with the hypothesis that recent species interactions have shaped the distribution of indigenous and alien turtles, although the precise ecological and evolutionary processes have not yet been determined.

Key words: Conservation biology; Freshwater turtle community; Interspecific interaction; Niche similarity; Species distribution model

---

*Corresponding author.
E-mail address: geoemyda.s@gmail.com

Introduction

The Japanese pond turtle (*Mauremys japonica*), Reeves' pond turtle (*M. reevesii*), and the red-eared slider (*Trachemys scripta elegans*), are widely distributed in Honshu, Shikoku, and Kyushu islands, Japan (Yasukawa et al., 2008; Lovich et al., 2011; Taniguchi et al., 2015). The endemic Japanese freshwater turtle *M. japonica* is most common in foothill areas, whereas it is usually absent or scarce in lowland environments (Yabe, 2002; Okada et al., 2005; Yamada et al., 2008; Tempaku et al., 2009; Kamezaki et al., 2017; Kagayama, 2019), although the turtles can be found in lowland areas in some areas of Japan (e.g., Yabe, 1996; Kohmatsu et al., 2000; Kosuge et al., 2003; Noda and Kamata, 2004; Taniguchi et al., 2015; Kagayama et al., 2017). In contrast, *M. reevesii* is most abundant in lowland environments (Yabe, 2002; Kosuge et al., 2003). Until recently, this distributional pattern has been interpreted as different habitat preferences between *M. japonica* and *M. reevesii*. However, the hypothesis about the relationship between *M. japonica* and *M. reevesii* has become controversial because recent studies have proposed that *M. reevesii* is not indigenous but rather introduced from mainland China and/or the Korean Peninsula (Hikida and Suzuki, 2010; Lovich et al., 2011; Suzuki et al., 2011).

A nationwide turtle survey conducted by the Nature Conservation Society of Japan demonstrated that *M. japonica* had become uncommon in many areas of Japan, and the most abundant freshwater turtle was the introduced red-eared slider *T. s. elegans* and *M. reevesii* (The Nature Conservation Society of Japan, 2014). Some studies have suggested that recent population declines of *M. japonica* have been caused not only by habitat degradation due to river alteration for flood control (Usuda et al., 2012) and predation by the introduced raccoon, *Procyon lotor* (Kosuge and Kobayashi, 2015), but also by interspecific interactions with alien turtles with similar ecological requirements (Yasukawa et al., 2008).

A recent study advocated that population declines and recent distribution patterns of *M. japonica* may be driven by interspecific interactions with the two alien turtle species (*M. reevesii* and *T. s. elegans*), based on a research result that *M. japonica* was abundant and widely distributed in lowland areas in the island where these alien turtles were absent (e.g., Tanegashima Island [Taniguchi et al., 2015]). Therefore, it is expected that *M. japonica* originally had a large distribution range, including large areas in the flatlands of Japan where recent species interactions with alien turtles have led to the reduction or elimination of native species, especially in lowland areas.

To examine the hypothesis of replacement of *M. japonica* with alien turtle species in lowland areas of Japan, large-scale and long-term field studies, such as removing alien turtle species from native turtle habitats to potentially demonstrate the increase in native turtle populations following eradication of the alien species, might provide the most compelling evidence, but would require much time and research efforts. However, there is a recent trend to use species distribution models (SDMs) to enable the prediction of suitable habitats for the target species under broad circumstances (Guisan and Thuiller, 2005). For example, Anderson et al. (2002) predicted the fundamental habitat range of two related indigenous South American pocket mice using SDMs and explained the mutually exclusive distribution ranges between the two native species based on environmental preferences and the competitive exclusion hypothesis. Warren et al. (2008) provided an approach that can evaluate niche similarity among two target species by quantitatively using the predicted SDMs. In the present study, we tested the hypothesis that recent distribution patterns of *M. japonica* were influenced by alien turtle species. If these turtles were segregated by differences in habitat preferences among the turtle species, the model would indicate that there was little overlap in suitable habitats and niche similarity among turtle species. On the other hand, if alien species displaced indigenous turtles, the model would indicate that these turtle species have large overlaps.

Therefore, the goal of this study was to test the hypothesis that recent species interactions by alien freshwater turtle species have molded the distribution of the indigenous turtle species. SDMs with presence-only data (MaxEnt and ENMTools; Warren et al., 2008) were applied to estimate the suitable habitat of the three turtle species within the distribution range of *M. japonica* and to evaluate the niche similarity among these turtle species.

Materials and Methods

Study area

In this study, we collected the locality records of three freshwater turtles in Honshu, Shikoku, Kyushu, and on adjacent islands in their distribution range in Japan (Yasukawa et al., 2008; see details in the Data acquisition subsection). Because the Hokkaido and Ryukyu archipelagos are not within the natural distribution ranges of *M. japonica*, we did not include these areas in our study region. Moreover, we removed the locality records of *M. japonica* from the Tohoku regions outside its natural distribution range (Yasukawa et al., 2008); however, alien turtle locality records from this region were included. These locality records (for three turtle species) were collected from flatland to foothill regions (elevation, mean=69.8 m, range=–0.9 to 1,043.6; slope, mean=3.2°, range=0–18.8) and various land use environments (e.g., forest, mean =319,236.3 m^2, range=0–1,099,423; paddies, mean=177,836.3 m^2, range=0–1,005,142; cropland, mean=62,937.1 m^2, range=0–979,679, n=2,889; these data were provided by the Ministry of Land, Infrastructure, Transport and Tourism of Japan [2009]). In addition, data were collected from various climatic environments (the highest temperature of the warmest month [August], mean=31.4°C, range=25.0–33.5; the lowest temperature of the coldest month [January], mean=0.15°C, range=–6.4 to 9.0; annual precipitation, mean=1,644.1 mm, range=943.2–3,339.1, n=2,889). The sources of topography and climate data are provided in the Data acquisition section.

Data acquisition

The longitude and latitude of the freshwater turtle (three species) localities were collected from multiple data sources from the early 1970s to the late 2010s (Ministry of the Environment of Japan, 1988, 1993, 2001; The Nature Conservation Society of Japan, 2014; Taniguchi et al., 2015; Kagayama et al., 2017; Ogano, unpublished data). These occurrence data were collected from past collection records, field visual surveys, capture (by hand and traps) studies, and photographs taken by citizens. A total of 811, 1,066, and 1,012 localities for *M. japonica*, *M. reevesii*, and *T. s. elegans*, respectively, were used (Fig. 1). Occurrences collected from artificial habitats, such as parks, shrines, and temple ponds, were excluded. Because these occurrences included the citizen-collected data, presence sites might be concentrated in areas that are easy to observe and have a high human population density. In addition, it was necessary to remove localities with the possibility of introducing the native species. To avoid biases in the spatial distribution of the occurrence data, one locality was chosen randomly from 1 km grid cells when multiple species localities occurred therein. Thus, in this study, the number of localities was 616 (*M. japonica*), 763 (*M. reevesii*), and 635 (*T. s. elegans*), respectively.

We selected four climatic and one topographic variable assuming that these variables have an effect on the distribution of freshwater turtle species (Fig. 2). The climatic variables included the highest temperature of the warmest month (August) (hereafter, max. temperature), the lowest temperature of the coldest month (January) (hereafter, min. temperature), annual precipitation, and total

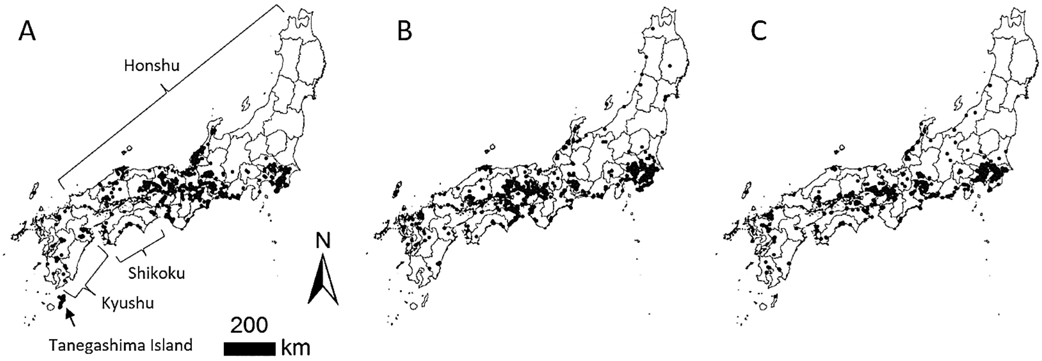


FIG. 1. Presence sites of freshwater turtles. (A) *Mauremys japonica* (n=811), (B) *Mauremys reevesii* (n=1066), (C) *Trachemys scripta elegans* (n=1012).

daylight hours from April to November, which were provided by the Japan Meteorological Agency (2012). The topographic factor was the mean slope provided by the Ministry of Land, Infrastructure, Transport and Tourism of Japan (2011). It was expected that climatic factors, such as the highest temperature of the warmest month (August), the lowest temperature of the coldest month (January), and total daylight hours limited the distribution of freshwater turtle species because these ectotherms required moderate temperatures and solar radiation to control their body temperature (Vitt and Caldwell, 2014). Furthermore, slope as the topographic factor and precipitation may affect the dispersal or establishment of freshwater turtles in the high-elevation regions because the distribution of turtles may be limited by the velocity of water currents (Buhlmann and Vaughan, 1991; Usuda et al., 2012; Kagayama, 2019). All five variables of grid data were divided by 1 km grid cells using ArcGIS 10.0 (ESRI, CA, USA), and we calculated only the total daylight hours from April to November using ArcGIS 10.0 and the Mesh Climate Value, which is a contiguous nationwide grid consisting of 1 km^2 cells because most freshwater turtles hibernate during winter in the water (Ultsch, 1989). In this study, we did not add land use and anthropogenic effects as variables (e.g., paddy, cropland, and distance from the city or road) because the number of samples would decrease if we arranged the presence sites by each variable in the same period. This might lead to a decrease in native turtle distribution sites in flatland regions and could cause erroneous results regarding suitable habitat distribution patterns of the native turtle species. Moreover, we did not select elevation, altitude, or latitude as variables because elevation usually is highly correlated with slope, and we already used climatic factors that may limit the vertical and horizontal distribution ranges of these ectotherms, such as air temperature during the warmest and coldest months, and annual precipitation, as variables.

Constructions of SDMs

We constructed SDMs for the three freshwater turtles, *M. japonica*, *M. reevesii*, and *T. s. elegans* using MaxEnt ver 3.3.3k (Phillips et al., 2006). MaxEnt predicts the occurrence probability for each grid cell as a function of the environmental variables based on presence-only data of target species and background environmental variables (Phillips et al., 2006). In the present study, the range of prediction for these turtles was within the distribution range of *M. japonica* (Yasukawa et al., 2008), including Honshu, Shikoku, and Kyusyu (Yasukawa et al., 2008), and we produced a buffer with a radius of 25 km from

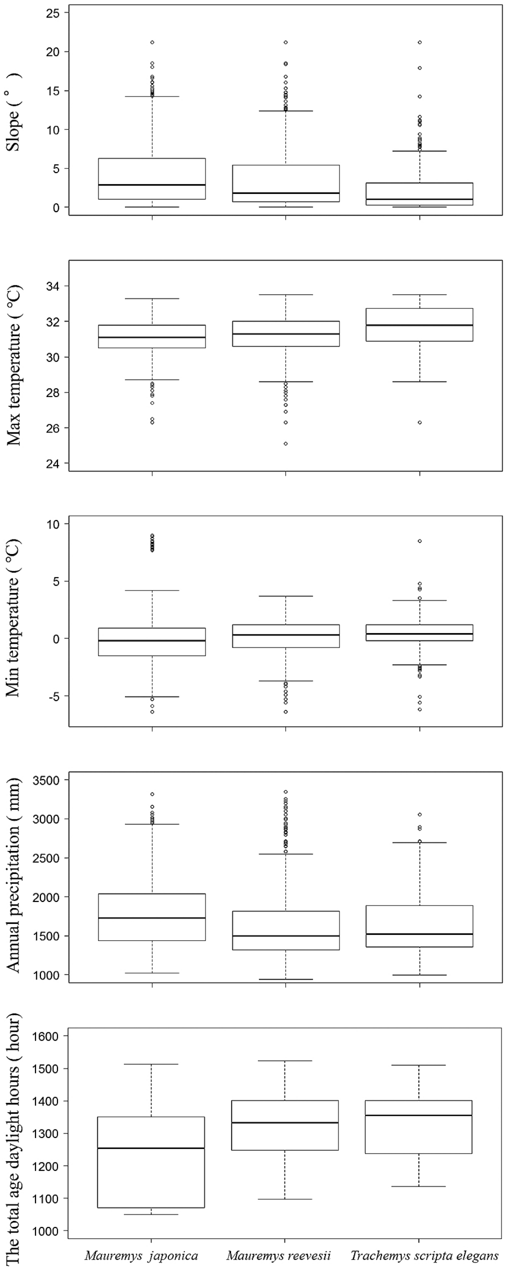


FIG. 2. Candidate environmental variables affecting habitat suitability of freshwater turtles. Data obtained from the occurrence records for the three species were used (*Mauremys japonica*, n=811; *Mauremys reevesii*, n=1,066; *Trachemys scripta elegans*, n=1,012).

the presence sites of all three turtle species. Indeed, surveys were conducted to define backgrounds as grid cells within these buffers and prevented background areas from being included as areas that we did not survey, such as high altitude areas (APPENDIX I). MaxEnt randomly sampled 10,000 background locations from covariate grids and a logistic output of MaxEnt was used, and the suitability value ranged from 0 (unsuitable habitat) to 1 (suitable habitat).

We performed MaxEnt analysis by randomly selecting 25% of the occurrence points as test points and ran 100 replications. In addition, we evaluated the accuracy of the model by the area under the curve (AUC) of the receiver operating characteristic plots. In general, values of AUC≥0.7 were regarded as good predictors (Hosmer et al., 2013).

Comparisons of the SDMs

To test the differences among SDMs, we used the framework of Warren et al. (2008) using ENMTools ver. 1.4.3 (Warren et al., 2010). We used the concept that compares niches provided by Peterson et al. (1999), niche similarity, which determines whether SDMs of related species predict one another's known occurrences better than expected under the null hypothesis that they provide absolutely no information about one another' s ranges (Takami and Osawa, 2016). In the present study, the background similarity test was implemented in ENMTools to test these questions. The measures of niche similarity that quantitatively compared niche models were based on the value of the sum of differences in suitable habitat probability between two species at all points in the objective area were provided (Warren et al., 2008). Then, in accordance with Warren et al. (2008), we used two statistical measures, Schoener's D (Schoener, 1968) and Warren's I (Warren et al., 2008), to measure niche similarities. Both similarity measures ranged from 0, where species predicted environmental tolerances did not overlap at all, to 1, where all grid cells were estimated to be equally suitable for both species (Warren et al., 2010). These similarity statistics were calculated for comparisons between (1) *M. japonica* and *M. reevesii*, (2) *M. japonica* and *T. s. elegans*, and (3) *M. reevesii* and *T. s. elegans*. To evaluate the differences between SDMs, background similarity tests were implemented in ENMTools. The test may be used to determine whether the SDMs obtained from two allopatrically distributed populations are more different than expected given the underlying environmental differences between the regions in which they occur (Warren et al., 2010). The test addresses this hypothesis by generating a null distribution for the SDM difference expected between one population and random occurrence points placed within the range of another population (Warren et al., 2010). We used this test to construct the null distribution of similarity statistics between the SDMs based on the localities of one species and those based on 100 replications of random points drawn from the geographic range of the other species (Peterson et al., 1999; Warren et al., 2008). Warren et al. (2008) showed that the inclusion of unsuitable habitat for a species can bias the result, the geographic range of each turtle species that generated random points was restricted to areas inside the 25 km buffer circles or cells involving the presence localities of each turtle species (APPENDIX II). We conducted bidirectional tests because the background of the similarity test can yield different results when the comparison is reversed (Warren et al., 2010). To determine whether the distribution of one species positively or negatively predicted that of the other species, the lower and upper 2.5% value of the null distribution were regarded to indicate that the SDMs of the two species were significantly dissimilar and similar, respectively (Takami and Osawa, 2016).

RESULTS

Constructions of SDMs

Three SDMs were constructed and high performance was evidenced by the relatively high AUC values (average test AUC: *M. japonica*, 0.75; *M. reevesii*, 0.82; *T. s. elegans*, 0.87). The predicted suitable habitat of *M. japonica*, *M. reevesii*, and *T. s. elegans* in Honshu, Shikoku, and Kyushu are shown in Fig. 3A, B, and C, respectively. In Fig. 3, each predicted suitable habitat mapped was extracted only over thresholds for each species. These thresholds, which were divided into categories based on whether they were suitable habitats or not, used the maximum training sensitivity plus specificity logistic threshold (Jiménez-Valverde and Lobo, 2007). These values were 0.41 (*M. japonica*), 0.37 (*M. reevesii*), and 0.29 (*T. s. elegans*). Figure 3 illustrates that the estimated suitable habitat of the three freshwater turtle species had a wide range distributed around Japan. The indigenous turtle species had the broadest suitable habitat among all three turtle species. On the other hand, the two alien species, *M. reevesii* (55,526 km^2) and *T. s. elegans* (47,031 km^2), had a narrower range than *M. japonica* (80,878 km^2). Furthermore, Figs 4 and 5 show the large overlap of suitable habitat among the native and two alien species within the predicted suitable habitat of *M. japonica*. The area of duplication was as follows: overlap of all three species (34,349 km^2), *M. japonica* and *M. reevesii* (8,096 km^2), *M. japonica* and *T. s. elegans* (3,561 km^2), and *M. japonica* only (34,872 km^2).

Among the three turtle species, the permutation importance of the three climatic variables, including max. temperature, min. temperature, precipitation, and slope, and the one topographic variable had particularly high values. Of the five environmental variables, the importance of max. temperature, min. temperature, and slope for *M. japonica*, min. temperature, precipitation, and slope for *M. reevesii*, and slope and min. temperature for *T. s. elegans* was higher than that of any other factors (Table 1).

Comparison of SDMs

Results of background similarity tests indi-

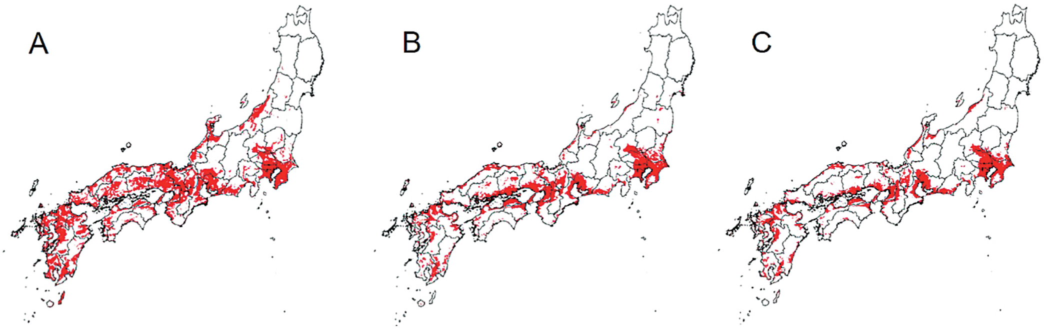


FIG. 3. Predicted suitable habitat of (A) *Mauremys japonica*, (B) *Mauremys reevesii*, and (C) *Trachemys scripta elegans*. Red grids indicate suitable habitats that were extracted over thresholds for each species.

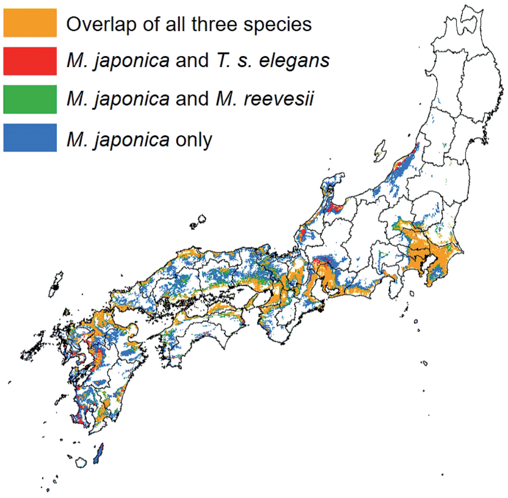


FIG. 4. *Mauremys japonica*'s predicted suitable habitat, and overlap area between *M. japonica* and alien turtle species.

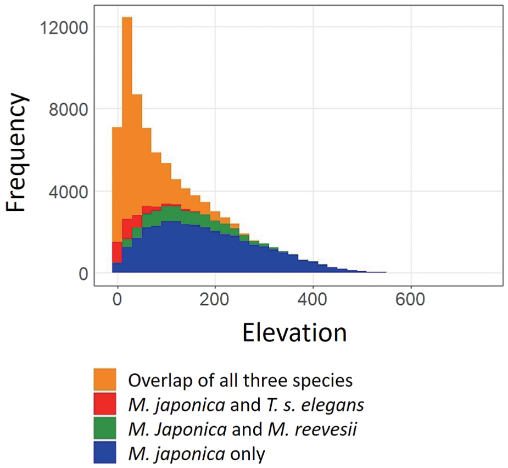


FIG. 5. Elevation of *Mauremys japonica*'s suitable habitat, and the overlapping area between *Mauremys japonica* and alien turtle species.

TABLE 1. Permutation importance of five environmental variables.

Environmental Variables	Permutation Importance (%)		
	M. japonica	*M. reevesii*	*T. s. elegans*
The highest temperature of the warmest month (August)	50.3	5.8	13.1
The lowest temperature of the coldest month (January)	18.6	52	38.6
Slope	11.3	16	30.9
The annual precipitation	9.3	23.1	12.5
The total age daylight hours (April–November)	10.5	3.1	4.9

TABLE 2. Results of the background similarity test. Similarity statistics and summary of null distributions (lower 0%, 2.5%, 97.5%, and 100% values) are shown. The directions of the background similarity tests are indicated by arrows as follows: occurrence localities of one species → geographic range of the other species in which background environmental data as random points were generated.

Species pair	Similarity statistics	Null distribution				Direction of niche similarity
		0%	2.5%	97.5%	100%	
M. japonica → *M. reevesii*	I=0.95*	0.921	0.923	0.936	0.937	Similar
	D=0.76*	0.718	0.725	0.749	0.751	Similar
M. reevesii → *M. japonica*	I=0.95*	0.861	0.864	0.886	0.887	Similar
	D=0.76*	0.607	0.611	0.645	0.650	Similar
M. japonica → *T. s. elegans*	I=0.87*	0.926	0.930	0.942	0.945	Dissimilar
	D=0.61*	0.734	0.742	0.770	0.771	Dissimilar
T. s. elegans → *M. japonica*	I=0.87*	0.751	0.752	0.776	0.779	Similar
	D=0.61*	0.470	0.471	0.501	0.506	Similar
M. reevesii → *T. s. elegans*	I=0.95*	0.879	0.880	0.899	0.901	Similar
	D=0.76*	0.637	0.638	0.672	0.676	Similar
T. s. elegans → *M. reevesii*	I=0.95*	0.755	0.756	0.778	0.782	Similar
	D=0.76*	0.472	0.476	0.502	0.507	Similar

* $P<0.001$, based on 100 randomizations (two-tailed).

cated that the ecological niches of the freshwater turtle species were significantly similar. In particular, the SDM of *M. japonica* positively predicted that of *M. reevesii* and vice versa (Table 2). The SDM of *M. reevesii* positively predicted that of *T. s. elegans* and vice versa (Table 2). However, the SDM of *T. s. elegans* positively predicted that of *M. japonica*, but it was not predicted in the opposite direction and the SDM of *M. japonica* negatively predicted that of *T. s. elegans* (Table 2).

DISCUSSION

This study revealed that climatic and topographic factors possessed high values in the permutation importance in SDMs for the three turtle species (Table 1), suggesting that these factors limited the distribution patterns of these turtles. Most freshwater turtles are ectotherms and require suitable ambient temperatures and solar radiation to maintain body temperature for their physiological and behavioral performance. Moreover, ambient temperature influences egg conditions and promotes embryonic development (hatching success) and sex determination of these turtles (Breitenbach et al., 1984; Bobyn and Brooks, 1994; Okada et al., 2010; Vitt and Caldwell, 2014). On the other hand, low ambient temperature during the hibernation season can kill hibernating turtles (St. Clair and Gregory, 1990). Therefore, temperature ultimately determines the distribution and population dynamics of freshwater turtles. Furthermore, micro-habitat environments, such as current velocity (e.g., Buhlmann and Vaughan, 1991; Usuda et al., 2012; Kagayama, 2019), may also be important. For example, Kagayama (2019) surveyed the distribution patterns of three freshwater turtle species in the Yorogawa River system (35°24'2.5842" N, 140°7'46.6896" E) and showed that *M. reevesii* and *T. s. elegans* were abundant in the lower regions of the river, whereas *M. japonica* was abundant in the middle and upper regions of the river. Moreover, the present study suggested that velocity may have negative effects on the abundance of the two alien species (*M. reevesii* and *T. s. elegans*). Therefore, the present study estimated the permutation importance of climatic and topological factors because slope and annual precipitation usually affect velocity in rivers.

Some studies have shown that *M. japonica* and the alien turtle species may have possessed allopatric distribution patterns (Yabe, 2002; Kosuge et al., 2003) because each turtle species has different habitat preferences. The predicted SDMs of the present study showed that *M. japonica* is a habitat generalist inhabiting broad environmental conditions (such as rivers, ponds, and marsh) from lowlands to foothill areas (Kosuge et al., 2003; Noda and Kamata, 2004; Yasukawa et al., 2008; Kagayama et al., 2017) and had the largest range of suitable habitats among the three turtle species examined in this study. However, most of *M. japonica*'s suitable area, especially in lowland areas, overlapped with those of *M. reevesii* and *T. s. elegans*, and suitable habitat where *M. japonica* occurs alone is the foothill region outside the overlapping ranges of *M. reevesii* and *T. s. elegans* (Figs. 4 and 5). Moreover, the background similarity test showed that native and alien turtle species had significant niche similarity. Therefore, the results of the present study support the assertion provided by Taniguchi et al. (2015), who reported that contemporary distribution patterns of *M. japonica* may be driven by interspecific interactions with the two alien turtle species (*M. reevesii* and *T. s. elegans*).

Recently, several studies suggested that alien turtle species reduced the population size of native turtles and displaced them (e.g., Cadi and Joly, 2003, 2004; Polo-Cavia et al., 2010, 2011; Yabe, 2014). Yabe (2014) showed that the dominant species had changed from *M. japonica* to *T. s. elegans* from 2005 to 2011 at several areas in Japan. This is probably due to competition for resources such as food and habitat, which led to a decline of *M. japonica*. On the other hand, both theoretical considerations and field studies strongly suggest that there has been reproductive interference (Gröning and Hochkirch, 2008) between the native and alien species, which has driven the substitution of native species by aliens (e.g., Konishi and Takata, 2004; Takakura et al., 2009). Hybridization between *M. japonica* and *M. reevesii* (Kato et al., 2010; Suzuki et al., 2014) could be a part of reproductive interference with the introduced *M. reevesii* and potentially cause negative effects on indigenous *M. japonica*. In the future, we need to clarify whether the substitution of *M. japonica* with *M. reevesii* or *T. s. elegans* occurred based on long-term monitoring of these turtles.

Recently, studies employing SDMs and ENMTools approaches have successfully evaluated the niche evolution and dynamics of hybridization zones between two native species (Warren et al., 2008; Takami and Osawa, 2016). SDMs and ENMTools were applied in this study to evaluate the niche similarity between native *M. japonica* and two alien turtle species. In the case of evaluating the SDMs of the alien species, we assumed that the distributions they attained were at equilibrium states in the introduced regions. Previous studies have pointed out that *M. reevesii* had been introduced from Korea since the late 18th century and from China since the 1970s (Hikida and Suzuki, 2010; Suzuki et al., 2011), and that *T. s. elegans* had been introduced from the United States since the 1920s (Kamezaki, 2015). Since both the species are now widespread and well-established in Honshu, Shikoku, and Kyushu, Japan (The Nature Conservation Society of Japan, 2014; Taniguchi et al., 2015), the assumption of an equilibrium distribution may be valid. Moreover, the absence of the two alien turtle species in the foothill regions in Japan could be explained by the habitat preference of each turtle species.

ACKNOWLEDGMENTS

We thank the Nature Conservation Society of Japan for permission to use locality data of freshwater turtles collected in a citizen-based study provided by The Nature Conservation Society of Japan (2014). We are also grateful to the anonymous reviewers for their valuable comments regarding our manuscript. This work was supported by the Environment Research and Technology Development Fund (4-1705) of the Environmental Restoration and Conservation Agency.

LITERATURE CITED

ANDERSON, R. P., PETERSON, A. T., AND GÓMEZ-LAVERDE, M. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* 98: 3–16.

BOBYN, M. L. AND BROOKS, R. J. 1994. Incubation conditions as potential factors limiting the northern distribution of snapping turtles, *Chelydra serpentina*. *Canadian Journal of Zoology* 72: 28–37.

BREITENBACH, G. L., CONGDON, J. D., AND VAN LOBEN SELS, R. C. 1984. Winter temperatures of *Chrysemys picta* nests in Michigan: effects on hatchling survival. *Herpetologica* 40: 76–81.

BUHLMANN, K. A. AND VAUGHAN, M. R. 1991. Ecology of the turtle *Pseudemys concinna* in the New River, West Virginia. *Journal of Herpetology* 25: 72–78.

CADI, A. AND JOLY, P. 2003. Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared slider (*Trachemys scripta elegans*). *Canadian Journal of Zoology* 81: 1392–1398.

CADI, A. AND JOLY, P. 2004. Impact of the introduction of the red-eared slider (*Trachemys scripta elegans*) on survival rates of the European pond turtle (*Emys orbicularis*). *Biodiversity and Conservation* 13: 2511–2518.

ERNST, C. H. AND LOVICH, J. E. 2009. *Turtles of the united states and Canada*. JHU Press, Baltimore.

GRÖNING, J. AND HOCHKIRCH, A. 2008. Reproductive interference between animal species. *The Quarterly Review of Biology* 83: 257–282.

GUISAN, A. AND THUILLER, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009.

HIKIDA, T. AND SUZUKI, D. 2010. The introduction of the Japanese populations of *Chinemys reevesii* estimated by the descriptions in the pharmacopias in the Edo Era. *Bulletin of the Herpetological Society of Japan* 2010: 41–46.

HOSMER JR, D. W., LEMESHOW, S., AND STURDIVANT, R. X. 2013. *Applied logistic regression*. John Wiley & Sons, Hoboken.

JAPAN METEOROGICAL AGENCY. 2012. *Mesh Climate Value.* http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html (accessed 12 March 2020)

JIMÉNEZ-VALVERDE, A. AND LOBO, J. M. 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica* 31: 361–369.

KAGAYAMA, S. 2019. Spatial distribution of the freshwater turtles in the Yorogawa River Basin, in Chiba Prefecture, Japan. *Bulletin of the Herpetological Society of Japan* 2019: 41–49.

KAGAYAMA, S., OGANO. D., AND HASEGAWA, M. 2017. Vertical distribution of the freshwater turtles in Chiba Prefecture, Japan. *Bulletin of the Herpetological Society of Japan* 2017: 156–161.

KAMEZAKI, N. 2015. Overview of the problems concerning freshwater turtles in Japan, especially *Trachemys scripta elegans*. *Bulletin of the Herpetological Society of Japan* 2015: 123–133.

KAMEZAKI, N., FUJIBAYASHI, N., AND KAWATA, M. 2017. Species composition and distribution of freshwater turtles in Okayama. *Kiraku* 14: 2–8.

KATO, H., KISHIDA, K., AND SASANAMI, T. 2010. Detection of hybrid individuals between *Mauremys japonica* and *Chinemys reevesii* by RAPD. *Biogeography* 12: 39–42.

KOHMATSU, Y., TSUJI, A., AND NOZAKI, K. 2000. Amphibian and Reptilian fauna in Naka-ikemi marsh, Turuga, Fukui, Japan. *Bulletin of the Herpetological Society of Japan* 2000: 85–88.

KONISHI, M. AND TAKATA, K. 2004. Impact of asymmetrical hybridization followed by sterile F 1 hybrids on species replacement in *Pseudorasbora*. *Conservation Genetics* 5: 463–474.

KOSUGE, Y. AND KOBAYASHI, R. 2015. Crisis of freshwater turtles caused by raccoons. *Bulletin of the Herpetological Society of Japan* 2015: 167–173.

Kosuge, Y., Ogano, H., and Hasegawa, M. 2003. Spatial distribution of the freshwater turtles along Koito River, Boso Peninsula. *Journal of the Natural History Museum and Institute, Chiba. Special Issue* 6: 55–58.

Lovich, J. E., Yasukawa, Y., and Ota, H. 2011. *Mauremys reevesii* (Gray 1831)—Reeves' turtle, Chinese three-keeled pond turtle. p. 050.1–050.10 *In*: A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, and J. B. Iverson, (eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5.* Chelonian Research Foundation, Lunenburg.

Ministry of Land, Infrastructure, Transport, and Tourism of Japan. 2009. *Land Use Mesh Data.* http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-L03-a.html (accessed 12 March 2020)

Ministry of Land, Infrastructure, Transport, and Tourism of Japan. 2011. *Elevation and Slope Mesh Data.* http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G04-a.html (accessed 12 March 2020)

Ministry of the Environment of Japan. 1988. Third National Survey on the Natural Environment. http://www.biodic.go.jp/reports2/3rd/ap_rep/index.html (accessed 25 April 2020)

Ministry of the Environment of Japan. 1993. Fourth National Survey on the Natural Environment. http://www.biodic.go.jp/reports/4-04/index.html (accessed 25 April 2020)

Ministry of the Environment of Japan. 2001. Fifth National Survey on the Natural Environment. http://www.biodic.go.jp/reports2/5th/ap_rep/index.html (accessed 25 April 2020)

Noda, H. and Kamata, N. 2004. Relationships between population traits and food habits in aquatic turtles. *Bulletin of the Herpetological Society of Japan* 2004: 102–113.

Okada, Y., Yabe, T., and Oda, S. I. 2010. Temperature-dependent sex determination in the Japanese pond turtle *Mauremys japonica* (Reptilia: Geoemydidae). *Current Herpetology* 29: 1–10.

Okada, Y., Yabe, T., Yamada, T., Kobayashi, H., Maezawa, K., and Oda, S. 2005. Distribution of freshwater turtles in western Mikawa area. *Yahagigawa Kenkyu* 9: 5–17.

Peterson, A. T., Soberón, J., and Sánchez-Cordero, V. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285: 1265–1267.

Phillips, S. J., Anderson, R. P., and Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.

Polo-Cavia, N., López, P., and Martín, J. 2010. Competitive interactions during basking between native and invasive freshwater turtle species. *Biological Invasions* 12: 2141–2152.

Polo-Cavia, N., López, P., and Martín, J. 2011. Aggressive interactions during feeding between native and invasive freshwater turtles. *Biological Invasions* 13: 1387–1396.

Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726.

St. Clair, R. C. and Gregory, P. T. 1990. Factors affecting the northern range limit of painted turtles (*Chrysemys picta*): winter acidosis or freezing?. *Copeia* 1990: 1083–1089.

Suzuki, D., Ota, H., Oh, H. S., and Hikida, T. 2011. Origin of Japanese populations of Reeves' pond turtle, *Mauremys reevesii* (Reptilia: Geoemydidae), as inferred by a molecular approach. *Chelonian Conservation and Biology* 10: 237–249.

Suzuki, D., Yabe, T., and Hikida, T. 2014. Hybridization between *Mauremys japonica* and *Mauremys reevesii* inferred by nuclear and mitochondrial DNA analyses. *Journal of Herpetology* 48: 445–454.

Takakura, K. I., Nishida, T., Matsumoto, T., and Nishida, S. 2009. Alien dandelion reduces the seed-set of a native congener through frequency-dependent and one-sided effects. *Biological Invasions* 11: 973–981.

Takami, Y. and Osawa, T. 2016. Ecological differentiation and habitat unsuitability maintaining a ground beetle hybrid zone. *Ecology and Evolution* 6: 113–124.

TANIGUCHI, M., UENO, S., MINE, K., AND KAMEZAKI, N. 2015. Distribution and density of freshwater turtles in Western Japan. *Bulletin of the Herpetological Society of Japan* 2015: 144–157.

TEMPAKU, M., OSAWA, S., AND KATSUNO, T. 2009. Relationships between the faunistic composition of freshwater turtles and the habitat in Miura Peninsula. *Landscape Research Japan* 72: 547–552.

THE NATURE CONSERVATION SOCIETY OF JAPAN. 2014. *Search for freshwater turtles in Japan. Nature Conservation Society of Japan reports (53)*. The Nature Conservation Society of Japan, Tokyo.

ULTSCH, G. R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. *Biological Reviews* 64: 435–515.

USUDA, H., MORITA, T., AND HASEGAWA, M. 2012. Impacts of river alteration for flood control on freshwater turtle populations. *Landscape and Ecological Engineering* 8: 9–16.

VITT, L. J., AND CALDWELL, J. P. 2014. *Herpetology: An Introductory Biology of Amphibians and Reptiles. 4th Edition*. Elsevier, Amsterdam.

WARREN, D. L., GLOR, R. E., AND TURELLI, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62: 2868–2883.

WARREN, D. L., GLOR, R. E., AND TURELLI, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33: 607–611.

YABE, T. 1996. Distribution of the turtles at Tado-cho in Mie Prefecture. *Mie Natural History* 3: 23–29.

YABE, T. 2002. Freshwater turtles of village forests. p. 176–184. *In*: S. Hiroki (ed.), *Ecology of village forests*. The university of Nagoya Press, Nagoya.

YABE, T. 2014. Crisis facing turtles in Japan: for constructing sustainable rural area. *Wildlife Forum* 18: 3–5.

YAMADA, Y., KAMIKIHARA, Y., AND SERIZAWA, S. 2008. Distribution of native and alien freshwater turtles in the central parts of Aichi Prefecture. *Science Report of the Toyohashi Museum of Natural History* 18: 35–45.

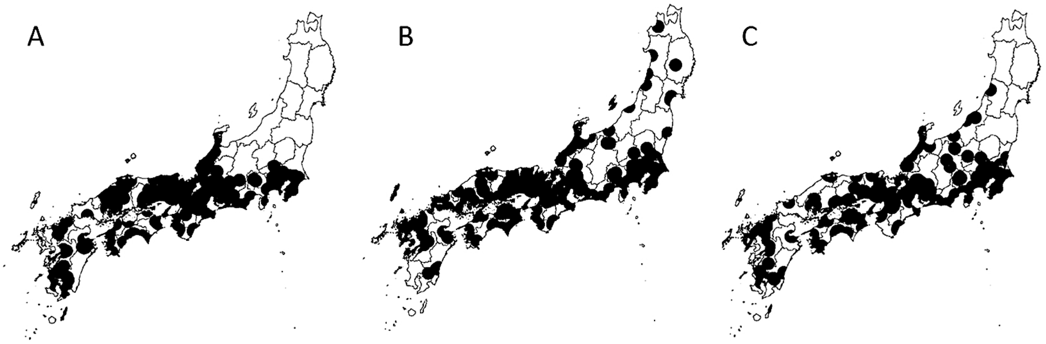
YASUKAWA, Y., YABE, T., AND OTA, H. 2008. *Mauremys japonica* (Temminck and Schlegel 1835)—Japanese pond turtle. p. 003.1–003.6 *In*: A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, and J. B. Iverson, (eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5*. Chelonian Research Foundation, Lunenburg.

Accepted: 26 June 2020

APPENDIX I

Definition of background area.

APPENDIX II



Definition of background area using the niche similarity test. (A) *Mauremys japonica*, (B) *Mauremys reevesii*, and (C) *Trachemys scripta elegans*.