

Climate change and the northward shift of *Cryptotympana facialis* in Japan: evidence from national survey data

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ABSTRACT: We developed a species distribution model of *Cryptotympana facialis* in Japan in order to investigate (1) the relationship between climate change and the northward shift of this species, (2) the existence of potential habitats in northern areas, and (3) the possibility of further northward shifts in the future. The distribution of *C. facialis* can be explained by life-history-related climate factors, including egg-hatching probability based on the sum of effective temperature, total precipitation during the rainy season, topographic slope, and the proportions of forest and urban areas, using an intrinsic Gaussian conditional autoregressive (CAR) model. The changes in potential habitat for *C. facialis* under climate change were projected using predicted climate conditions for 2070. In the parameter estimates of the CAR model, hatching probability, precipitation, and urban area were positive factors, while slope and forest area were negative factors. The fixed effects of the CAR model showed that more potential habitats exist in the north than in the current range of the species in western Japan. Moreover, our projection showed areas of suitable habitat increasing under all climate change scenarios. The current distribution of *C. facialis* is not in a state of equilibrium, possibly due to its low speed of dispersal. The distribution of *C. facialis* will expand to northern areas without climate warming, but climate warming will increase the amount of potential habitat. We emphasize the importance of considering life-history-related climatic factors, non-climatic factors, and spatial autocorrelation when modeling species distributions under climate change.

KEY WORDS: Bear cicada · Global warming · Insect · Life history · Niche model · Range shift · Spatial autocorrelation · Species distribution model

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1. INTRODUCTION

Northward shifts have been reported for various animals in a wide range of taxonomic groups, such as arthropods, fish, and birds (Thomas & Lennon 1999, Hickling et al. 2006), and this trend has often been explained in the context of climate change. Northward shifts of insect groups, including the Lepidoptera, Hemiptera, and Odonata, have also occurred in various regions (e.g. Parmesan et al. 1999, Hickling et al. 2005, 2006, Yukawa et al. 2007, Mason et al. 2015). Researchers have argued that insect population dynamics are generally sensitive to climate,

and particularly to temperature and humidity (Parmesan et al. 1999, Kiritani 2006). However, the relationship between climate change and the northward shift of insects is not always a simple causal association. Even if climatic conditions allow insects to extend their ranges northward under climate change, ecological constraints, such as the lack of suitable habitat, may prevent their expansion into particular localities (Hill et al. 2002). In addition, other factors, such as changes in human activity, may promote range expansion of species without regard to climate change (Iverson et al. 2011, Saito et al. 2012, 2016), and this range expansion may appear to

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be a northward shift. To evaluate changes in species distribution realistically, it is also important to consider dispersal capacity (Jaeschke et al. 2013, Urban et al. 2013, Saito et al. 2016). To manage ecosystems adequately under climate change, it is necessary to understand the relationship between northward shifts and climate change, while incorporating non-climatic factors and dispersal capacity.

The cicadas are an insect group with characteristic traits, including large bodies, exuviae that tend to remain on the tree, and male calling songs. They inhabit mainly warm temperate and tropical zones. Since their characteristic traits make it easy to recognize changes in their populations and communities, cicadas are often used for long-term monitoring and assessment as important biodiversity and environmental indicators (e.g. Hirose 1977, Katsura & Okuno 1995, Shiyake 2012, Tokue et al. 2013, Sato & Sato 2015). Moreover, environmental education through the observation of cicadas (e.g. Shimoyamada 2009) is an established practice. The experience gained from such activities indirectly promotes environmental awareness and ecosystem conservation (Dearborn & Kark 2010). However, some cicadas cause human-wildlife conflict as a result of their loud calls (e.g. Cyranoski 2007, Kim et al. 2014), their capacity for crop damage (e.g. Itô & Nagamine 1974), and the damage they cause to optical fiber cables by egg laying (e.g. Cyranoski 2007, Itou et al. 2010). Therefore, studying cicadas is important for both conserving ecosystems and controlling damage to human activities.

Cryptotympana facialis (Walker 1858) (Heteroptera: Cicadidae), which mainly inhabits western Japan (Hayashi & Saisho 2015), has recently expanded into northern areas (Numata & Shiyake 2007, Ikeda 2015). Although the geographical distribution of *C. facialis* can be explained by annual mean temperature (Kiritani & Yukawa 2010), the relationship between its distribution and climate may not be so simple when considered in the context of the life history of the species. *C. facialis* emerges from its underground nymph stage during the summer approximately every 7 yr (Numata & Shiyake 2007). Although an increase in the survival rate of overwintering eggs has been proposed as the cause of northward range expansion, the likelihood of this is low because the eggs are already known to be highly tolerant of low temperatures (Moriyama & Numata 2009). Moreover, low temperatures in winter do not increase the mortality of nymphs (Moriyama & Numata 2009), because the soil provides thermal buffering to these proficient diggers, irrespective of their

cold hardiness (Hoshikawa et al. 1988). Therefore, the northward shift of *C. facialis* in Japan may have little association with recent global warming. However, high humidity and the sum of effective temperatures (SET) are key climatic factors that influence hatching in *C. facialis* (Moriyama & Numata 2006, 2008), and these climatic factors may play a part in determining their geographical range. This illustrates the importance of life-history knowledge in understanding the northward shift of *C. facialis*.

Numata & Shiyake (2007) proposed that the migration range expansion of *C. facialis* was caused by low dispersal speed due to its short dispersal distance, and field experiments in Osaka indicated that the migration range of the species was narrow (Numata & Shiyake 2007). Unoccupied but potentially suitable habitat may perhaps exist north of the current geographical range of *C. facialis*. If that is the case, it is possible to regard the current western Japan distribution of the species as still undergoing historical expansion toward northern areas. To evaluate the impact of climate change on the range shifts of *C. facialis*, it is therefore necessary to analyze the distribution of potential suitable habitat.

Species distribution models (SDMs) allow the identification of potential suitable habitat based on relationships between species occurrence and factors such as climate (Guisan & Thuiller 2005). When the distribution of a range-expanding species is modeled, it is necessary to incorporate dispersal processes because the parameters of habitat suitability may not be accurately estimated for species undergoing range expansion (Fukasawa et al. 2009, Saito et al. 2012, 2016). Although it is necessary to use the history of range expansion (i.e. past distribution) when incorporating dispersal processes into an SDM, obtaining such data is often difficult. In fact, the past distribution of *C. facialis* is unclear. Moreover, the development of distribution of a species is also affected by non-climatic factors (e.g. human activity and topography) (Early & Sax 2014) and by evolutionary processes (e.g. local adaptation) that are difficult to incorporate into an SDM (Record et al. 2013). To resolve these problems, it is best to use an SDM incorporating spatial autocorrelation (Record et al. 2013). In this way, relationships between northward shifts and climate change can be evaluated more realistically.

In this study, we first constructed an SDM for *C. facialis* in Japan, incorporating life-history-related climate conditions, non-climatic factors, and spatial autocorrelation. Based on the SDM, we then tested for the existence of potential habitats in northern

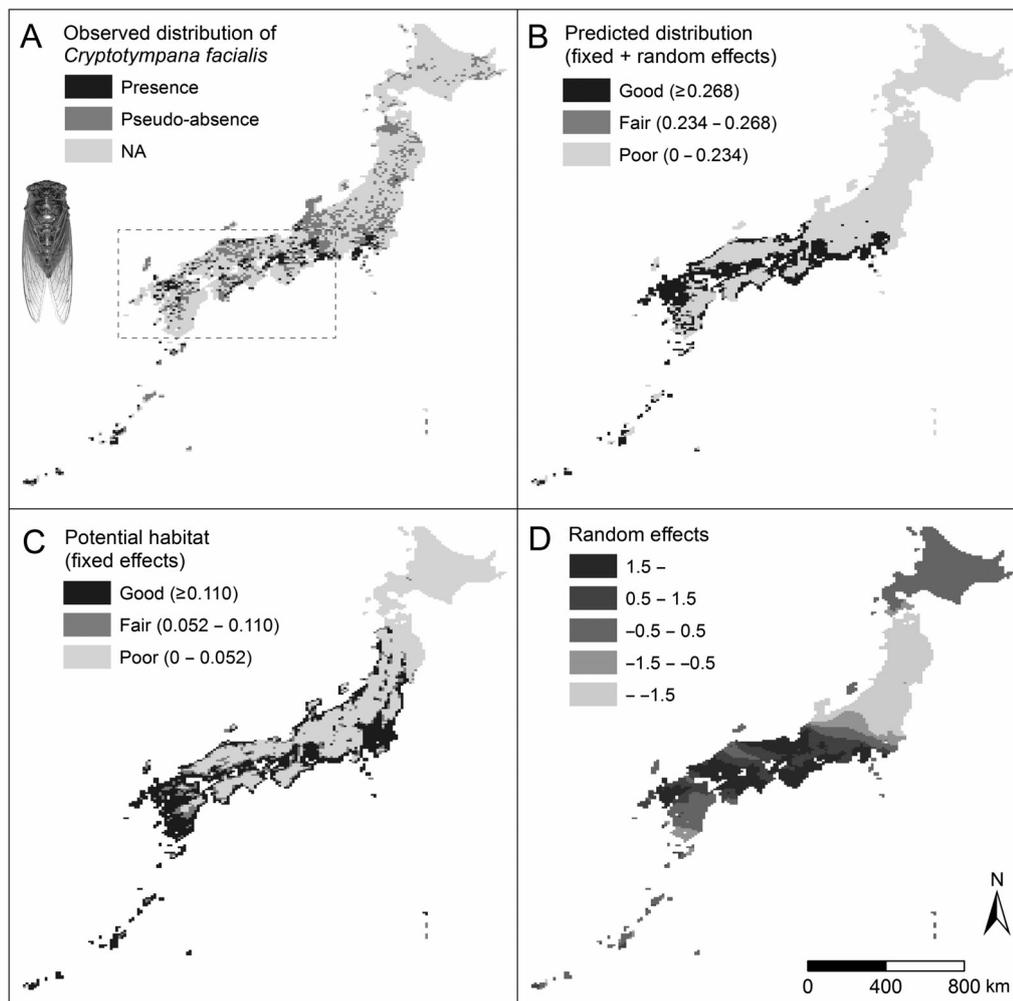


Fig. 1. The spatial patterns of (A) observed presence/pseudo-absence of *Cryptotympana facialis*, (B) predicted distribution based on fixed and random effects, (C) potential habitat based on fixed effects, and (D) spatial random effects: ρ of the conditional autoregressive (CAR) model. The area enclosed by the dotted line in Panel A shows the area used for validation of the CAR model. For definitions of 'good', 'fair', and 'poor' habitat see Section 2.4. NA: no records of cicadas

areas, and projected the possibility of a northward shift in the future.

2. MATERIALS AND METHODS

2.1. Data collection

Current distributional information for *Cryptotympana facialis* in Japan was taken from the results of the fifth National Survey of the Natural Environment (Ministry of the Environment Japan 2002). This survey was conducted by experts who recorded the occurrence of various insects in 45" \times 30" cells (approximately 1 \times 1 km). We changed the resolution to 7'30" \times 5' (approximately 10 \times 10 km), because the original cell size was too detailed for cicadas. The survey attempted to collect comprehensive occurrence records, including specimens, from all over Japan through 1998, and therefore the data set from this survey included very old records (e.g. 1930s). In

this study, we used occurrence records after 1983. Moreover, the data set could not provide absolute presence or absence data. Therefore, we designated all the cicada occurrence cells as background, and extracted pseudo-absence data (cells where *C. facialis* was not observed but other cicada species were observed) from the background. We assumed that an expert would observe all the cicada species in the cell, so cells where *C. facialis* was not observed (but other cicada species were observed) represented areas where the probability of finding that species was very low and consequently represented 'absences' (Mateo et al. 2010). Because the cells with no records of any cicadas might not have been surveyed by an expert, we treated these cells as 'NA'. Using these methods, we identified 334 present cells and 1080 pseudo-absent cells in the whole of Japan (4545 cells total) (Fig. 1A).

As climate-related factors, we used egg-hatching probability based on temperature as well as total precipitation during the early summer rainy season (i.e.

Japanese 'Baiu' in May to July) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/c068p013_supp.pdf). To calculate hatching probability based on temperature, we obtained the monthly mean temperature from WorldClim v1.4 (Hijmans et al. 2005) and calculated the annual SET, that is, the sum of positive differences between the daily mean temperatures and 14.3°C for each cell. The temperature threshold was reported by Moriyama & Numata (2008). By turning the SET into an equation following Moriyama & Numata (2011), we obtained a spatially explicit probability of egg hatching based on SET (Fig. S1 in the Supplement). High humidity in early summer acts as a trigger for egg hatching in *C. facialis* (Moriyama & Numata 2006, 2011). Thus, we calculated total precipitation (mm) from May to July (i.e. the early summer rainy season) in each cell using data from WorldClim (Fig. S1 in the Supplement). The value of current climate data from WorldClim is representative of the years 1950–2000.

The non-climatic factors we incorporated were topography and land use. Because *C. facialis* prefers flat land (Kinjo & Azuma 1991), we used slope (°) as a topographic factor, recording the mean value in each cell based on 50 m resolution elevation data obtained from the Geographical Survey Institute (2001) (Fig. S1 in the Supplement). As a land-use factor, we used the proportion of forest, since forests are the main habitat of *C. facialis* (Hayashi 1982, Kinjo & Azuma 1991). We also used the proportion of urban area, because the population of *C. facialis* has increased in urban landscapes in recent years (Numata & Shiyake 2007). The proportions of forest and urban area were extracted from a land-use map in conjunction with a vegetation map based on the fifth National Survey of the Natural Environment (Ministry of the Environment Japan 1999) (Fig. S1 in the Supplement).

2.2. Statistical modeling

We constructed the SDM of *C. facialis* to evaluate the effect of climate change on the distribution of the species. The model explains the distribution (presence or pseudo-absence) of *C. facialis* by the following environmental factors: egg-hatching probability, total precipitation in the rainy season, slope, and proportions of forest and urban areas. However, in the context of species distribution, the presence or absence of species at 1 location is likely associated with its presence or absence at neighboring locations (i.e. spatial autocorrelation). Therefore, we used an intrinsic

Gaussian conditional autoregressive (CAR) model incorporating spatial random effects (see Latimer et al. 2006). The CAR model was expressed as follows:

$$y_i \sim \text{Bernoulli}(p_i) \quad (1)$$

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha + \mathbf{x}'_i\beta + \rho_g \quad (2)$$

where the response variable y_i represents the presence or pseudo-absence of *C. facialis* in cell i (not including NA cells) and its distribution approximates the Bernoulli distribution, p_i is the probability of occurrence in cell i , \mathbf{x}'_i is a vector of environmental factors associated with cell i , and α and β are vectors of the associated coefficients. Each cell i belongs to a cell g (all cells in Japan including NA), and ρ_g is the spatial random effect of the cell g . The value of ρ_g adjusts the probability of occurrence dependent upon the values of ρ in cell g 's spatial neighborhood cells h .

The model assumed a vague Gaussian prior for the regression parameters $\beta \sim N$ (mean = 0, precision = 0.01), where precision = 1/variance. The prior for the effect is defined conditionally as:

$$\rho_g | \rho_h, g \neq h, \tau \sim N\left(\frac{1}{n_g} \sum_{g \sim h} \rho_h, \frac{1}{n_h \tau}\right) \quad (3)$$

where τ is a precision hyperparameter, n_g is the number of neighbors of node g , and $g \sim h$ indicates that the 2 nodes g and h are neighbors. The unknown precision hyperparameter τ controls the smoothness of the spatial random effect, and the prior is defined on a logarithmic scale. In this study, we defined the 4 cells adjacent to a focal cell as a neighborhood.

The parameter of the model was fitted using integrated nested Laplace approximations (Rue et al. 2009). This approach is a statistical inference method for latent Gaussian Markov random field models, and it substitutes stochastic sampling with deterministic approximations based on a clever use of the Laplace approximation and on numerical integration. The use of integrated nested Laplace approximations was motivated by their computational efficiency in approximating posterior marginal probabilities, in comparison with Markov chain Monte Carlo simulations (Rue & Martino 2007, Martino et al. 2011). This approach has the advantage of a large sample size of spatial data, complex spatial random effects, and a substantial number of fixed effect combinations to be fitted.

To confirm the utility of the CAR model, we also constructed a generalized linear model (GLM) without spatial autocorrelation by the same method as the CAR model. The GLM was expressed as follows:

$$y_i \sim \text{Bernoulli}(p_i) \quad (4)$$

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha + x'_i \beta \quad (5)$$

The prior for the fixed parameters and the approach for fitting parameters were performed as with the CAR model.

We compared the CAR model with the GLM based on the importance and significance of the variables and the deviance information criterion (DIC; Spiegelhalter et al. 2002), an index of model fitness. DIC is a generalization of Akaike's information criterion (AIC), and is calculated from the mean deviance adjusted for the estimated number of parameters in the model (Spiegelhalter et al. 2002). As for AIC, a model with a smaller DIC value is better.

The CAR and GLM analyses were conducted with the `inla` function in the INLA v0.0-1404466487 package (Rue et al. 2014) in the R v3.0.2 software environment (R Core Team 2013).

2.3. Relative importance and significance of environmental factors

The relative importance of each variable in the CAR model and GLM was evaluated by the absolute values of standardized coefficients in the model. A larger absolute value indicates high importance of the variable. When the 95 % confidence interval (CI) of the coefficient did not overlap zero, we judged that the variable had statistical significance.

2.4. Definition of suitable habitat based on thresholds

We used the parameters of the CAR model to estimate the predicted distribution and potential habitats of *C. facialis*, based on Kadoya et al. (2009). The predicted distribution was calculated using fixed effects (i.e. effects of environmental factors) and the value of ρ estimated for each cell as spatial random effects (i.e. spatial autocorrelation), and potential habitats were calculated using fixed effects only.

We calculated 2 threshold sets to define a suitable habitat for *C. facialis* in its predicted distribution and its potential habitat based on the CAR model. One threshold was adjusted to minimize the difference between sensitivity and specificity (Jiménez-Valverde & Lobo 2007, Lobo et al. 2008). We defined a cell with a value higher than the threshold as 'good' habitat. However, the values of this threshold may be too

strict. Thus, we also used the value above which the model classifies correctly 90 % of the present cells as another threshold. The loose threshold is a conservative value that is often used in SDM studies (e.g. Rebelo & Jones 2010, Bosso et al. 2013). We defined a cell that is lower than the strict threshold but higher than the loose threshold as 'fair' habitat. A cell with a value lower than the loose threshold was defined as 'poor' habitat.

2.5. Validation

To validate the accuracy of estimations by the CAR model, we calculated the area under the curve (AUC) based on receiver operating characteristic analysis (Fielding & Bell 1997), using the predicted values (predicted distribution and potential habitat) and the distribution data (presence or pseudo-absence). An AUC of ≥ 0.7 is assessed as moderate accuracy (Fischer et al. 2003). In the predicted distribution, we calculated the AUC for all of Japan except for cells with no records of distribution. The AUC of the potential habitat was calculated using the western part of Japan (Fig. 1A), because the distribution of *C. facialis* in that area is stable.

Since coarse climate data was used in the SDM, it was necessary to check for false positives when evaluating potential habitats in northern areas. We compared the value of potential habitat in the Tohoku region (Fig. 2A) with detailed climate data from 114 local meteorological observatories of the Japan Meteorological Agency. In *C. facialis*, the threshold SET for hatching was 715.3 degree days (Moriyama & Numata 2008). We calculated the SET based on the normal value of daily mean temperature from 1981 to 2010 at each local meteorological observatory, and confirmed whether the cell with potential suitable habitat exceeded 715.3 degree days.

2.6. Scenario analysis under future climate conditions

To project changes in the distribution of potential habitat for *C. facialis* under climate change, we prepared hatching probability based on SET and precipitation in the rainy season in 2070 based on down-scaled global climate model data from CMIP5 (the fifth phase of the Coupled Model Intercomparison Project) that was published in 2013 by the Intergovernmental Panel on Climate Change (IPCC). However, differing values of future climate based on dif-

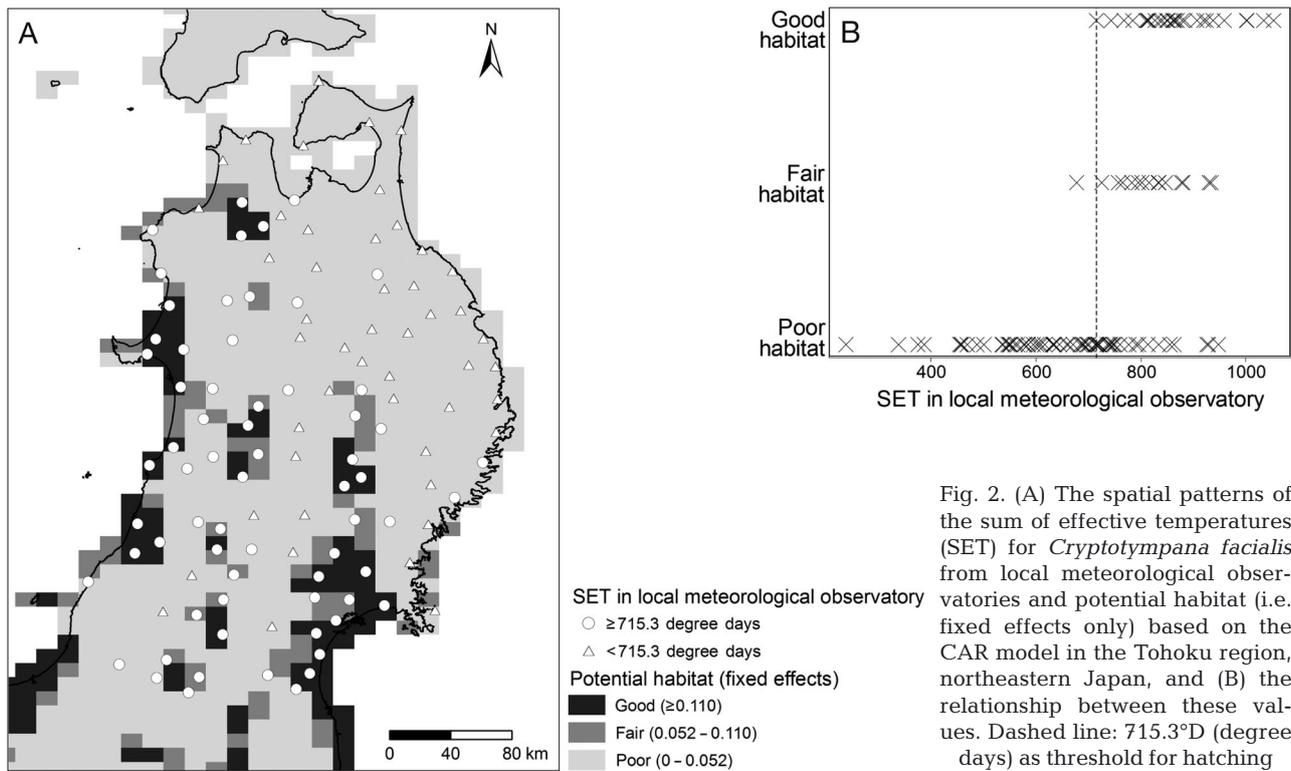


Fig. 2. (A) The spatial patterns of the sum of effective temperatures (SET) for *Cryptotympana facialis* from local meteorological observatories and potential habitat (i.e. fixed effects only) based on the CAR model in the Tohoku region, northeastern Japan, and (B) the relationship between these values. Dashed line: 715.3°D (degree days) as threshold for hatching

ferent global climate models will alter the projection of the distribution of *C. facialis* in response to the selected global climate model. To consider this uncertainty, we selected data from 4 different global climate models: CCSM4 (CC), HadGEM2-ES (HE), MIROC5 (MC), and MRI-CGCM3 (MG). Moreover, in each global climate model, we used 4 representative concentration pathways (RCP2.6, RCP4.5, RCP6.0, and RCP8.5) that are greenhouse gas scenarios (Figs. S2 & S3 in the Supplement at www.int-res.com/articles/suppl/c068p013_supp.pdf), that is, we used 16 climate change scenarios for projecting future potential habitat. By assigning hatching probability based on SET and precipitation in the rainy season under each scenario to the CAR model, we projected future potential habitat. All global climate model data were obtained from WorldClim.

We compared the number of cells with good and fair habitat in the predicted current distribution (i.e. prediction using fixed and random effects of the CAR model based on current climate conditions), the current potential habitats (i.e. prediction using only fixed effects of the CAR model based on current climate conditions), and the projected future distribution of potential habitats (i.e. prediction using only fixed effects of the CAR model based on future climate conditions). From this comparison, we tested whether (1) the current distribution of *C. facialis* has

reached an equilibrium state and (2) a future distribution of potential habitats exists in northern areas.

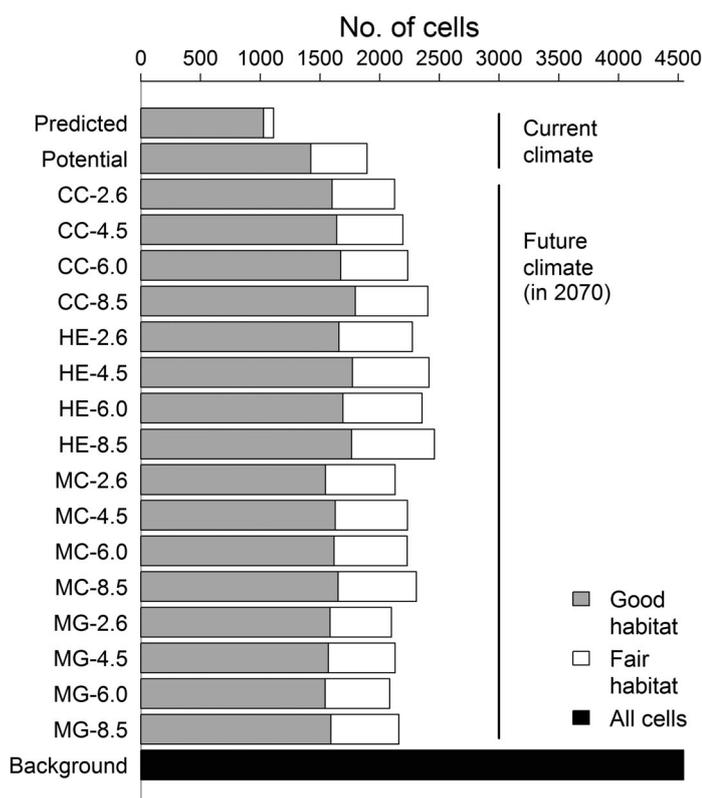
3. RESULTS

The CAR model incorporating spatial autocorrelation fitted the distribution of *Cryptotympana facialis* in Japan better than the GLM, as confirmed by the DIC values of 966.7 (CAR) and 1185.7 (GLM) (Table 1). In the CAR model, hatching probability based on SET, precipitation in the rainy season, and the proportion of urban area were positive factors, and the slope and proportion of forest area were negative factors (Table 1). The statistical significance and relative importance of the parameters of the GLM were similar to those of the CAR model. The relative importance of hatching probability based on SET, as indicated by the standardized coefficient in each model, showed the large contribution that climate factors make to the distribution of *C. facialis*. However, the slope parameter differed between CAR and GLM. A significant effect of slope was detected in CAR only.

The values of strict and loose thresholds of the predicted distribution were 0.268 and 0.234, respectively. The prediction map based on the thresholds of the predicted distribution seemed to be restructuring the

Table 1. Parameter estimates and deviance information criterion (DIC) values of an intrinsic Gaussian conditional autoregressive (CAR) model incorporating spatial autocorrelation, a generalized linear model (GLM) without spatial autocorrelation, and an intercept-only GLM. The parameters of these models were fitted using integrated nested Laplace approximations (Rue et al. 2009). Hatching probability means egg-hatching probability calculated from the annual sum of effective temperatures for each cell using 14.3°C as the lower threshold (Moriyama & Numata 2008, 2011). Precipitation indicates total precipitation in the early summer rainy season (May to July) in Japan

Variable	Coefficient				Median of standardized coefficient
	Median	Lower limit of 95% CI	Upper limit of 95% CI	SD	
CAR model (DIC = 966.7)					
Intercept	-5.383	-7.541	-3.606	1.006	-3.969
Hatching probability	2.987	1.699	5.033	0.831	1.360
Precipitation	0.003	0.001	0.004	0.001	0.658
Slope	-0.059	-0.112	-0.009	0.026	-0.449
Proportion of forest	-2.423	-3.412	-1.443	0.501	-0.780
Proportion of urban area	4.190	2.461	6.051	0.915	0.399
GLM (DIC = 1185.7)					
Intercept	-6.365	-8.265	-4.880	0.865	-3.000
Hatching probability	4.103	2.734	5.909	0.811	1.871
Precipitation	0.003	0.002	0.003	0.000	0.607
Slope	0.009	-0.027	0.045	0.018	0.071
Proportion of forest	-1.802	-2.534	-1.075	0.372	-0.580
Proportion of urban area	4.084	2.848	5.409	0.653	0.389
Intercept-only GLM (DIC = 1548.0)					
Intercept	-1.174	-1.299	-1.053	0.063	-



distribution of *C. facialis* (Fig. 1B). In the potential habitat, the values of strict and loose thresholds were 0.110 and 0.052, respectively. The map of potential habitats based on thresholds showed that a suitable habitat for *C. facialis* existed in the north as well as in the current range of the species (Fig. 1C). High values for random effects (i.e. spatial autocorrelation) were found in western Japan (Fig. 1D).

The AUCs of the predicted distribution (i.e. fixed and random effects) and of the potential habitat (i.e. fixed effects only) were 0.945 and 0.800, respectively. Although the AUC of the potential habitat was lower than that of the predicted distribution, the value was only of moderate accuracy. Moreover, we tested for false positives for the potential habitat in the Tohoku region using SET based on detailed data from local meteorological observatories. The SET in all good habitat and most fair habitat exceeded 715.3 degree days (Fig. 2B). At the same time, a

variety of SETs were found in the cells with poor habitat.

Based on the CAR model, we identified a future potential habitat for *C. facialis* under different climate change scenarios (Fig. S4 in the Supplement at www.int-res.com/articles/suppl/c068p013_supp.pdf). In the potential habitat, the numbers of cells with good and good + fair habitat were 1424 and 1894, respectively (Fig. 3). These values were larger than those of the predicted current distribution. Our scenario analysis showed that the numbers of cells with suitable habitat increased under all climate change scenarios (Fig. 3), although the increase was relatively low.

Fig. 3. The number of cells of predicted current distribution (i.e. fixed and random effects) of *Cryptotympana facialis*, current potential habitat (fixed effects only), future potential habitat under each climate change scenario in 2070, and background (i.e. all of Japan). Climate change scenarios were based on downscaled global climate model data from CMIP5 (IPCC Fifth Assessment). We selected CCSM4 (CC), HadGEM2-ES (HE), MIROC5 (MC), and MRI-CGCM3 (MG), and used 4 representative concentration pathways (RCP2.6, RCP4.5, RCP6.0, and RCP8.5) in each global climate model

4. DISCUSSION

4.1. Validity and interpretation of the SDM

The CAR model fit the distribution of *Cryptotympana facialis* in Japan better than the GLM (Table 1), and it exhibited good accuracy based on the AUCs (0.945 of predicted distribution and 0.800 of potential habitats). Moreover, most of the potential suitable habitats in the Tohoku region, which is the northern limit of potential habitats, satisfied the SET requirement based on detailed climate data. Because low temperatures in the winter do not increase mortality in the nymph stage (Moriyama & Numata 2009), potential habitats in the Tohoku region may exist. Thus, we can at least avoid false positives in our estimates in northern areas. These results support the validity of the estimation by our SDM based on the CAR model.

According to the fixed effects of the CAR model (Table 1), climate-related factors, hatching probability based on SET, and precipitation in the rainy season had positive effects on the distribution of *C. facialis* in Japan. These results are supported by previous studies showing the importance of SET and precipitation in the rainy season for hatching eggs (Moriyama & Numata 2006, 2008, 2011). In particular, the large absolute value of the standardized coefficient of hatching probability based on SET indicates the importance of climate as a factor determining the distribution of *C. facialis*. With respect to topography (slope) in our SDM, *C. facialis* preferred flat land, as noted by Kinjo & Azuma (1991). Although a previous study in the Fuji-Hakone-Izu region of Japan (Hayashi 1982) pointed out that *C. facialis* inhabits broad-leaved forests, our SDM showed a negative effect of forest area on the distribution of the species. Other studies indicated that *C. facialis* might prefer relatively open forests or anthropogenically disturbed forests (Hamaguchi 1995, Katsura & Okuno 1995). In that case, the proportion of forest area might be identified as a negative factor, because open and disturbed forests often exist in landscapes with little forested area. Another land-use factor, the proportion of urban area, was a positive factor in the distribution of *C. facialis*. Previous studies reported that *C. facialis* often dominates in urban landscapes for the following reasons: increase in hatching success as a result of changes in phenology caused by climate warming and the urban heat island phenomenon (Moriyama & Numata 2011), high desiccation tolerance of fully developed embryos in a dry urban environment (Moriyama &

Numata 2010), high burrowing ability of newly hatched nymphs under the impact of urban soil compaction (Moriyama & Numata 2015), and low predation rate in the urban environment of which tree cover is fragmented (Takakura & Yamazaki 2007). In addition, cicada nymphs may move long distances as a result of human activities such as planting and intentional release (Ministry of the Environment Japan 2002, Nagata 2013, Hayashi & Saisho 2015, Ikeda 2015), and the movement destination will often be an urban landscape (Hayashi & Saisho 2015, Ikeda 2015). The positive effect of urban areas may therefore reflect various urban landscape processes.

The values of spatial autocorrelation estimated as random effects tended to be high in western Japan, with a stable distribution compared to its recent distribution in eastern Japan (Fig. 1D). This result is consistent with the report that the distribution of *C. facialis* is expanding northward, and it indicates that the geographical distribution of *C. facialis* has been limited to western Japan for specific reasons. A niche-based model incorporating spatial autocorrelation for the range-expanding *Bombus terrestris* in Hokkaido indicated that its spread represents a phase of dispersal from established feral populations (Kadoya et al. 2009). In our study, the random effects of the CAR model may reflect the limited dispersal abilities of *C. facialis*. Field experiments in Osaka (Numata & Shiyake 2007) found that the dispersal distance of *C. facialis* was short, and this trait may restrict range expansion.

4.2. Suitable habitat under current and future climates

Our SDM showed that potential suitable habitats for *C. facialis* existed in more northern areas in Japan, even under current climate conditions (Fig. 1). It is at least possible that *C. facialis* could spread to the Tohoku region without climate warming. This indicates that the current distribution of *C. facialis* is not yet in a state of equilibrium, which may be explained by the limited dispersal abilities of the species, as described above. Therefore, our results support the suggestion of Numata & Shiyake (2007) that *C. facialis* has not yet completed its range expansion due to its low dispersal speed. Normal dispersal and long-distance movement by planting and intentional release (Ministry of the Environment Japan 2002, Nagata 2013, Hayashi & Saisho 2015, Ikeda 2015), as opposed to an increase in suitable habitat as a result of climate warming, may be contributing to the recent northward shift of *C. facialis* in Japan.

On the other hand, potential suitable habitats increased under all future climate change scenarios (Fig. 3). In light of the large effects of climatic factors in the CAR model, it is not surprising that climate warming increases potential suitable habitat for *C. facialis* in northern areas of Japan. Eventually, the expansion of potential habitats as a result of climate warming may promote new colonization by normal dispersal and accidental long-distance jumps (Robinet & Roques 2010).

4.3. Implications and limitations

Our results demonstrate the importance of considering non-climatic factors and spatial autocorrelation when modeling a species distribution under climate change, and are thus in agreement with previous studies (Davis et al. 1998, Jaeschke et al. 2013, Record et al. 2013, Early & Sax 2014). Although the influence of climate factors on species distributions is not in doubt, we emphasize that other factors (geographic factors, land use, and dispersal processes) are also important. In species with low dispersal ability, such as *C. facialis*, the effects of dispersal limitations may be especially notable. It will require careful analysis to associate northward shifts of such species with climate warming. To avoid misleading overestimates, it is necessary to consider other environmental factors and biological processes as well as climate change. Life-history-related climatic factors such as hatching probability based on SET and precipitation in the rainy season should be incorporated into analyses of species distributions, along with simple climatic factors such as mean temperature, in the same way that physiological knowledge needs to be better integrated into SDMs (Kearney & Porter 2009). The response of the distribution of a species to climate change is often taxonomically specific (Hickling et al. 2006, Mair et al. 2012, Mason et al. 2015), and differences in the traits of species are one of the causes of this specificity (e.g. Beckmann et al. 2015). Life-history knowledge should be recognized as a key in species distribution analysis. Exploring the relationships between species distribution and multiple factors, including climate, geography, land use, and life history, will help us to more accurately evaluate the effects of climate change.

In the management of nuisance insects that can be intentionally or unintentionally released, it is essential to project the potential distribution of the species correctly. If the potential distribution is underesti-

mated, management will lag behind. For example, according to our model, *C. facialis* will colonize the Tohoku region if released in potential habitats, and characteristic nuisance behaviors will be reported, including its loud buzz and damage to optical fiber cables from oviposition (e.g. Cyranoski 2007). Moreover, changes in distribution may indirectly affect other species through biotic interactions (e.g. Boggs & Inouye 2012, Li et al. 2015). Therefore, it is necessary to validate estimates and projections by monitoring future changes in distribution.

The distribution data used in our study provide a snapshot of the geographical range of *C. facialis*. The males of *C. facialis* sometimes move long distances while calling, although most of the females do not move at a local scale (Hayashi & Saisho 2015). We must therefore be careful in making judgments about the colonization of new areas based on cicada occurrence data (i.e. presence or absence). To confirm the colonization of *C. facialis*, long-term monitoring based on exuviae and on the presence of females is required. Moreover, although a rich collection of data on distribution and population density from past to present is needed for correct evaluation, data of that quality are rarely available (Kuussaari et al. 2009). Thus, limited distribution data are often used, as in our study, and care must be taken to use such data most effectively. When making estimates from limited data, an SDM approach is still one of most useful tools for decision-making (Iverson & McKenzie 2013). Data on non-climatic factors are currently readily available, and the methodology of spatial autocorrelation is widely used. Assessments of the impact of climate change on various insects will continue to depend on the quality of the data.

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