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Ecological Character Displacement in Non-Congeneric Frogs

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Character displacement is phenotypic divergence driven by competition (ecological character displacement) or reproductive interference (reproductive character displacement). Although previous studies have examined these phenomena separately, recent evidence suggests that reproductive interference can drive both reproductive and ecological character displacement, in that certain traits are related to both competition and reproduction. Thus, to evaluate the effect of competition, the effect of reproductive interference must be excluded. Here, we analysed ecological character displacement between non-congeneric frogs, which show little reproductive interference. *Odorrana amamiensis* inhabits the Amami and Tokunoshima Islands, Japan, whereas its non-congeneric competitor *Babina subaspera* inhabits the Amami Island. We tested three of the Schluter (2000) criteria for ecological character displacement: phenotypic changes in *O. amamiensis* between the two islands, phenotypic change related to prey preference, prey availability between the two islands. We demonstrated that the three criteria in Schluter (2000) were likely to be satisfied, indicating the occurrence of ecological character displacement in non-congeners without reproductive interference. Thus, we conclude that competition is potentially the main driver of this phenotypic divergence, and that non-congeners may be a suitable model for evaluating ecological character displacement in a variety of organisms, as the influence of reproductive interference can be excluded.

Key words: ecological character displacement, non-congener, competition, evolution, speciation, frog, conservation

INTRODUCTION

Character displacement is phenotypic divergence caused by natural selection, which can reduce resource competition or reproductive interference amongst species (Brown and Wilson, 1956; Schulter, 2000). This phenomenon produces a geographical pattern in which species differ to a greater extent in their sympatric zones than in their allopatric zones (Brown and Wilson, 1956; Schulter, 2000). There are two types of character displacement: ecological character displacement, which is related to resource use, and reproductive character displacement, which is related to reproduction (Brown and Wilson, 1956; Schulter, 2000). These types of character displacement are important mechanisms underlying diversification, and numerous studies have explored these two phenomena separately (Schulter, 2000). However, recent evidence suggests that reproductive interference can drive reproductive as well as ecological character displacement, as certain traits may be related to both competition and reproduction (Pfennig and Pfennig, 2005; Konuma and Chiba, 2007; Pfennig and Pfennig, 2009).

Konuma and Chiba (2007) have theoretically described the occurrence of ecological character displacement as a consequence of reproductive interference. Additionally, Pfennig and Pfennig (2005) have reported that body size shift in spadefoot toad (*Spea multiplicata*) likely resulted from both reproductive and ecological character displacements with its congeneric species (*S. bombifrons*). The effect of competition on ecological character displacement remains obscure (Konuma and Chiba, 2007; Pfennig and Pfennig, 2009). Thus, excluding the potential effect of reproductive interference is important for evaluating the effect of competition on ecological character displacement (Pfennig and Pfennig, 2009).

A majority of the previous studies reporting ecological character displacement have focused on congeneric species (Schulter, 2000; Simberloff et al., 2000; Dayan and Simberloff, 2005; Pfennig and Pfennig, 2009; Nosil, 2012). Because congeneric species often exhibit similar traits related to resource use, they often show competitive interactions (Schulter, 2000; Dayan and Simberloff, 2005). Hence, congeneric species are a suitable model to examine effects of competition on ecological character displacement (Schulter, 2000). However, congeneric species have similar reproductive traits, and often show reproductive interference (Gröning and Hochkirch, 2008). Distinguishing the effects of competition and reproductive interference on character displacement in congeneric species can thus be

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challenging (Pfennig and Pfennig, 2009).

In the present study, we examined the effect of competition on ecological character displacement in two non-congeneric frogs with little reproductive interference (Gröning and Hochkirch, 2008): Amami tip-nosed frog (*Odorrana amamiensis*), which inhabits Amami and Tokunoshima Islands in southern Japan, and Otton frog (*Babina subaspera*), which is restricted to Amami Island (Maeda and Matsui, 1999). Thus, Amami Island is a sympatric zone for the species, while the Tokunoshima Island is the allopatric zone. The two species are phylogenetically distantly related non-congenerics. *Odorrana amamiensis* inhabits the forest floor in the non-breeding season and breeds in mountain streams, whereas *B. subaspera* inhabits the forest floor in the non-breeding season but breeds in stagnant water pools (Maeda and Matsui, 1999). Both species prey upon ground-dwelling organisms. These species potentially share food resources despite being both phylogenetically and reproductively different. Thus, such non-congeners can serve as a study model in which species do not show reproductive interference but compete with each other for resources, enabling the evaluation of the independent effect of competition on ecological character displacement.

Schulter (2000), by compiling results from several studies (e.g., Grant, 1972; Arthur, 1982; Schluter and McPhail, 1992; Strong et al., 1979), proposed six characteristics of ecological character displacement. An increase in the number of criteria satisfied is associated with an increase in probability. Based on the criteria in Schluter (2000), we tested three hypotheses: (1) *Phenotypic change in allopatric vs. sympatric populations—O. amamiensis* individuals on Tokunoshima Island (allopatric zone) are larger than *O. amamiensis* individuals on Amami Island (sympatric zone); (2) *Phenotypic change related to prey preference—O. amamiensis* individuals on Tokunoshima Island prefer larger prey than do *O. amamiensis* individuals on Amami Island; (3) *Prey availability*—arthropod communities on Amami and Tokunoshima Islands are highly similar.

MATERIALS AND METHODS

Study area and species

Amami Island is located in the Nansei Islands in southern Japan and covers an area of 712 km^2 (Fig. 1). Average annual temperature is 21.5°C, and average annual rainfall is 2941 mm. The island is primarily covered by broad-leaved evergreen trees, such as chinquapin (*Castanopsis sieboldii*). Tokunoshima Island is located approximately 50 km south of Amami Island and covers an area of 248 km^2 (Fig. 1). Average annual temperature is 21.6°C, and average annual rainfall is 1912 mm. The island has a mountain forest at the centre, which is covered by broad-leaved evergreen trees. These islands are subtropical and are home to many endemic species. Owing of their high biodiversity, these islands are listed on United Nations Educational, Scientific and Cultural Organization's provisional list of candidates for World Natural Heritage sites.

O. amamiensis is a relatively large (56–101 mm) terrestrial frog inhabiting both Amami and Tokunoshima Islands (Maeda and Matsui, 1999; Matsui et al., 2005). *Babina subaspera* is a terrestrial frog, which is larger (93–140 mm) than *O. amamiensis* and restricted to Amami Island (Maeda and Matsui, 1999). Both species are endemic to the middle Nansei Islands and are listed as Endangered species in the IUCN Red List of Threatened Species (Kaneko and Matsui, 2004a; Kaneko and Matsui, 2004b).

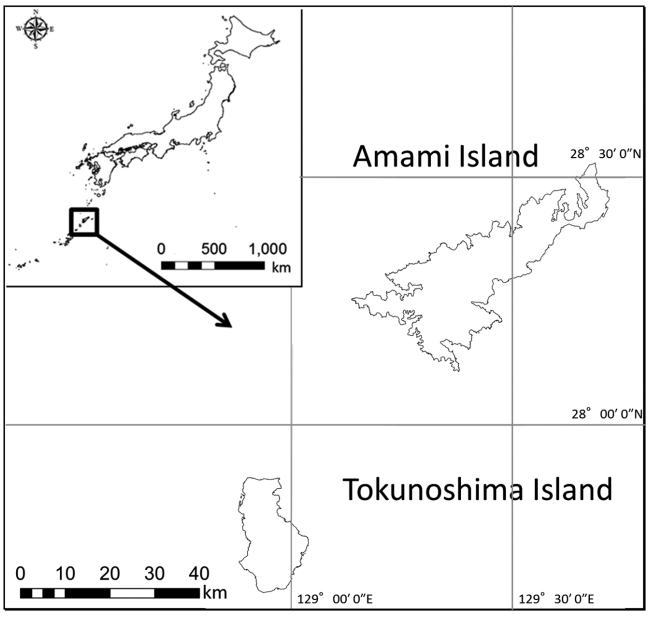


Fig. 1. Map showing the locations of Amami and Tokunoshima Islands in southern Japan.

Sample collection

We searched for *O. amamiensis* frogs on forest roads on Amami and Tokunoshima Islands at night (20:00–01:00) from June to August in 2016 (50 days) by driving at a constant speed of approximately 10 km/h. When a frog was detected visually, the researcher captured the frog using a net and recorded the morphological trait of snout–vent length (SVL) to the closest 0.1 mm using a caliper. After measuring the morphological trait, we collected gut contents by inserting forceps into the frogs' mouths. After collecting gut contents, we sampled the fourth finger of the hind limb (the longest finger) to avoid repeat measurement. Then, we released the frogs at the capture site.

Similarly, we collected *B. subaspera* on Amami Island from June to August in 2004 and 2005 (13 days). We took measurements and collected gut contents from the frogs in a similar manner. Because this species is endangered species, we should avoid disturbing them as much as possible from the conservation aspect. In this study, we used the data collected in 2004 and 2005 and did not collect alternative data in 2016. To assess frog prey, we captured ground-dwelling organisms from the two islands using sticky traps from June to August 2016. We set five traps along the forest road 10 m apart at each site, which were 300 m apart in each area (Supplementary Table S1). Each area had five sites (Supplementary Table S1). We conducted trapping in five areas in Amami Island and 4 areas in Tokunoshima Island for 3–5 days per area (Supplementary Table S1). Trapping areas are mainly covered by broad-leaved evergreen trees. In total, we set up 434 sticky traps on Amami Island and 370 on Tokunoshima Island. Although different numbers of sticky traps might lead to difference in the number of organisms captured, we considered the bias in the calculation mentioned below. We recorded the taxa and their abundances to as fine a scale as possible.

We obtained SVL of 165 individuals of *O. amamiensis* from the sympatric population, 63 individuals of *O. amamiensis* from the allopatric population and 53 individuals of *B. subaspera*. We obtained gut contents from 124 individuals from the sympatric population of *O. amamiensis*, 50 individuals from the allopatric population of *O. amamiensis* and 47 individuals of *B. subaspera* (Supplementary Table S2).

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Hypothesis testing

To test for the presence of ecological character displacement in our model system, we tested three of the six criteria for ecological character displacement proposed by Schluter (2000), as follows:

(1) *Phenotypic change amongst populations*: Population and species differences must represent an evolutionary shift and not just species sorting. (i.e. the differences between sympatric and allopatric populations should be intraspecific);

(2) *Phenotypic change matches prey preference*: Shift in resource use should match changes in morphology or other phenotypic traits;

(3) *Prey availability*: Food resource differences between sites of sympatry and allopatry must be controlled;

We chose to test only the following three criteria because the other three were difficult to evaluate in our study system:

(4) *Competition amongst species*: Independent evidence should be gained that similar phenotypes compete for resources;

(5) Chance should be ruled out as an explanation of the pattern, and;

(6) Phenotypic differences amongst populations and species should have a genetic basis.

Hypothesis 1. Phenotypic change amongst populations

We examined intraspecific morphological differences between the Amami Island population of *O. amamiensis* (sympatric with potential competitor) and the Tokunoshima Island population of *O. amamiensis* (allopatric with potential competitor).

We tested whether there was a statistically significant difference in SVL between the 2 *O. amamiensis* populations using Welch two-sample t-test. We predicted that SVL of the allopatric population of *O. amamiensis* would be greater than SVL of the sympatric population of *O. amamiensis* because the allopatric population was released from potential competition with *B. subaspera*.

Hypothesis 2. Phenotypic change matches prey preference

We predicted that the allopatric population of *O. amamiensis* consumed larger prey than did the sympatric population, because the Tokunoshima Island population was free from the potential competitor *B. subaspera*. We determined prey size on the basis of gut contents. First, we measured dry weight of the gut contents. When we found remnants of a ground-dwelling organism, we estimated dry weight on the basis of allometric formula, with which we tested the relationship between the remnant length (i.e., leg length) and dry weight by a linear regression model (Supplementary Table S3). We applied generalised linear mixed models (GLMM) to test the difference in dry weight of gut contents between the two *O. amamiensis* populations. Normal distribution was considered error distribution, and logit link function was specified. We used log-transformed dry weight of the gut contents per individual as the response variable and the two islands as the explanatory variables. We added individual difference as a random effect to consider individual variation.

In addition, we predicted that food segregation had already occurred between *O. amamiensis* and *B. subaspera* populations on Amami Island because food segregation is an inherent component of sympatric competition (Schluter, 2000). The allopatric *O. amamiensis* population, however, was released from competition for food. Therefore, we predicted that there would be a significant difference in prey size between *B. subaspera* population and the sympatric *O. amamiensis* population, but not in prey size between *B. subaspera* population and the allopatric *O. amamiensis* population. To test this hypothesis, we measured the dry weight of gut contents. When we found remnants of ground-dwelling organisms, we estimated dry weight on the basis of allometric calculations. We applied GLMM to test the differences in size of prey between *B. subaspera* and the two island populations of *O. amamiensis*. Normal distribution was considered error distribution, and logit link function was specified. We used log-transformed dry weight of the gut contents per individual as the response variable and species and island as explanatory variables. We added individual difference as a random effect to consider individual variation.

Hypothesis 3. Prey availability

We examined the similarity in ground-dwelling fauna, which was the main prey of the frogs, to evaluate the food resource similarity between the two islands. We calculated Pianka's α similarity index, which takes the number of taxa and their abundances into account (Pianka, 1973; Nakamura, 2000).

$$\text{Pianka's } \alpha = \sum PAi \cdot PBi \,/\, \sqrt{\sum PAi^2 \cdot \sum PBi^2}$$

$$(PAi = nAi/NA,\ PBi = nBi/NB)$$

$$(0 \le \alpha \le 1)$$

where *NA* is the total number of individuals in area *A*, and *nAi* is the total number of individuals of species *i* in area *A*. *NB* is the total number of individuals in area *B*, and *nBi* is the total number of individuals of species *i* in area *B*.

RESULTS

Hypothesis 1. Phenotypic changes

Snout–vent length of the allopatric *O. amamiensis* population was significantly greater than that of the sympatric *O. amamiensis* population (median 96.4 mm vs 83.0 mm, respectively; $P = 0.001$; Fig. 2).

Hypothesis 2. Prey preference

We identified seven classes, 13 orders and 4 families of prey, including beetles (Coleoptera), earthworms (Annelida)

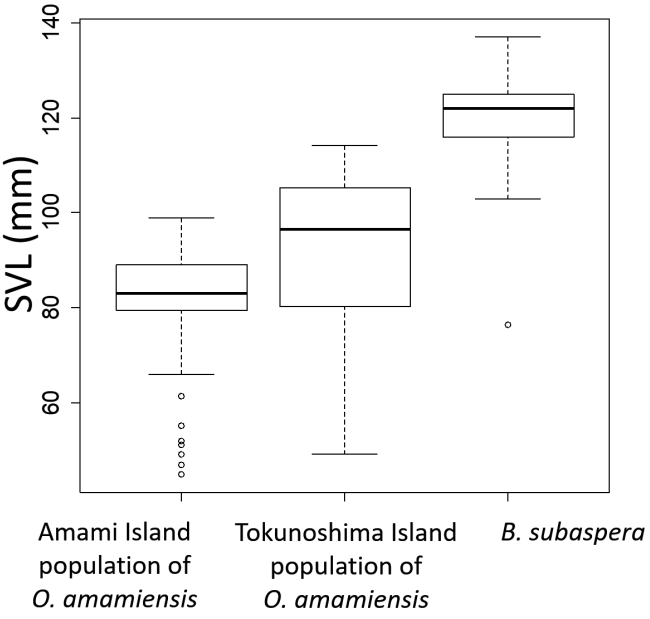


Fig. 2. Box and whisker plots illustrating differences in snout–vent length (SVL) in *Odorrana amamiensis* from Amami Island, *O. amamiensis* from Tokunoshima Island and *Babina subaspera* from Amami Island. The whiskers represent the maximum and minimum (excluding outliers); the top and bottom of the box represent the upper and lower quartiles, respectively; the centre line within the box represents the median.

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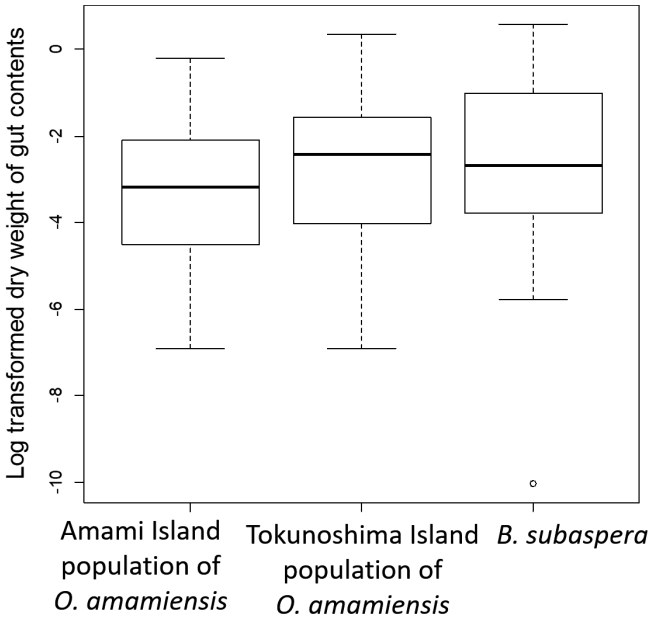


Fig. 3. Box and whiskers plot illustrating differences in log-transformed the dry weight of the gut contents of *Odorrana amamiensis* from Amami Island, *O. amamiensis* from Tokunoshima Island and *Babina subaspera* from Amami Island. The whiskers represent the maximum and minimum (excluding outliers); the top and bottom of the box represent the upper and lower quartile, respectively; the centre line within the box represents the median.

and camel crickets (Rhaphidophoridae) from the gut contents of the *O. amamiensis*' sympatric population. We identified seven classes, nine orders and three families of prey, including camel crickets (Rhaphidophoridae), from the gut contents of *O. amamiensis*' allopatric population (Supplementary Table S2).

GLMM revealed that the dry weight of the gut contents of the allopatric *O. amamiensis* population was significantly higher than the dry weight of the gut contents of the sympatric *O. amamiensis* population ($P < 0.01$; Fig. 3; Supplementary Table S4).

We identified nine classes, 15 orders and four families of prey from the gut contents of *B. subaspera*, including crabs (Decapoda) and camel crickets (Rhaphidophoridae) (Supplementary Table S2).

GLMM revealed a significant difference in prey size between *B. subaspera* population and the sympatric *O. amamiensis* population ($P < 0.001$; Fig. 3; Supplementary Table S5) but no significant difference in prey size between *B. subaspera* population and the allopatric *O. amamiensis* population ($P = 0.416$; Fig. 3; Supplementary Table S5).

Hypothesis 3. Prey availability

We identified eight classes, 19 orders and six families of ground-dwelling fauna on Amami Island and nine classes, 20 orders and five families of ground-dwelling fauna on Tokunoshima Island (Supplementary Table S6). Pianka's α similarity index was 0.982 ($0 \leq \alpha \leq 1$).

DISCUSSION

All three hypotheses tested in this study were consistent with our predictions, indicating a possibility of the presence of ecological character displacement between species. Individuals from the allopatric *O. amamiensis* population were significantly larger than those from the sympatric population. Prey size of the allopatric *O. amamiensis* population was significantly larger than that of the sympatric population, suggesting that intraspecific morphological divergence occurred and that resource use shift corresponded to morphological divergence. Moreover, *B. subaspera* consumed significantly larger prey than the sympatric Amami Island populations, whereas prey size did not significantly differ between *B. subaspera* and the allopatric *O. amamiensis* population. Therefore, food segregation may be present between *B. subaspera* and the sympatric *O. amamiensis* population. Additionally, arthropod fauna between Amami and Tokunoshima Islands was highly similar. Hence, our findings suggest that competition between non-congeneric species without reproductive interference can drive ecological character displacement.

Our results are consistent with previous reports demonstrating ecological character displacement as a result of competition. Schluter (1986) have reported that *Geospiza fuliginosa* and *G. difficilis* from the Galapagos Islands consumed more nectar on islands on which the carpenter bee, *Xylocopa darwini*, was absent. Moreover, *G. fuliginosa* and *G. difficilis* were significantly smaller on islands on which the carpenter bees were present. Similarly, Yom-Tov (1993) reported that body size of the striped mouse, *Rhabdomys pumilio*, in southern Africa was larger in areas in which potential competition with larger herbivores was excluded. These findings suggest that ecological character displacement can occur between species of different genera that show no reproductive interference. However, these previous studies did not assess the similarity of food resources between sympatric and allopatric zones, which is an essential component of ecological character displacement. In our study, ground-dwelling fauna—the main food resource of the studied frogs—was similar between the islands; thus, we could evaluate ecological character displacement between non-congeneric frogs.

Previous studies have considered competition as an important driver of evolutionary diversification, and many studies have reported ecological character displacement. Stuart and Losos (2013) have reported 144 case studies that satisfied at least one of the Schluter (2000) criteria for ecological character displacement, with fewer organisms considered strong candidates of ecological character displacement (satisfying more than four criteria). Known examples of strong candidates of ecological character displacement are restricted to a few groups, such as anoles, sticklebacks and Darwin's finches (Dayan and Simberloff, 2005; Stuart and Losos, 2013). In this study, we demonstrated that our study model satisfied at least three of the six criteria for ecological character displacement (Schluter, 2000), and this is one of the few case studies conducted in Anura (Martin and Pfenning, 2011).

We could not investigate the other three of the Schluter (2000) 6 criteria for ecological character displacement. *O. amamiensis* is endemic to Amami and Tokunoshima Islands; therefore, it is difficult to replicate the study elsewhere to satisfy the fifth criterion, i.e., ruling out chance. Many previ-

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ous studies often lacked replication because researchers were unable to completely control their study design in the field study (McDowall, 1998; Gehlbach, 2003; Davies et al., 2007; Gurd, 2008). Our study also lacks replication; hence, we did not completely prove ecological character displacement. However, our study presents a rare case, suggesting that ecological character displacement is likely to occur in non-congeners. Moreover, this case study will contribute to a better understanding of evolutionary mechanism in nature (Stuart and Losos, 2013). We could not examine fourth criteria sufficiently. We found that there was a significant difference in prey size between *B. subaspera* and the sympatric *O. amamiensis* population ($P < 0.001$; Fig. 3; Supplementary Table S5) but no significant difference in prey size between *B. subaspera* and the allopatric *O. amamiensis* population ($P = 0.416$; Fig. 3; Supplementary Table S5). This result suggests that food segregation has occurred in sympatric zone by competition. However, we will need to examine resource competition between *O. amamiensis* and *B. subaspera* by measuring prey capture efficiency in the field or laboratory enclosure to satisfy the fourth criteria. We intend to examine such a test in future studies. To satisfy the final criterion—genetic bases for phenotypic differences—we need to evaluate the difference in growth between the two island populations of *O. amamiensis* in the laboratory (Grudemoa and Johannesson, 1999; Schluter, 2000), which we intend to perform in a future study. Additionally, although we focused on differences in morphological characters and resource use between allopatric and sympatric *O. amamiensis* populations and *B. subaspera* population, we did not evaluate differences in morphological characters and resource use between *B. subaspera* populations allopatric with *O. amamiensis*. *B. subaspera* inhabits Kakeroma Island located to the south of Amami Island (Maeda and Matsui, 1999). In future, we intend to examine the differences in morphological characters and resource use amongst allopatric *B. subaspera* populations. Additionally, we were unable to consider sexual dimorphism in *O. amamiensis* because we could capture only five males in each island. *O. amamiensis* females are generally larger than their male counterparts; therefore, we might have to consider the sexual difference. However, the maximum size of males was 81.0 mm in Tokunoshima Island and 68.1 mm in Amami Island. Moreover, a previous study reported that the maximum size of males, which participated in breeding in the Amami Island population, was 71.7 mm ($n = 21$) (Iwai et al., 2015). Thus, males from Tokunoshima Island seemed to be larger than those from Amami Island, and sexual dimorphisms would not influence our conclusion. We intend to collect more male samples in near future. In addition, we were unable to consider the age structure of *O. amamiensis*. However, a previous study reported that the maximum size of females, which participated in breeding in the Amami Island population, was 99.9 mm ($n = 7$) (Iwai et al., 2015), and the maximum size of females in the Tokunoshima Island population in our sample was 114.1 mm. Although our sample from Tokunoshima Island might not be matured, individuals in the Tokunoshima Island population were larger than the matured individuals from Amami Island. This indicates that the age structure would not influence our result. We collected the fourth finger of the hind limb, which will allow us assess the age structure by observing the arrested growth lines. We will examine it to reveal the relationship between the age and body size of *O. amamiensis* individuals from Amami Island and Tokunoshima Island in a future study.

In the present study, we focused on the competition with *B. subaspera* as a driver of the body size shift of *O. amamiensis*, while there may be other possibilities leading to the body size shift; for example, *O. splendida*, which inhabits only Amami Island, might be a potential competitor of *O. amamiensis*. This species is also a large frog species in Amami Island; therefore, they might be competitors to *O. amamiensis*. However, habitat use is likely to differ amongst *O. amamiensis*, *B. subaspera* and *O. splendida*. Both *O. amamiensis* and *B. subaspera* individuals inhabit the entire mountain forest in Amami Island, whereas *O. splendida* individuals inhabit localised environments, such as a forest near the mountainous stream (Matsui and Maeda, 2018). Hence, *O. amamiensis* can be an important competitor of *O. splendida*; however, *O. splendida* could not be an important competitor for *O. amamiensis.* Therefore, *B. subaspera*, rather than *O. splendida*, is likely to be the major driver of the body size shift of *O. amamiensis*.

The two populations of *O. amamiensis* studied do not differ genetically (Matsui et al., 2005). Matsui (1994) has described the Tokunoshima Island population to be larger than the Amami Island population. However, the sample size was small ($n = 5$), and they did not focus on the ecological and evolutionary significance of morphological differences between the two populations. Our study demonstrated that these island populations were ecologically and morphologically divergent, suggesting the presence of a peculiar species interaction, giving rise to ecological divergence on each island. Therefore, to conserve evolutionary processes on these two islands, both Amami and Tokunoshima Island populations should be conserved. Since 2000, the Ministry of the Environment has been trying to eradicate an invasive species of mongoose on Amami Island (Watari et al., 2008; Watari et al., 2013; Fukasawa et al., 2013; Komine et al., 2016). Recently, the Ministry of the Environment and local governments have taken initiatives to reduce feral cat populations on these islands. Continuing such projects will benefit the conservation of *O. amamiensis* on these islands.

In conclusion, phenotypic divergence and resource use shift in *O. amamiensis* may be explained by ecological character displacement between this species and *B. subaspera*. Non-congeneric species show little reproductive interference, which is another driver of ecological character displacement; thus, the observed ecological divergence phenomenon was likely driven by competition between these non-congeneric species. Our results indicate that non-congeneric species can be a more successful model for evaluating ecological character displacement in a variety of organisms because the influence of competition on ecological character displacement can be partitioned from the influence of reproductive interference in non-congeneric species. In this study, we focused on the ecological divergence of *O. amamiensis* alone, and future studies should examine the phenotypic divergence and resource use shift in *B. subaspera*. Additionally, we efforts should be made to conserve populations of *O. amamiensis* on both islands to preserve the unique evolutionary processes arising from

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species interactions.

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COMPETING INTERESTS

We have no competing interests.

AUTHOR CONTRIBUTIONS

Hirotaka Komine designed the study, collected field data, carried out statistical analysis and drafted the manuscript. Yuya Watari collected field data and helped to draft the manuscript. Koichi Kaji helped to design the study and draft the manuscript. All authors gave final approval for publication.

SUPPLEMENTARY MATERIALS

Supplementary materials for this article are available online (URL: https://bioone.org/journals/supplementalcontent/10.2108/zs190037/10.2108.zsj.36.410.s1.pdf).

Supplementary Table S1. Trapping design to capture ground-dwelling fauna using sticky traps on Amami and Tokunoshima Islands. We set five traps along forest road 10 m apart at each site, which was placed 300 m apart in each area. One area has five sites. We conducted trapping in five areas in Amami Island and four areas in Tokunoshima Island for 3–5 days per area. Trapping areas are mainly covered by broad-leaved evergreen trees. In total, we set up 434 sticky traps on Amami Island and 370 on Tokunoshima Island.

Supplementary Table S2. Gut contents of *Babina subaspera* from Amami Island, *Odorrana amamiensis* from Amami Island and *Odorrana amamiensis* from Tokunoshima Island.

Supplementary Table S3. Relationship between the remnant length (i.e. leg length) and dry weight of camel crickets (*Rhaphidophoridae*) by linear regression model.

Supplementary Table S4. Results of generalised linear mixed models testing the difference in dry weight of gut contents between 2 populations of *Odorrana amamiensis* from Amami and Tokunoshima Islands, respectively.

Supplementary Table S5. Results of generalised linear mixed models testing the difference in the dry weight of gut contents between *Babina subaspera* from Amami Island and the sympatric *Odorrana amamiensis* population from Amami Island and between *B. subaspera* from Amami Island and the allopatric *O. amamiensis* population from Tokunoshima Islands.

Supplementary Table S6. Ground-dwelling fauna captured using sticky traps set on Amami and Tokunoshima Islands.

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