Parallel environmental factors drive variation in insect density and plant resistance in the native and invaded ranges

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Abstract. Geographic variation in the traits of a species is shaped by variation in abiotic conditions, biotic interactions, and evolutionary history of its interactions with other species. We studied the geographic variation in the density of the lace bug, *Corythucha marmorata*, and the resistance of tall goldenrod *Solidago altissima* to the lace bug herbivory in their native range in the United States and invaded range in Japan. We conducted field surveys and reciprocal transplant experiments to examine what abiotic and biotic factors influence variation in lace bug density, and what ecological and evolutionary factors predict the resistance of the host plant between and within the native and invaded ranges. Lace bug density was higher throughout the invaded range than in the native range, higher in populations with warmer climates, and negatively affected by foliage damage by other insects in both ranges. The higher lace bug density in warmer climates was explained by the shorter developmental time of the lace bugs at higher temperatures. The resistance of *S. altissima* to lace bugs was higher in populations with lace bugs compared to populations without lace bugs in both native and invaded ranges, indicating that the evolutionary history of the interaction with the lace bugs was responsible for the variation in *S. altissima* resistance in both ranges. The present study revealed that abiotic and biotic factors, including temperature and other herbivorous insects, can drive the geographic variation in lace bug density, which in turn selects for variation in plant resistance in both in the native and invaded ranges. We conclude that the novel combination of factors such as higher temperature and lower number of other herbivorous insects is responsible for the higher lace bug density in the invaded range than in the native range.

Key words: *biological invasion;* Corythucha marmorata; *exotic insects; plant defense; plant–insect interaction;* Solidago altissima.

Introduction

Species interactions may vary geographically due to local variation in abiotic conditions and biotic community structure. This may lead to geographical differences in species traits through evolution (Endler and Houde 1995, Thompson 2005, Craig et al. 2007, Soria-Carrasco et al. 2014). Plant–herbivorous-insect interactions comprise a major proportion of all species interactions and are fundamental to the community structure of terrestrial ecosystems (Futyma and Agrawal 2009). Plants may suffer from herbivorous insects that vary geographically, leading to local adaptation and variation in their resistance over a wide geographical range (Lankau and Strauss 2008, Züst et al. 2012).

Geographic differences in abiotic conditions, quality or quantity of host plants, and density of natural enemies are known to be ecological and environmental factors explaining the variation in density and species composition of herbivorous insects (Pennings and Silliman 2005,

Marczak et al. 2011, Woods et al. 2012, Anstett et al. 2014, Barrios-Garcia et al. 2014, Abdala-Roberts et al. 2016, Bhattarai et al. 2017). However, only a few studies have evaluated multiple ecological and evolutionary factors that interact to generate the geographic variation in herbivorous insect density. In addition, the time scale over which the geographic variation is shaped is not well understood. A recent study has shown that the latitudinal cline in traits related to herbivory can be shaped in <100 yr (Bhattarai et al. 2017). To determine the ecological and evolutionary processes that produce these variations, and the timescale over which they form, a combination of field studies over broad geographic scales and manipulative experiments is necessary.

The biological invasion of plants into new environments provides an important opportunity to study the evolution of plant defenses to herbivorous insects in a contemporary time scale. When a plant invades a new area, differences in plant community, herbivorous insect community, abiotic environment, and plant genotype that colonize the new location can affect the evolutionary dynamics of plant–herbivorous-insect interactions (Leimu et al. 2012). In a new geographical range, exotic plants are free from various herbivorous insects (i.e., the enemy

release hypothesis; Elton 1958, Keane and Crawley 2002), but they are often colonized by a few native insects in the invaded range (Parker et al. 2006). Moreover, some of the herbivorous insects in the native range are occasionally introduced to the invaded range, either accidentally or intentionally for biological control (Van Klinken and Edwards 2002, Zangerl and Berenbaum 2005). The density and population growth of exotic herbivorous insects may differ between the native and invaded ranges because the plant-herbivorous insect interactions take place in a novel abiotic, biotic, and genetic context.

Climate is critical in determining the differences in density of herbivorous insects in the native and invaded ranges (Bezemer et al. 2014), because the life history of insects and plant phenology are strongly influenced by temperature (Raghu et al. 2006, Cleland et al. 2007, Mitton and Ferrenberg 2012). In addition, the presence or absence of other herbivorous insects may influence the strength of the focal plant–herbivorous-insect interaction in the invaded range (Leimu et al. 2012, Strauss 2013). For example, resistance traits to the focal herbivorous insect could be antagonistically constrained due to restriction in signal transduction pathways (i.e., jasmonic acid pathway or phytohormonal cross talk), or the strength of the antagonistic response could be genetically determined (Stam et al. 2014). However, studies are lacking on how these factors interact to shape the variation in the herbivorous insect density, and how rapidly they cause the evolution in plant resistance between native and invaded ranges. Measuring geographical variation in herbivorous insect communities and local adaptation of defensive plant traits within and among native and invaded ranges will allow us to understand the role of multiple factors shaping the evolutionary dynamics of plant-herbivorous insect interactions. Comparing the herbivorous insect community and plant resistance of the invaded populations with those of the source populations in the native range can also help to trace the changes in plant resistance during the invasion process.

The interaction between tall goldenrod, *Solidago altissima* (Asteraceae), and the lace bug, *Corythucha marmorata* (Tingidae; Hemiptera), provides an ideal system for understanding local adaptation in a plant to an herbivorous insect during the invasion process. *Solidago altissima* is an herbaceous perennial native to old-field habitats in North America. Several studies have explored genetic variability in goldenrod's resistance to herbivorous insects (Maddox and Root 1987, Craig et al. 2007, Utsumi et al. 2011, Uesugi et al. 2013) and indicated that herbivorous insects are the major agent of natural selection on defensive traits of *S. altissima* (Meyer and Root 1993, Bode and Kessler 2012). In Japan, *S. altissima* was introduced 100 yr ago and it has extensively invaded abandoned fields across the country (Shimizu 2003). Sakata et al. (2015) showed that *S. altissima* populations in southeastern U.S. are most closely related to the predominant genetic lineage in Japan, suggesting that they are the source populations. *Corythucha*

marmorata is one of the major herbivorous insects on *S. altissima* in its native range of North America (Cappuccino and Root 1992), and it was introduced to Japan 15 yr ago, and is still expanding its distribution. A previous study demonstrated that this invasion of lace bugs caused rapid evolution of elevated resistance in *S. altissima* in Japan (Sakata et al. 2014).

The aim of the present study was (1) to examine which abiotic and biotic factors drive variation in the lace bug density between and within the native and invaded ranges and (2) to examine the effect of the evolutionary history with the interaction of lace bugs on the resistance of the host plant *S. altissima*. Because lace bugs exert strong selection on resistance in *S. altissima* in Japan (Sakata et al. 2014), elucidating the abiotic and biotic factors that determine lace bug density will lead to further understanding of the underlying mechanisms responsible for the evolution of *S. altissima* resistance during the invasion process. To examine which biotic and abiotic factors drive variation in the density of lace bugs, we conducted the following surveys and experiments. First, we conducted geographical surveys to measure the effect of abiotic and biotic factors on the density of lace bugs in natural populations of *S. altissima* in the United States and Japan. Second, we conducted a growth chamber experiment to test whether developmental time and number of offspring in the next generation of lace bugs differed between and within the ranges. To examine ecological and evolutionary factors that drive variation in *S. altissima* resistance, we conducted a reciprocal transplant experiment, and a common garden experiment to compare the resistance of *S. altissima* from populations that vary in the evolutionary history of the interaction with lace bugs in both ranges. We demonstrated that parallel environmental factors drive variation in insect density and plant resistance in the native and invaded ranges, and novel combinations of these factors rapidly shaped the differences in the herbivorous insect density between native and invaded ranges.

METHODS

Field survey

We surveyed 16 *S. altissima* natural populations in the midwest United States from Minnesota to Texas (1900 km), and seven populations in the southeastern United States from Florida to Louisiana during July and August in 2012–2014, as well as 50 populations in Japan (1,500 km) during June and July in 2011–2012 (Appendix S1: Fig. S1, Table S1). Populations were identified as aggregations of plants in areas such as riversides and abandoned agricultural fields. All surveyed populations were at an early successional stage with patch sizes of 25–50 m^2. The distance between any two adjacent populations was at least 1 km. We randomly surveyed three ramets per genotype for 5–10 genotypes, which were distinguished by their clumped distribution.

Clumps were separated by at least 5 m from each other to increase the probability that they were genetically distinct. For each ramet, the number and family (species if possible) of insects, including herbivorous insects and predators, levels of lace bug herbivory, and the number of damaged leaves excluding lace bug herbivory were recorded. Lace bug herbivory is distinguished from other insect herbivory by their yellow feeding scars. Herbivorous insects were categorized into four feeding guilds: sucker, galler, chewer, and miner. Gallers and miners were counted as the number of stem and leaf galls and leaf mines instead of the number of individuals. In addition, the level of lace bug herbivory was assessed by classifying the leaves damaged by the lace bug into four levels: (1) no damage, (2) <33% damage, (3) 33–66% damage, and (4) >66% damage of total leaf area. Subsequently, we counted the number of leaves indicating each damage level, added the values for all four levels, and finally divided this figure by the total leaf number.

We used meteorological data collected by the national weather stations closest to the surveyed populations. Mean annual temperature and precipitation were obtained from the National Oceanic and Atmospheric Administration and the Japan Meteorological Agency (data *available online*).[5,6]

First, we explored factors influencing the number of herbivorous insect families and their density observed using generalized linear mixed models (GLMMs). The number of herbivorous insect families per plant population and individuals per ramet were selected as response variables, while range (USA or Japan), mean annual temperature, and annual precipitation were set as explanatory variables. For insect density, we also included number of leaves per ramet as an explanatory variable, because the number of leaves may affect colonization by herbivorous insects. We included the two climate variables instead of latitude because they are important environmental factors for insects and plants (Anstett et al. 2014, Agrawal et al. 2015, Moreira et al. 2015). These two climate measures were not correlated to each other, while annual temperature was correlated with latitude. We included plant genotypes nested within a population as a random effect.

Next, we explored factors influencing the number and damage level of lace bugs in two ways using GLMMs. Prior to the analysis, we excluded populations without lace bugs in both ranges so that data consisted only of populations with lace bugs. First, we analyzed the presence/absence of both lace bugs and lace bug damage with GLMMs with a binomial distribution. The presence/absence of lace bugs and damage level per ramet were selected as response variables, and range (United States or Japan), mean annual temperature, annual precipitation, foliage damage by other herbivorous insects (number of leaves damaged by other herbivorous insects

divided by number of total leaves), number of leaves per ramet, and the interaction term of range and other foliage damage were set as explanatory variables. We included other foliage damage because lace bugs may be influenced by foliage damage by other herbivorous insects owing to competitive or facilitative interactions, and range × other foliage damage because the effect of the foliage damage on lace bugs may differ between the United States and Japan. We included genotypes nested within a population as a random effect. Second, we analyzed the lace bug density and the damage level in ramets with lace bugs using GLMMs with a Poisson distribution. The number of lace bugs and damage level per ramet were selected as response variables, and the same explanatory variables and random effect used in the GLMMs for the presence/absence of lace bugs were included.

Finally, we analyzed relationships between the density of lace bugs and other herbivorous insects (categorized by feeding guilds) in the United States using GLMMs with a Poisson distribution. The number of lace bugs per ramet was selected as a response variable, and the number of leaves per ramet and the number of insects of each of the four guilds were set as explanatory variables. We included plant genotypes nested within a population as a random effect. In addition, we analyzed the relationship between the density of lace bugs and *Uroleucon* aphids that was another abundant insect beside lace bugs on *S. altissima* populations in Japan.

Reciprocal transplant experiment

We conducted a reciprocal transplant experiment in common gardens in the USA and Japan to examine the resistance and tolerance (i.e., the ability of plants to mitigate negative fitness loss by herbivory) of *S. altissima* populations with and without lace bugs in both ranges based on the field survey. We replicated gardens in two ranges to determine the difference in the degree of adaptation of lace bugs to *S. altissima* between ranges. Rhizome segments of 10 genotypes were collected in each population from plants at least 5 m apart from the field survey of 12 populations in the United States in 2012 (seven populations with high lace bug density and five populations without lace bugs), and nine populations in Japan in 2011 (four populations with an 11-yr history of lace bug establishment and five lace bug uninvaded populations; Appendix S1: Table S1). The rhizome segments were planted in a greenhouse at the Center for Ecological Research, Kyoto University, Japan, and cultivated for more than one growing season to minimize maternal effects.

In April 2013 in Japan and May 2013 in the United States, rhizomes were cut into 6 cm long segments with a diameter of 5 mm. Two ramets each of identical genotypes from populations in both the United States and Japan (800 plants in total in each garden) were planted in pots and grown in gardens in both the United States (University of Minnesota Duluth Research and Field

Studies Center; 46.86° N, 92.03° W) and Japan (Center for Ecological Research; 34.97° N, 135.96° E). In June 2013 in Japan and July in the United States, all but one shoot were eliminated to equalize plant size for each ramet. The mean daily temperature during the experiment was 30° and 25°C in Japan and the United States, respectively. Each plant was inoculated with two adult male and two adult female lace bugs, which were collected from areas around each garden. All plants were then covered with nonwoven fabric bags (500 mm wide, 2000 mm tall). The number of lace bugs and damage levels were measured using the same method as in the field survey in the fourth week from the start of the experiment. We measured lace bug population growth and damage level in the fourth week as indices of resistance of *S. altissima* because the fourth week is an appropriate time for measuring the population growth of lace bugs (Sakata et al. 2014). Both indices were used to complementarily evaluate plant resistance.

We explored factors influencing plant resistance using GLMMs with a Poisson distribution. We set garden location (United States or Japan), evolutionary history with lace bugs (plant populations with or without lace bugs), plant country origin (United States or Japan), latitude of the plant population, and the interaction terms among garden, plant country origin, and evolutionary history with lace bugs as explanatory variables for resistance. For lace bug population growth rate, the number of lace bugs was set as a response variable, and the natural logarithm of the initial population size (i.e., four individuals) was entered into the model as an offset term. For damage levels, damage scores were set as a response variable and the natural logarithm of number of leaves was entered into the model as an offset term. Since lace bugs caused rapid evolution of resistance in *S. a;tissima* in Japan, we predicted that differences in plant resistance were influenced by the evolutionary history with lace bugs as well as the environmental factors. Data taken from the same genotype are thought to be correlated each other, and we sampled several genotypes from each population. Therefore, we included genotypes nested within a population as a random effect for all models to account for this nested correlation structure.

Aboveground vegetative production (number of leaves, height, and stem width) was measured at the start and end of the experiment four weeks later to estimate tolerance in each population. The variables of growth rate in plant height, width, and increase in leaf number were calculated by dividing the final measurements in the fourth week by the initial measurements. Reproductive traits were assessed for plants grown in Japan; we were not able to assess reproductive traits in the United States since most plants were frost damaged before they flowered. Flowers were examined every four days during the blooming season from 1 September to 15 November. For an index of sexual reproduction, the number of flowers was calculated by the following equation obtained from Sakata et al. (2014): number of flowers = $e^{0.11H + 0.05W + 3.15}$, where H and W are height and width of the capitulescence, respectively. All plants were harvested on 30 November 2013, and the total number of rhizomes was counted and their length was measured. Tolerance in each population was estimated as the slope of the linear regression of the plant growth and reproductive traits against the lace bug damage level in the fourth week, which is a measure of tolerance that has been supported by other studies in *S. altissima* (Hakes and Cronin 2012, Sakata et al. 2014). To explore factors influencing tolerance, we set the same as explanatory variables for resistance.

Common garden experiment: comparison of S. altissima *resistance between the source and invaded populations*

To elucidate the temporal changes in *S. altissima* resistance during invasion, we conducted a common garden experiment in 2015, which compared the resistance of the four populations in the putative source area, southeastern United States (TL, FL2, BR, and HT) and the four populations with an 11-yr lace bug establishment history in Hyogo, Japan (KN, KR, KRN, and KM), and three uninvaded populations from Sado and Yamagata, Japan (ST, SU, and Y). Rhizome segments of 10 genotypes were collected from plants at least 5 m apart at the field survey populations in southeastern United States in 2014. In April 2015, rhizomes were planted and grown in the garden in Japan at the Center for Ecological Research in the same way as in the reciprocal transplant experiment and the plant resistance indices were measured.

We analyzed the relationship between resistance indices (i.e., lace bug population growth rate and damage level) and the evolutionary history with lace bugs (i.e., southeastern populations with lace bugs in the United States, lace bug uninvaded populations in Japan, and populations with an 11-yr lace bug establishment history in Japan) using GLMMs with a Poisson distribution. The two resistance indices were selected as response variables and the population category was set as an explanatory variable. We included genotypes nested within a population as a random effect. When the effect of the population category was significant, we tested for differences in resistance among population categories using Tukey's post hoc test on least-squared means, holding the overall type I error rate at 5% using the lsmeans package, version 2.21 (Lenth 2015) of R.

Growth chamber experiment: effect of temperature, plant and insect origins on growth traits of lace bugs

We conducted a growth chamber experiment in the United States and Japan to examine whether growth traits of lace bugs differed between and within ranges. In 2012, 10 *S. altissima* genotypes per site were collected from two sites in the United States: one in the south with high lace bug density (Kansas [KS]) and the other in the north with low density (Minnesota [MN]), and one site

with high density in Japan (CER). These genotypes were grown in the common garden in both the United States and Japan for more than one growing season. We collected lace bugs from the same three sites where *S. altissima* plants were collected (KS, MN, and CER). Since no difference was found in lace bug growth traits among populations in Japan (Sakata et al. 2014), we only used plants from one site (CER). In June 2014 in Japan (July in the United States), four ramets of each genotype (eight ramets in the United States) were cut to the same size (roots were cut off and stem height was 15 cm with four leaves) and placed in a plastic container (10 cm wide, 15 cm tall) with a wet flower sponge. We cannot exclude the possibility that cutting stems might affect the defensive and nutritional traits of *S. altissima* by induced responses in the plants (Uesugi et al. 2013). However, it is beyond the scope of the experiment, because we aimed to compare the relative lace bug growth traits between and within ranges. Two female and two male lace bug adults were added to each plant and two temperature treatments were applied (20° and 30°C). We selected these two temperatures because the mean temperature in August when we conducted the field survey was 29.6°30.1°C in KS and CER, and 19.5° 21.0°C in MN where lace bugs were collected. Lace bug origins and *S. altissima* origins were fully crossed, producing nine different combinations. Two growth chambers were used to replicate each temperature to account for unknown factors influencing the difference between temperature treatments on lace bug growth (10 genotypes × 3 sites × 4 ramets = 120 plants for each lace bug origin). Lace bugs were checked every two days, and the following measurements were recorded: (1) the number of days that the first emerged nymph was observed from the time when the eggs were first observed, (2) the number of days that the first emerged adult was observed from the time when the first nymph was observed, and (3) the number of individuals including both adults and nymphs of the following generation at the end of the experiment (after one generation). Body length and width of five each male and female adults per population per treatment were also measured.

We analyzed the above three measurements and lace bug body size (length and width) using GLMMs with Poisson and Gaussian distributions, respectively. The lace bug traits were selected as response variables and lace bug origin, plant origin, temperature, and their interaction terms were set as explanatory variables. We included plant genotypes nested within a population as a random effect. When the effect of the variable was significant, we tested for differences in lace bug traits among lace bug categories and plant origin using Tukey's post hoc test on least-squared means, with the overall type I error rate at 5% using the lsmeans package of R.

In all the GLMM analyses we have described, the significance of main effects and interaction was determined using a likelihood ratio test, compared to chi-square distribution. All the analyses were conducted using the lme4 package (Bates et al. 2011) and car package (Fox and Weisberg 2011) of R 3.0.1 (R Development Core Team 2013).

RESULTS

Field survey

A wide range of herbivorous insect taxa from different feeding guilds was found in the United States (Appendix S2: Table S1, Fig. S1). The most common insects in the United States besides lace bugs were blister galler *Asteromyia carbonifera*, stem galler *Eurosta solidaginis*, bunch gallers *Procecidochares atra* and *Rhopalomyia solidaginis*, leaf miner *Microrhopala vittata*, leaf chewer Tortricidae sp., and leaf suckers Cicadellidae sp. and Membracidae sp. Lace bugs accounted for 39% of all observed insects in the United States. In contrast, in Japan, two exotic insect species dominated, with *C. marmorata* and the aphid *Uroleucon nigrotuberculatum* accounting for 61% and 37% of all observed insects, respectively. The number of herbivorous insect families per population and density per ramet were affected by range (Table 1), and the number of families was greater in the United States than in Japan (mean ± SE; United States, 11.85 ± 1.09; Japan, 3.31 ± 1.07), but the number of insects per ramet was greater in Japan than in the United States (United States, 2.13 ± 1.10; Japan, 8.59 ± 1.08). Mean annual temperature ($b \pm SE$, 0.11 ± 0.01; b refers to the estimate) and number of leaves per ramet ($b \pm SE$, 0.53 ± 0.03) positively affected herbivorous insect density, while annual precipitation positively affected the number of insect families ($b \pm SE$, 0.0004 ± 0.0001).

Lace bugs were absent in six populations where the mean annual temperature was lower than 12°C in the United States (HB, DL, FB, CA, CL, and DLP) in our survey, although low densities of lace bugs were observed in CA and DL during previous surveys in 2010–2012 (T. Craig, *personal observation*). We found different patterns between the analyses of lace bug presence/absence and lace bug density. Increasing foliage damage by other herbivorous insects had a positive effect on the presence of lace bugs and on the presence of lace bug damage (lace bug, $b \pm SE$, 1.93 ± 2.68; damage, 2.26 ± 2.63,

TABLE 1. Generalized linear mixed models (GLMMs) that predict number of families of herbivorous insects per *Solidago altissima* population (n = 73; United States n = 23, Japan n = 50), and total density of herbivorous insects per *S. altissima* ramet (n = 1720; United States n = 1034, Japan n = 686).

Effect	No. families		Density	
	χ^2	P	χ^2	P
Range	109.72	<0.0001	101.64	<0.0001
Annual temperature	0.08	0.78	66.04	<0.0001
Annual precipitation	7.74	0.005	6.48	0.01
No. leaves			233.04	<0.0001

Appendix S2: Table S2). On the other hand, lace bug density decreased as the foliage damage by other herbivorous insects increased. Moreover, lace bug density had a greater rate of decrease in the United States than in Japan as other foliage damage increased (United States, $b \pm$ SE, -0.53 ± 0.08; Japan, -0.28 ± 0.06; Fig. 1b). Lace bug density was higher in Japan than in the USA (lace bug mean $\pm$ SE; United States, 4.88 ± 1.11; Japan, 6.59 ± 1.07, Appendix S2: Table S2). Mean annual temperature and precipitation had no effect on lace bug presence, but lace bug density in both ranges was positively affected by mean annual temperature ($b \pm$ SE, 0.15 ± 0.03; Fig. 1a). Lace bug damage exhibited the same pattern as lace bug density, and so only the results of the lace bug density are shown (Fig. 1).

In the United States, the number of gallers and chewers had a significantly positive relationship with the number of lace bugs, while miners and suckers did not (Appendix S2: Table S3). We did not find a significant relationship between the numbers of lace bugs and *Uroleucon* aphids in Japan (GLMM, $\chi^2 = 0.85$, $P = 0.36$, $n = 499$).

Traits of S. altissima *in the reciprocal transplant experiment*

Both lace bug population growth and lace bug damage levels on *S. altissima* were significantly higher in the Japanese garden than in the U.S. garden (Fig. 2a, b), but did not differ by latitude of the plant origin (Appendix S3: Table S1). The effect of plant country origin was significantly influenced by the garden (garden × plant country origin), depending on the evolutionary history with lace bugs (plants from populations with or without lace bugs; Appendix S3: Table S1; Fig. 2c, d). Plants from populations without lace bugs had higher

damage levels than plants from populations with lace bugs in both ranges (Appendix S3: Table S1; Fig. 2b). None of the tolerance indices were significantly influenced by the plant country origin, evolutionary history with lace bugs, or latitude (Appendix S3: Table S2).

Solidago altissima *resistance in the source and invaded populations*

Lace bug population growth and damage level were both significantly greater (indicating lower plant resistance) in lace bug uninvaded populations in Japan than in the native populations in southeastern United States and in populations with an 11-yr lace bug establishment history in Japan (Fig. 2e, f). In addition, the populations with 11-yr lace bug establishment history showed significantly lower population growth, indicating higher plant resistance than the U.S. populations (Fig. 2e), but this trend was not significant for lace bug damage level (Fig. 2f).

Comparison of growth traits of lace bugs in the USA and Japan

Temperature significantly affected the developmental time of lace bugs (i.e., number of days for eggs to hatch and from hatched to adult emergence). Total developmental time from egg to adult emergence was 10 days shorter on average at 30°C (mean $\pm$ SE, 21.40 ± 0.55 d) than at 20°C (31.59 ± 0.68 d), but neither plant origin nor lace bug origin affected developmental time (Appendix S4: Table S1). Lace bug origin influenced the number of individuals in the next generation differently among plant origins (lace bug origin × plant origin), depending on temperature (Appendix S4: Table S1; Fig. 3c, d). The number of Kansas lace bugs in the next generation was greater on *S. altissima* from Duluth than
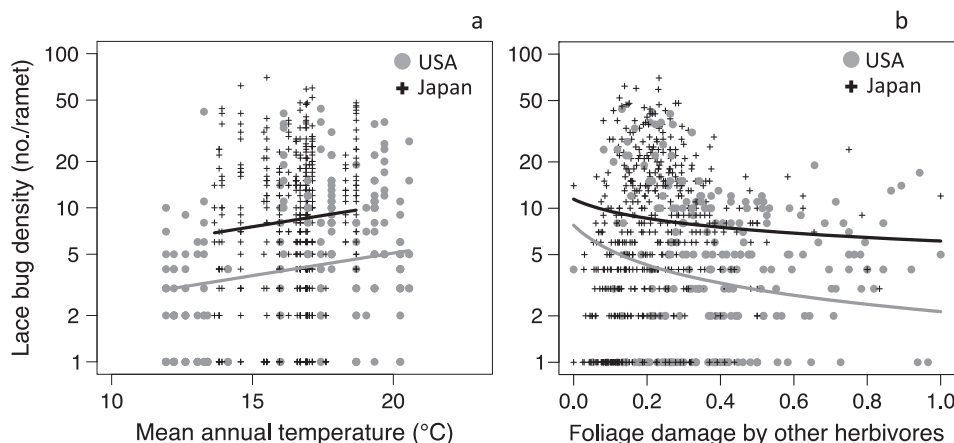

FIG. 1. Relationship between number of lace bugs per ramet of *Solidago altissima* and (a) mean annual temperature and (b) foliage damage (proportion) by other herbivores in natural populations. Foliage damage by other herbivores was scored as number of leaves with damage by herbivores excluding lace bugs divided by number of total leaves per ramet. Gray circles and black cross symbols/lines refer to the United States and Japan, respectively. Lines represent predicted relationships by the results of the GLMM in Appendix S2: Table S2. Each point represents a goldenrod genotype (5–10 genotypes per population).
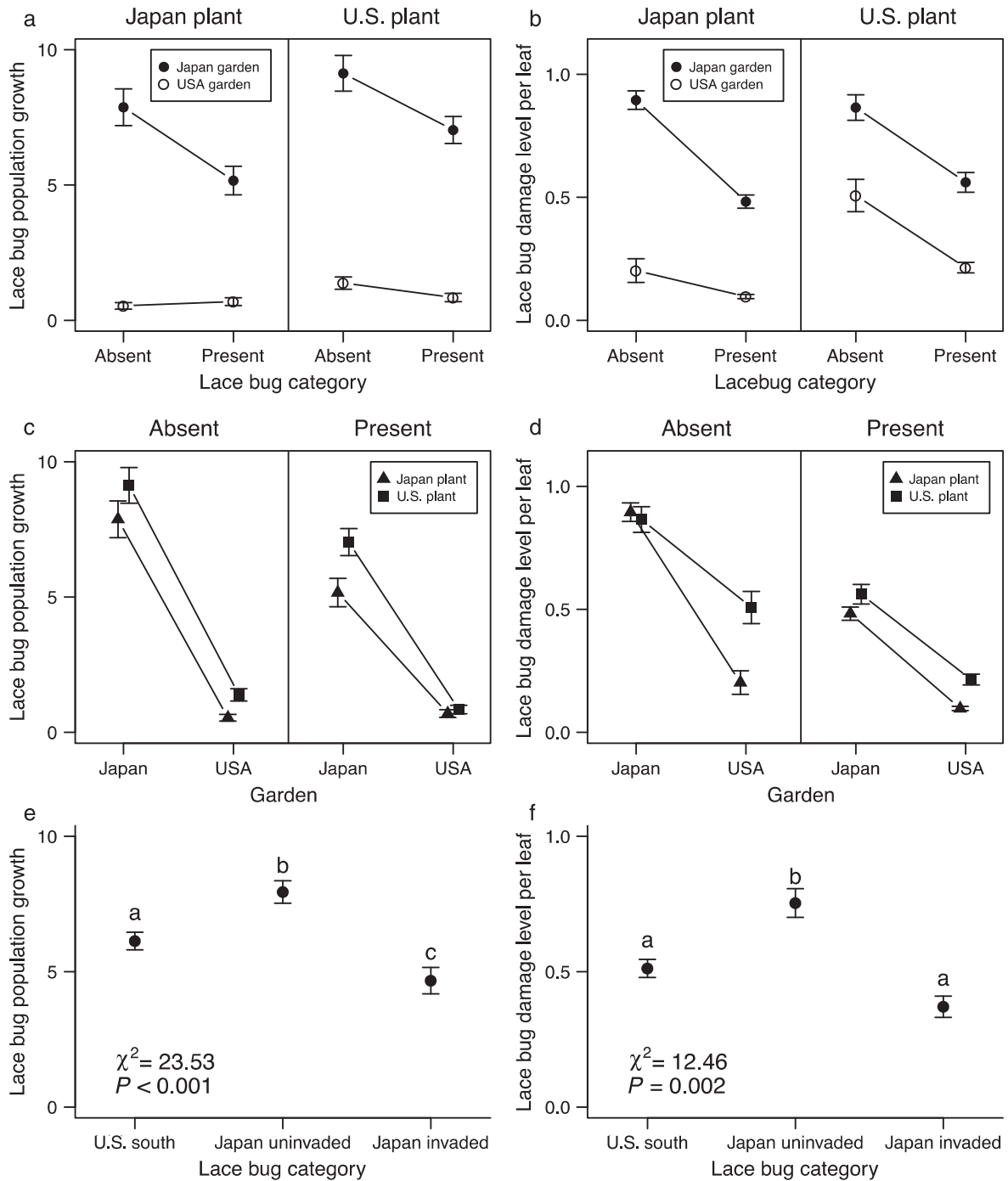
FIG. 2. Least square means (±SE) of lace bug population growth and damage rate of ramets of *Solidago altissima* by plant origin and lace bug history in Japan and the United States measured (a–d) in the reciprocal transplant experiment and (e, f) in the common garden experiment in Japan. Different letters indicate significant differences ($P \leq 0.05$).

on Japanese plants at 20°C ($P < 0.0001$; Fig. 3c), while the number of Japanese lace bugs on Kansas plants was greater than on Japanese plants ($P < 0.0001$; Fig. 3d). The body size of lace bugs was not affected by any of the three treatments, and showed no difference among lace bug origins (GLMM, $\chi^2 = 2.95$, $n = 180$, $P = 0.23$).

DISCUSSION

We draw two major findings from this study. First, abiotic and biotic factors, including temperature and other herbivorous insects, explained the geographic variation in lace bug density in both the native and invaded
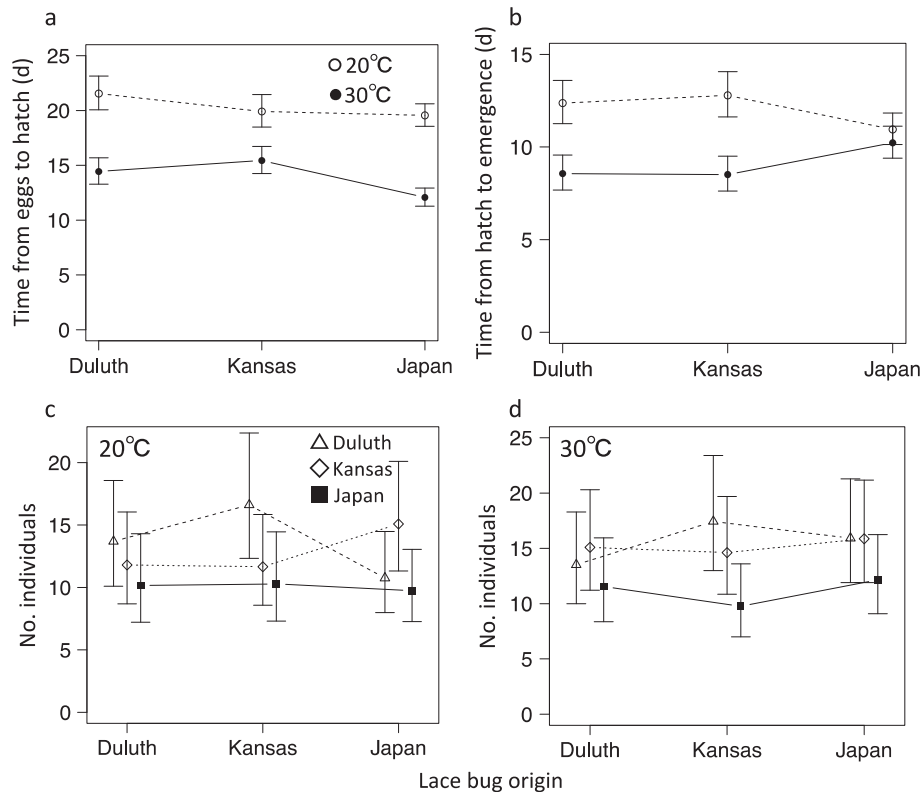
Fig. 3.   (a and b) Least square means (±SE) of developmental time in 20°C and 30°C. Symbols refer to temperature treatment. (c and d) Number of lace bugs in the following generation in 20°C and 30°C. Symbols refer to the plant origin.

ranges. Moreover, the novel combination of these factors in Japan may have caused the greater lace bug density in Japan than in the United States. Second, the evolutionary history of the interaction with lace bugs was responsible for the variation in *S. altissima* resistance in both ranges. Below, we discuss the basis for these conclusions.

Effects of temperature on lace bug density

Lace bug density was higher in warmer climates in both ranges, and when the mean annual temperature was below 12°C, their densities were extremely low or zero in the United States. The developmental time was shorter at the higher temperature (i.e., 30°C) in the growth chamber experiment, which would lead to a higher population growth rate in warmer climates. The shorter developmental time at higher temperatures was also reported in another lace bug species *Stephanitis takeyai* (Tsukada 1994). On the other hand, the number of individuals per generation was not influenced by temperature, and the Japanese lace bugs did not have a greater number of next generation individuals compared to the U.S. lace bugs. Therefore, lace bugs exhibited parallel positive response to the mean annual temperature (i.e., higher lace bug density with higher temperature) in both ranges due to shorter developmental time at higher temperature. In addition, the 5°C higher temperature at the Japanese

reciprocal transplant garden than at the U.S. garden would explain the greater lace bug population growth and damage level in the Japanese garden. Lu et al. (2015) also documented that warm climate increased overwintering survival of an insect introduced as a biocontrol and thus, increased the damage on the plant in the invaded range.

Effects of other herbivorous insects on lace bug density

In the United States, *S. altissima* plants supported more diverse taxa of herbivorous insects than in Japan, while the number of insects per ramet was higher in Japan due to the greater number of lace bugs and aphids. However, because of their small size, the per capita fitness impact of the lace bugs or aphids on *S. altissima* is likely to be smaller than that of larger insects that attack more important plant tissues such as the stem gallers. The decreased diversity in herbivorous insects in the invaded range is consistent with other studies comparing herbivory between ranges on *Solidago* sp. (Roháčová and Drozd 2009) and other plants (Wolfe 2002, Liu and Stiling 2006, Maurel et al. 2013). We conclude that *S. altissima* in Japan has been released from attack by its diverse herbivorous insects in the native range with the exception of two exotic insects: lace bugs and *Uroleucon* aphids.

A positive relationship between foliage damage by other herbivorous insects and lace bug presence was found, but

there was a negative relationship between foliage damage by other herbivorous insects and lace bug density. Moreover, when the foliage damage by other herbivorous insects increased, lace bug density decreased at a higher rate in the United States than in Japan, showing that lace bugs exhibited a nonparallel negative response to the foliage damage by other herbivorous insects between ranges. However, a negative correlation was not detected at the level of feeding guilds in the United States. These results suggest the following possibilities. First, the variation in plant quality, such as in nitrogen content, may have affected the presence of foliage-feeding insects and lace bugs in a similar way. Second, the negative genetic correlations (i.e., trade-offs) between resistance to lace bugs and other foliage feeding insects may exist, since multiple herbivorous insect species can impose selection on resistance of plants known as diffuse evolution (Leimu and Koricheva 2006, Wise and Rausher 2013). These negative correlations may be greater in the United States where numerous herbivorous insects have been established for a longer time period, and therefore had exerted stronger selection on plant resistance compared to Japan. Alternatively, the leaf damage by early-emerged herbivorous insects prior to lace bug colonization may had induced defenses or decreased the plant quality that decrease lace bug density (Karban and Baldwin 1997, Kessler and Baldwin 2002, Ohgushi 2005, Helms et al. 2013).

Other potential factors responsible for lace bug density

The developmental time of lace bugs differed neither among plant origins nor among lace bug origins, indicating that it was likely influenced by temperature alone. The number of lace bug individuals in the following generation differed among plant origins and among lace bug origins, but we did not find significant differences between the United States and Japan. However, we cannot eliminate the possibility that unmeasured traits such as the oviposition rate may differ between ranges. Evolution in insect traits has been reported in studies where both a plant and its associated herbivorous insect invaded a new area. For instance, the parsnip specialist webworm, *Depressaria pastinacella*, has evolved a higher furanocoumarin detoxification rate in the invaded range because of the absence of other host plants with lower furanocoumarin content (Berenbaum and Zangerl 2006). A ragweed specialist leaf beetle, *Zygoramma suturalis*, evolved an expanded host plant range in its invaded range because the ragweed, *Ambrosia trifida*, had reduced resistance in the invaded range (Fukano et al. 2016). Because generalist and specialist herbivorous insects differ in their response to plant defenses (Ali and Agrawal 2012), the fact that the lace bug is a generalist herbivorous insect feeding on several other Asteraceae plants in Japan (Kato and Ohbayashi 2009, Y. Sakata personal observation) may be one of the reasons why lace bugs have not been adapted to the variation of resistance of *S. altissima* within and between ranges.

Even when the variation in mean annual temperature and leaf damage by other insects were considered in the field survey, the Japanese plants supported greater lace bug density than did the USA plants. This may be due to the difference in the plant defense to lace bugs between ranges, which we did not measure in the field survey. Although we did not determine the nature of the resistant traits of *S. altissima* against lace bugs, secondary chemical compounds rather than physical traits are likely responsible for the resistance. This is because we did not find any relationships between physical traits (e.g., leaf trichome or leaf toughness) and resistance to lace bugs (Sakata 2016). *Solidago altissima* is known for its diverse anti-nutritive compounds (Uesugi and Kessler 2016). In addition, Uesugi and Kessler (2016) found that Japanese *S. altissima* with an early stage of lace bug invasion showed lower production of leaf secondary metabolites such as diterpene acids than in the USA. Although we did not find difference in plant resistance between ranges in the garden experiments, the effect of plant resistance on lace bug density in natural populations may differ between ranges. In future studies, it will be important to establish a causal link between specific plant defensive traits and lace bug herbivory, and to examine whether the geographic variation in the defensive traits explain the geographic variation in lace bug evolutionary history and density.

In addition, there may be differences in predation by natural enemies between the USA and Japan. In our previous experiment, lace bugs were eaten by generalist predators such as jumping spiders (Salticidae), lacewing nymphs (Chrysopidae), mantis imago (Mantidae), and harvestman (Opiliones) in both Japan and the United States (Sakata 2016). Although an egg parasitoid wasp of the lace bug, *Anugrus virginiae*, was recorded in Missouri, USA (Puttler and Triapitsyn 2006), it has not been recorded in any other regions throughout the United States, and we did not observe any lace bug parasitoids in any of the developmental stages in the present study. No other predators of lace bugs have been recorded in North America (Neal and Schaefer 2000). Although it is unlikely that differential predation results in the difference in lace bug density between ranges, it would be necessary to examine the predation on lace bugs throughout the season across sites to compare the effect of natural enemies on lace bug density.

We also cannot eliminate the possibility that other environmental factors may influence the geographic variation in lace bug density such as the degree of isolation of the populations (Cappuccino and Root 1992), or the soil characteristics such as soil biota communities, water content, and chemical composition (van Geem et al. 2013).

Effects of evolutionary history of the interaction with lace bugs on S. altissima *resistance*

The reciprocal transplant experiment showed that *Solidago altissima* resistance to lace bugs was higher in

populations with lace bugs than in populations without lace bugs in both native and invaded ranges. This is consistent with the findings of Sakata et al. (2014) that *S. altissima* resistance increased in populations with a longer period of establishment by lace bugs in Japan. This implies that the local adaptation of *S. altissima* defenses results from the evolutionary history of its interaction with lace bugs in both its native and invaded ranges. Measurement of the selection differentials of lace bugs on plant resistance is necessary to determine whether lace bugs exert selection on *S. altissima* resistance, and this is an important next step in studies of this interaction. Latitude did not affect the resistance to lace bugs in either range. In addition, there was no latitudinal difference in resistance either within the lace bug-present populations or within the lace-bug-absent populations in the United States (Y. Sakata, *unpublished data*). Therefore, *S. altissima* resistance to lace bugs is unlikely to be determined solely by the latitudinal difference but it is instead determined by the evolutionary history of the interaction with lace bugs influenced by abiotic and biotic factors.

The putative source of the Japanese *S. altissima* populations is southeastern U.S. populations where lace bug herbivory and plant resistance to lace bugs are high, suggesting that highly resistant *S. altissima* genotypes were introduced to Japan. The low plant resistance in lace bug uninvaded populations in Japan suggests that the frequency of the resistant genotypes declined through the following 100 yr when plants were free from lace bug herbivory. However, the frequency of resistant *S. altissima* genotypes increased again after reassociation with the lace bugs in the last decade (Sakata et al. 2014). This temporal dynamics of resistance could be explained by the cost in maintaining resistance shown by the existence of the tradeoff between resistance and flower production (Sakata et al. 2014).

Moreover, the Japanese plants exposed to lace bugs for 11 yr showed lower lace bug population growth than the putative source populations in the southeastern United States. This suggests that within a decade, the *S. altissima* that invaded Japan may have evolved resistance to lace bugs that exceeds that of the source populations. The scenario of temporal dynamics of losing and regaining plant defense is consistent with other studies of an exotic plant and an exotic insect (Zangerl and Berenbaum 2005, Fukano and Yahara 2012). However, our results are the first to indicate that the resistance of plant populations in the invaded range may exceed that of the source populations. Our results suggest that the novel combinations of abiotic and biotic factors in the invaded range have led to a higher lace bug density than the native range, resulting in the rapid evolution of resistance of *S. altissima* within a decade. This highlights that when invasive plants are reassociated with the native herbivorous insects in a novel environment, they may quickly regain resistance to their herbivorous insects.

Conclusions

Our results clearly demonstrated that abiotic and biotic factors cause parallel variation in lace bug density in the native and invaded ranges, and that the novel combination of these factors in the invaded range may cause greater lace bug density than in the native range. We found parallel positive responses to increasing temperature in lace bug density in both ranges, while other recent studies have shown nonparallel responses along the latitudinal gradients in herbivory between invasive and native plant genotypes (i.e., greater herbivory in lower latitude on native genotypes but not on invasive genotypes; Bezemer et al. 2014, Cronin et al. 2015). This equivocal inconsistent pattern suggests that the response to climates by herbivorous insects depends on the evolutionary history of the plant–herbivorous-insect interactions. In addition, we found a nonparallel response in lace bug density to other herbivorous insect damage between native and invaded ranges. The effect of the other herbivorous insects on plants can be an important mechanism predicting the herbivory by exotic insects including biological control agents. Finally, our study showed that, although the evolutionary history of the interaction with the herbivorous insect was very short in the invaded range, it could predict the exotic plant resistance in the same manner as it did in the native range. Together with recent studies, our research highlights the importance of considering differences in multiple ecological and evolutionary factors determining plant–herbivorous-insect interactions between native and invaded ranges over a wide geographical scale to understand the mechanisms and consequences of species invasion (Colautti and Barrett 2013, Agrawal et al. 2015, Cronin et al. 2015). Such research will be of great help to unravel how the combinations of ecological and evolutionary factors interact to shape plant–herbivorous-insect interactions.

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