bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Niche filtering, not interspecific resource competition, explains the geographical co-occurrence of butterfly species

Ryosuke Nakadai[12*†], Koya Hashimoto[1*], Takaya Iwasaki[3], Yasuhiro Sato[14]

[1]Center for Ecological Research, Kyoto University, Hirano 2-509-3, Otsu, Shiga, 520-2113 Japan

[2]Current address: Faculty of Science, University of the Ryukyus, Senbaru 1, Nishihara, Okinawa, 903-0213 Japan.

[3]Department of Biological Sciences, Faculty of Science, Kanagawa University, Tsuchiya 2946, Hiratsuka, Kanagawa 259-1293 Japan

[4]Current address: Department of Plant Life Sciences, Faculty of Agriculture, Ryukoku University, Yokotani 1-5, Otsu, Shiga 520-2194 Japan.

[*]Equal contribution

[†]*Author Correspondence:* R. Nakadai

Faculty of Science, University of the Ryukyus, Senbaru 1, Nishihara, Okinawa 903-0213, Japan.

E-mail: r.nakadai66@gmail.co.jp

Running head: Co-occurrence of butterfly species

Keywords: butterfly, co-occurrence, dispersal ability, climatic niche, herbivorous insect, host use, taxonomic relatedness

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Abstract

The relevance of interspecific resource competition in the context of community assembly by herbivorous insects is a well-known topic in ecology. Most previous studies focused on local species assemblies, that shared host plants. Few studies evaluated species pairs within a single taxon when investigating the effects of host plant sharing at the regional scale. Herein, we explore the effect of plant sharing on the geographical co-occurrence patterns of 229 butterflies distributed across the Japanese archipelago; we use two spatial scales (10 × 10 km and 1 × 1 km grids) to this end. We considered that we might encounter one of two predictable patterns in terms of the relationship between co-occurrence and host-sharing among butterflies. On the one hand, host-sharing might promote distributional exclusivity attributable to interspecific resource competition. On the other hand, sharing of host plants might promote co-occurrence attributable to filtering by resource niche. At both grid scales, we found significant negative correlations between host use similarity and distributional exclusivity. Our results support the thesis that the butterfly co-occurrence pattern across the Japanese archipelago is better explained by filtering via resource niche rather than interspecific resource competition.

Introduction

Efforts to understand community assembly processes are of major importance in ecological research (Diamond 1975, Cavender-Bares et al. 2009). All of dispersal limitations, environmental filtering via both abiotic and biotic niches, and interspecific interactions are thought sequentially to determine local community structures (reviewed by Cavender-Bares et al. 2009). Of the various relevant factors, the significance of interspecific interaction has often been assessed by examining how different species co-occur spatially even when they share similar niches (Diamond 1975, Gotelli and McCabe 2002). As different species with similar niches likely prefer similar

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

environmental habitats, but may compete strongly, recent studies have often compared the significance of interspecific interactions (in terms of community assembly patterns) from the viewpoint of niche filtering (Webb et al. 2002, Mayfield and Levine 2010).

In terrestrial ecosystems, many plant species are used by various herbivorous insects as both food resources and habitats, suggesting that host use plays key roles in both competition and filtering via resource niches. Earlier studies described niche partitioning between co-occurring herbivores and considered that partitioning was attributable to interspecific competition (Ueckert and Hansen 1971, Benson 1978, Waloff 1979, Augustyn et al. 2016). Conversely, other studies described the frequent co-occurrence of multiple herbivorous insect species on shared host plants despite the fact that extensive niche overlap was in play (Ross 1957, Rathcke 1976, Bultman and Faeth 1985, Hashimoto and Ohgushi 2017); the cited authors argued that the effects of interspecific competition were relatively weak in terms of community organization (Lawton and Strong 1981, Schoener 1983, Strong et al. 1984, Tack et al. 2009). Whether the importance of competition was or was not supported, most previous studies focused on how host plants shape the local assemblages of herbivorous insects. Therefore, the question of whether interspecific resource competition is critical in terms of shaping herbivore communities remains highly controversial (reviewed by Kaplan and Denno 2007). Very little is known about the extent to which the results of the cited studies can be extrapolated to describe patterns, at the regional scale, of the distribution of herbivorous insects within a single taxon.

The effects of interspecific competition and filtering via resource niches on the co-occurrence patterns of herbivorous insects must be considered when attempting to explain differences in species traits, with the exception of host use. For example, climatic niches (often associated with differences in potential geographical distributions in the absence of interspecific interactions; Warren et al. 2008, Takami and Osawa 2016) may drive niche filtering, which may in turn mediate the impact of host use on

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

assembly patterns. In addition, taxonomic relatedness should reflect niche similarity; the niche of any organism should be partly determined by its phylogenetic history (Webb et al. 2002). Thus, the outcomes of competition within shared niches should reflect both resource and climatic factors (Mayfield and Levine 2010). As such factors may correlate with host use by individual species, any focus on host use alone may yield misleading results. Furthermore, dispersal ability may complicate assembly patterns; these are often associated with both the extent of the geographical range and other factors (Kneitel and Chase 2004). A high dispersal ability may enhance the extent of co-occurrence. Thus, when attempting to explore the effects of competition and filtering via resource niches on distribution patterns, it is important to consider all of taxonomic relatedness, climatic niche preferences, and dispersal ability.

In the present study, we explored whether interspecific competition or niche filtering better explained the geographical co-occurrence of a group of herbivorous insects. We expected to discern one of two patterns when evaluating the significance of interspecific competition in terms of the geographical patterns of species co-occurrence. One possibility was that sharing of host plants would be associated with exclusive distributions attributable to resource competition. The alternative was that sharing of host plants would promote species co-occurrence attributable to filtering via resource niches. The former pattern predicts that a positive correlation would be evident between host use similarity (i.e., the extent of sharing of host species) and the exclusiveness of geographic distribution. The latter pattern predicts that the correlation would be negative. We focused on herbivorous butterflies of the Japanese archipelago, for the following reasons. First, butterfly host specificity is relatively high; the insect larvae are mostly leaf chewers (Novotny et al. 2010). Second, the Biodiversity Center of Japan has extensive records of butterfly distributions. Third, forewing length (easily measured on photographs) is a useful index of butterfly dispersal ability (Chai and Srygley 1990; Shirôzu 2006). Finally, and most importantly, a great deal is known about the hosts

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

used by butterfly species (Saito et al. 2016). Thus, data on Japanese butterflies can be used to explore the effects of host plant sharing and other factors on the co-occurrence patterns at regional scales. Specifically, we determined the effect of host use similarity on the exclusivity of geographical distribution between pairs of entirely herbivorous Japanese butterflies; we considered taxonomic relatedness, climatic niche similarities, and overall dispersal abilities in the course of our work.

Methods

Study area

The Japanese archipelago, including the Ryukyu Islands, forms a long chain of continental islands lying off the eastern coast of Asia. The latitudinal range of the archipelago (22°N to 45°N) embraces hemi-boreal, temperate, and subtropical zones. The mean temperatures in the coldest and warmest months are −19.0°C and 31.5°C, respectively; the annual precipitation ranges from 867 to 3,908 mm (Kubota et al. 2014).

Study organisms

The Japanese archipelago hosts over 280 species of butterflies of five families (the Papilionidae, Pieridae, Lycaenidae, Nymphanidae, and Hesperiidae) (Shirôzu 2006). Over 95% of the larvae of Japanese butterflies feed on plants (Honda 2005). The host plants are diverse and include both dicots and monocots (Saito et al. 2016). Lycaenid butterflies include two non-herbivorous species, but all species of all other families are exclusively herbivorous.

Metadata compilation

Butterfly census data are available on the website of the Biodiversity Center of Japan, Ministry of the Environment (http://www.biodic.go.jp/index_e.html). We used the results of the fourth and fifth censuses (1988 to 1991 and 1997 to 1998, respectively) of the National Survey of the Natural Environment in Japan

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

(http://www.biodic.go.jp/kiso/15/do_kiso4.html). This database includes records of 273 species/subspecies of butterflies from the entire Japanese archipelago, in grid cells of latitude 5 min and longitude 7.5 min (the Japanese Standard Second Mesh). These grid dimensions are about 10 km × 10 km, and this grid is described below as the "10-km grid." Furthermore, the Biodiversity Center also contains records from grid cells of latitude 30 s and longitude 45 s (the Japanese Standard Third Mesh). These grid dimensions are about 1 km × 1 km, and this grid is described below as the "1-km grid." As processes driving community assemblies may vary between spatial scales (Cavender-Bares et al. 2009), we evaluated data from both grids. We summarized data at the species level, and converted all records into the presence or absence (1/0) of a species in each grid. We used the taxonomy of Shirôzu (2006).

Data on host plants and forewing length were evaluated as possible variables explaining, respectively, host use and dispersal ability. The host plants of 278 butterfly species/subspecies were obtained from the data of Saito et al. (2016). Dispersal ability was evaluated by reference to adult wing length. We compiled wing data on 284 species using published illustrations (Shirôzu 2006). We used Image J software (Abramoff et al. 2004) to extract forewing lengths (in cm) from plates that included centimeter scale bars. Multiple forewing lengths were extracted when individual, sexual, and/or geographical variations were evident.

We assembled data on the distributions, host plants, climatic niches (described below), and forewing lengths of 229 butterfly species. Twenty-four species were excluded from the analysis, for the following reasons. First, the taxonomic status of three species (*Papilio dehaanii*, *Pieris dulcinea*, and *Eurema hecabe*) changed in the interval between the fourth and fifth biodiversity censuses (Inomata 1990; Shirôzu 2006). Thus, we excluded these species because identifications were unreliable. Second, we excluded three species of non-herbivorous butterflies (*Taraka hamada*, *Spindasis takanonis*, and *Niphanda fusca*). Finally, we excluded a further 18 species because the

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

models used to evaluate their ecological niches failed to satisfy the criteria that we imposed (the details are in Appendix S2).

Data analysis

Species distribution exclusiveness. We used the checkerboard scores (C-scores; Stone and Roberts 1990) to evaluate the exclusivity of distributions between each species pair. We set r_i and r_j as the numbers of grids in which species *i* and *j*, respectively, were present; the checker unit C_{ij} associated with the two species was defined as: $C_{ij} = (r_i - S_{ij}) \times (r_j - S_{ij})$, where S_{ij} indicates the extent of co-presence (i.e., the number of grid cells shared by the two species). Thus, the checker unit became larger as the two species occurred more commonly in different grid cells. We simulated null models to allow the observed checker units to be compared with stochastic distributions. We used the method of Jonsson et al. (2001) to describe the frequencies of species occurrence and randomized the presence/absence matrices for each pair of butterfly species. The null models were run 999 times for each species pair. C_{obs} and C_{null} were the checker units of the observed and null distributions, respectively; the checker unit was standardized as: $C_{std} = (C_{obs} - C_{null})/SD_{null}$, where SD_{null} indicates the standard deviation of all checker units of the null models. The checker unit of the null model, C_{null}, was the average checker unit of all null models. Thus, positive and negative values of C_{std} indicate that two species are allopatrically and sympatrically distributed, respectively, to extents greater than indicated by the null models. All statistical analyses were performed with the aid of R software version 3.2.0 (R Core Team 2015).

Climatic niche similarities. We used ecological niche modeling (ENM) (Franklin 2010) to evaluate climatic niche similarities among butterfly species (Warren et al. 2008). ENM associates distributional data with environmental characteristics, thus estimating the response functions of, and the contributions made by, environmental variables. Furthermore, potential distributional ranges may be obtained by projecting model data onto geographical space. In the present study, potential distributional ranges

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

estimated by ENM should be influenced by abiotic environmental variables alone (climate and altitude); we did not consider interspecific interactions among butterflies or dispersal abilities in this context. Thus, comparisons of potential distribution patterns estimated by ENM allow evaluation of climatic niche similarities among butterfly species. The maximum entropy algorithm implemented in MaxEnt ver. 3.3.3e software (Phillips et al. 2006) was employed in ENM analyses (Appendix S2 contains the details). The logistic outputs of MaxEnt analyses can be regarded as presence probabilities. Finally, we then used Schoener's (1968) *D* statistic to calculate climatic niche similarities between pairs of butterfly species, based on the MaxEnt outputs. $P_{x,i}$ and $P_{y,i}$ were the probabilities (assigned by MaxEnt) that species *x* and *y* would mesh to the extent of *i* on a geographic scale; the climatic niche similarity between the two species was defined as: $D_{env} = 1 - 0.5 \times \Sigma|P_{x,i} - P_{y,i}|$, where D_{env} ranged from 0 (no niche overlap) to 1 (completely identical niches). The probability assigned to the presence of species *x* in grid *i* was $P_{x,i} = p_{x,i} / \Sigma p_{x,i}$, where $p_{x,i}$ was the logistic Maxent output for species *x* in grid *i*.

Explanatory variables. We evaluated both host use similarity and other factors that might explain exclusive species distributions (i.e., taxonomic relatedness). We calculated the total dispersal abilities of species pairs and climatic niche similarities (as explained above). Host use similarity was calculated as 1 minus Jaccard's dissimilarity index (Koleff et al. 2003) when host plant species were shared by two butterflies. The taxonomic relatedness of each species pair was classified as: 2: in the same genus; 1: in the same family; and 0: in different families. The total dispersal ability was calculated as the sum of the ln(forewing lengths) of each species pair.

Statistical tests. We used the Mantel test, in which the response matrix yielded pairwise C_{std} data, and which included explanatory matrices, to examine the effects of host use similarity and other factors (i.e., taxonomic relatedness, climatic niche similarity, and total dispersal ability) on the exclusivity of butterfly distribution.

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

We calculated Spearman's correlations because one of the explanatory variables (taxonomic relatedness) was a rank variable. *P*-values were determined by running 9,999 permutations. In addition, when analyzing correlations between host use similarity and other explanatory matrices, we ran Mantel tests with 9,999 permutations, and calculated Spearman's correlations. We used partial Mantel tests, in which the response matrix yielded pairwise C_{std} data, and in which a matrix of host use similarity including the other three explanatory matrices served as a co-variable, to evaluate the effects of confounding factors associated with host use similarity on the exclusivity of butterfly distribution. We ran 9,999 permutations and calculated Spearman's correlations. We employed the vegdist function of the vegan package (Oksanen et al. 2015) and the mantel function of the ecodist package (Goslee and Urban 2007) implemented in R. We performed all analyses using data from both the 10-km and the 1-km grids.

Results

The standardized checkerboard scores (C_{std} values) of most species pairs were negative, indicating that, in general, Japanese butterflies were more likely to co-occur than expected by chance (Fig. 1). The Mantel test showed that host use similarity was significantly, and negatively, correlated with the C_{std} values at both geographical scales (Fig. 1, Table 1a); all three explanatory variables exhibited significant negative correlations with the C_{std} values at both scales (Table 1a). Host use similarity was significantly and positively correlated with both taxonomic relatedness and climatic niche similarity, but we found no significant correlation with total dispersal ability (Table 1b). The partial Mantel tests revealed negative correlations between the C_{std} values and host use similarity, attributable to both taxonomic relatedness and dispersal ability, at both geographical scales (Table 1c). In contrast, we found a significant positive correlation in terms of climatic niche similarity in the 10-km grid dataset, but no significant correlation in the 1-km grid dataset (Table 1c).

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Discussion

Significant negative correlations were clearly evident between the C_{std} scores and host use similarities at both grid scales (Fig. 1, Table 1a), indicating that pairs of Japanese butterflies were more likely to share host plants than not. Significant negative correlations between C_{std} scores and host use similarities were evident after controlling for other potentially confounding factors, with the exception of climatic niche similarity (Table 1c). Interspecific resource competition (i.e., a positive correlation between the C_{std} score and host use similarity) was detected only after controlling for the effects of climatic niche similarity in the 10-km grid data, but the correlation coefficient was low (Table 1c). Our results are consistent with the idea that interspecific resource competition is too weak to organize communities of herbivorous insects effectively (Lawton and Strong 1981, Strong et al. 1984). Rather, our results suggest that the geographic pattern of species co-occurrence among Japanese butterflies is better explained by niche filtering. However, the niche axes that drive the observed patterns remain unclear because the factors tested exhibited mutual correlations (Table 1b).

The most likely explanation of our data is that the relative strength of structuring via resource competition may be weaker than that associated with niche filtering. As the geographical distributions of host plants would be expected to be strongly associated with the local climatic environment, the impacts of resource and climatic niche filtering may combine to ensure that butterfly species sharing host plants assemble in the same places. In addition, the dispersal of adult butterflies from the patches in which they were born may counteract the structuring force imposed by interspecific competition. Indeed, co-occurrence was facilitated by the overall total dispersal ability (Table 1a). However, negative correlations between the C_{std} scores and host use similarity were evident even when we controlled for the effects of total dispersal ability (Table 1c). This means that dispersal alone may not explain the weak

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

impact of resource competition on the co-occurrence patterns of Japanese butterflies. Other potential factors reducing the effects of interspecific resource competition may also be in play; we did not address these topics in the present study. For example, the presence of natural enemies is known to reduce interspecific competition during community assembly markedly (Strong 1982, Nakadai and Kawakita 2017). It is very difficult to assess the effects of natural enemies at regional scales.

The negative correlation evident between taxonomic relatedness and the C_{std} scores (Table 1a) suggests that niche filtering is in play among Japanese butterflies, given that taxonomic relatedness serves as a proxy of niche similarity including host use. Indeed, we found significant (positive) correlations between host use similarity and the taxonomic relatedness of Japanese butterflies (Table 1b), as has often been shown for other herbivorous insects (e.g., Nyman et al. 2010). Moreover, when host use similarity was controlled using the partial Mantel test, taxonomic relatedness did not significantly affect co-occurrence at the 10-km grid scale (Appendix S1: Table S4). These results suggest that, at least at the 10-km grid scale, the effects of taxonomic relatedness largely reflect host use similarity.

In the present study, we used ENM to evaluate the effects of climatic niche similarity on co-occurrence patterns. When we controlled for the effects of such niche similarity, the negative correlations between the C_{std} scores and host plant similarities disappeared at both spatial scales (Table 1c). This suggests that the explanatory power of climatic niche filtering is stronger than that of resource niche filtering. It should be noted that, although ENM has been widely used to quantify climatic niches (e.g., Kozak et al. 2008, Warren et al. 2008, Takami and Osawa 2016), ENM data should be treated with caution (Peterson et al. 2011, Warren 2012, Warren et al. 2014). For example, Warren et al. (2014) noted that ENM always includes non-targeted factors that limit real distributions if those distributions correlate spatially with environmental predictors. Such confounding effects may cause overestimation of any positive correlation between

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

climatic niche similarity and butterfly co-occurrence, and may also cause the effects of host use similarity to be underestimated when controlling for the effects of climatic niche similarity. The use of ENM to study species co-occurrence patterns requires careful consideration; more case studies evaluating the relative importance of climatic niches are required.

Conclusions

The significance of interspecific resource competition in terms of the structuring of herbivorous insect communities is a source of long-standing controversy. Many researchers have sought to explain the general patterns of relationships between the co-occurrence of, and the use of different niches by, herbivorous insects. However, the data remain limited because most previous studies employed narrow taxonomic and spatial scales. In this context, our study is the first to provide a comprehensive picture of the co-occurrence patterns among a single taxonomic group over a large region. Co-occurrence of Japanese butterflies is more likely to be driven by niche filtering than interspecific resource competition. It is essential to employ broad taxonomic and spatial scales when attempting to reveal general patterns of community assembly among herbivorous insects. Future studies should explore the relative importance of each assembly stage not only ecologically but also over evolutionary time (Rabosky 2009). Such work would answer the important question: “Why have herbivorous insects become one of the most diverse groups of the natural world?”

Acknowledgement

We thank K. Kadowaki for his comments and advice on our manuscript. We also thank the Biodiversity Center of Japan, Ministry of the Environment, Japan, for allowing access to butterfly data at the 1-km grid scale. This work was supported by a grant from the Grant-in-Aid Program for JSPS Fellows (grant no. 15J00601).

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Literature cited

Abramoff, M. D., P. J. Magalhães, and S. J. Ram. 2004. Image processing with ImageJ. Biophotonics international 11:36–42.

Augustyn, W. J., B. Anderson, and A. G. Ellis. 2016. Experimental evidence for fundamental, and not realised, niche partitioning in a plant-herbivore community interaction network. Journal of Animal Ecology 85:994–1003.

Benson, W. W. 1978. Resource Partitioning in Passion Vine Butterflies. Evolution 32:493–518.

Bultman, T. L. and S. H. Faeth. 1985. Patterns of intra- and inter- specific association in leaf-mining insects on three oak host species. Ecological Entomology 10:121–129.

Cantor, S. B., C. C. Sun, G. Tortolero-Luna, R. Richards-Kortum, and M. Follen. 1999. A Comparison of C/B Ratios from studies using receiver operating characteristic curve analysis. Journal of Clinical Epidemiology 52:885–892.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

Chai, P., and R. B. Srygley. 1990. Predation and the flight, morphology, and temperature of neotropical rainforest butterflies. The American Naturalist 135:748–765.

Diamond, J. 1975. Assembly of species communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, pp 342–444

Franklin, J. 2010. Mapping species distributions: spatial inference and prediction. Cambridge University Press.

Goslee, S. C. and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22:1–19.

Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. Ecology 83:2091–2096.

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Hashimoto, K., and T. Ohgushi. 2017. How do two specialist butterflies determine growth and biomass of a shared host plant? Population Ecology 59:17–27.

Honda, K. 2005. Larval feeding habit and host selection. In: Honda K, Kato Y (eds) Biology of butterflies. University of Tokyo Press, Tokyo, pp 255–301 (in Japanese).

Inomata, T. 1990. Keys to the Japanese butterflies in natural color. Hokuryukan.

Jonsson, B. G. 2001. A null model for randomization tests of nestedness in species assemblages. Oecologia 127:309–313.

Kaplan, I., and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. Ecology Letters 10:977–994.

Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: Linking spatial scales and species coexistence. Ecology Letters 7:69–80.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72:367–382.

Kozak, K. H., C. H. Graham, and J. J. Wiens. 2008. Integrating GIS-based environmental data into evolutionary biology. Trends in Ecology and Evolution 23:141–148.

Kubota, Y., T. Hirao, S. Fujii, T. Shiono, and B. Kusumoto. 2014. Beta diversity of woody plants in the Japanese archipelago: the roles of geohistorical and ecological processes. Journal of Biogeography 41:1267–1276.

Lawton, J. H. and D. R. Strong. 1981. Community patterns and competition in folivorous insects. The American Naturalist 118:317–338.

Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology letters 13:1085–1093.

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Nakadai, R., and A. Kawakita. 2017. Patterns of temporal and enemy niche use by a community of leaf cone moths (*Caloptilia*) coexisting on maples (*Acer*) as revealed by metabarcoding. Molecular Ecology

Novotny, V., S. E. Miller, L. Baje, S. Balagawi, Y. Basset, L. Cizek, K. J. Craft, F. Dem, R. A. I. Drew, J. Hulcr, J. Leps, O. T. Lewis, R. Pokon, A. J. A. Stewart, G. Allan Samuelson, and G. D. Weiblen. 2010. Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. Journal of Animal Ecology 79:1193–1203.

Nyman, T., V. Vikberg, D. R. Smith, and J.-L. Boevé. 2010. How common is ecological speciation in plant-feeding insects? A “Higher” Nematinae perspective. BMC Evolutionary Biology 10:266.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’Hara. 2015. Vegan: community ecology package [https://cran.r-project.org/web/packages/vegan/index.html].

Peterson, A. T., J. Soberon, R. G. Pearson, R. P. Anderson, E. Martinez-Meyer, M. Nakamura, M. B. Araújo 2011. Ecological niches and geographic distributions. Monographs in Population Biology. Princeton University Press. Princeton. New Jersey, USA

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

Rabosky, D. L. 2009. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. Ecology Letters 12: 735– 743.

Rathcke, B. J. 1976. Competition and co-existence within a guild of herbivorous insects. Ecology 57:76–87.

R Core Team 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Ross, H. H. 1957. Principles of natural coexistence indicated by leafhopper populations. Evolution 11:113–129.

Saito, M. U., U. Jinbo, M. Yago, O. Kurashima, and M. Ito. 2016. Larval host records of butterflies in Japan. Ecological Research 31:491–491.

Schoener, T. W. 1968. The anolis lizards of bimini: Resource partitioning in a complex fauna. Ecology 49:704–726.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist 122:240–285.

Shirôzu, T. 2006. The butterflies of Japan in color. In Japanese. Gakken Holdings, Tokyo, Japan.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. Oecologia 85:74–79.

Strong, D. R. 1982. Harmonious coexistence of *Hispine* beetles on *Heliconia* In experimental and natural communities. Ecology 63:1039–1049.

Strong, D. R., J. H. Lawton, and S. R. Southwood. 1984. Insects on plants. Community patterns and mechanisms. Harvard University Press, Cambridge, MA.

Tack, A. J. M., O. Ovaskainen, P. J. Harrison, and T. Roslin. 2009. Competition as a structuring force in leaf miner communities. Oikos 118:809–818.

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

Ueckert, D. N., and R. M. Hansen. 1971. Dietary overlap of grasshoppers on sandhill rangeland in northeastern Colorado. Oecologia, 8: 276-295.

Waloff, N. 1979. Partitioning of resources by grassland leafhoppers (Auchenorrhyncha, Homoptera). Ecological Entomology 4:379-385.

Warren, D. L., M. Cardillo, D. F. Rosauer, and D. I. Bolnick. 2014. Mistaking geography for biology: inferring processes from species distributions. Trends in Ecology & Evolution 29:572–580.

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. Evolution 62:2868–2883.

Warren, D. L. 2012. In defense of 'niche modeling'. Trends in Ecology & Evolution 27:497–500.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Supporting information

Appendix S1: Table S1. The Japanese butterfly species analyzed in the present study.

Appendix S1: Table S2. Summary of the MaxEnt data at the 10-km grid scale.

Appendix S1: Table S3. Summary of the MaxEnt data at the 1-km grid scale.

Appendix S1: Table S4. Correlations among host use similarity (Host), taxonomic relatedness (Taxon), climate niche similarity (Climate), and total dispersal ability (Dispersal), at two spatial scales. (a) Summary of Mantel test data on pairwise correlations between the explanatory matrices. (b) Summary of partial Mantel test data on standardized C_{std} scores between pairs of butterfly species. The "Taxon-Dispersal" data (b) were obtained using the datasets at either grid mesh scale.

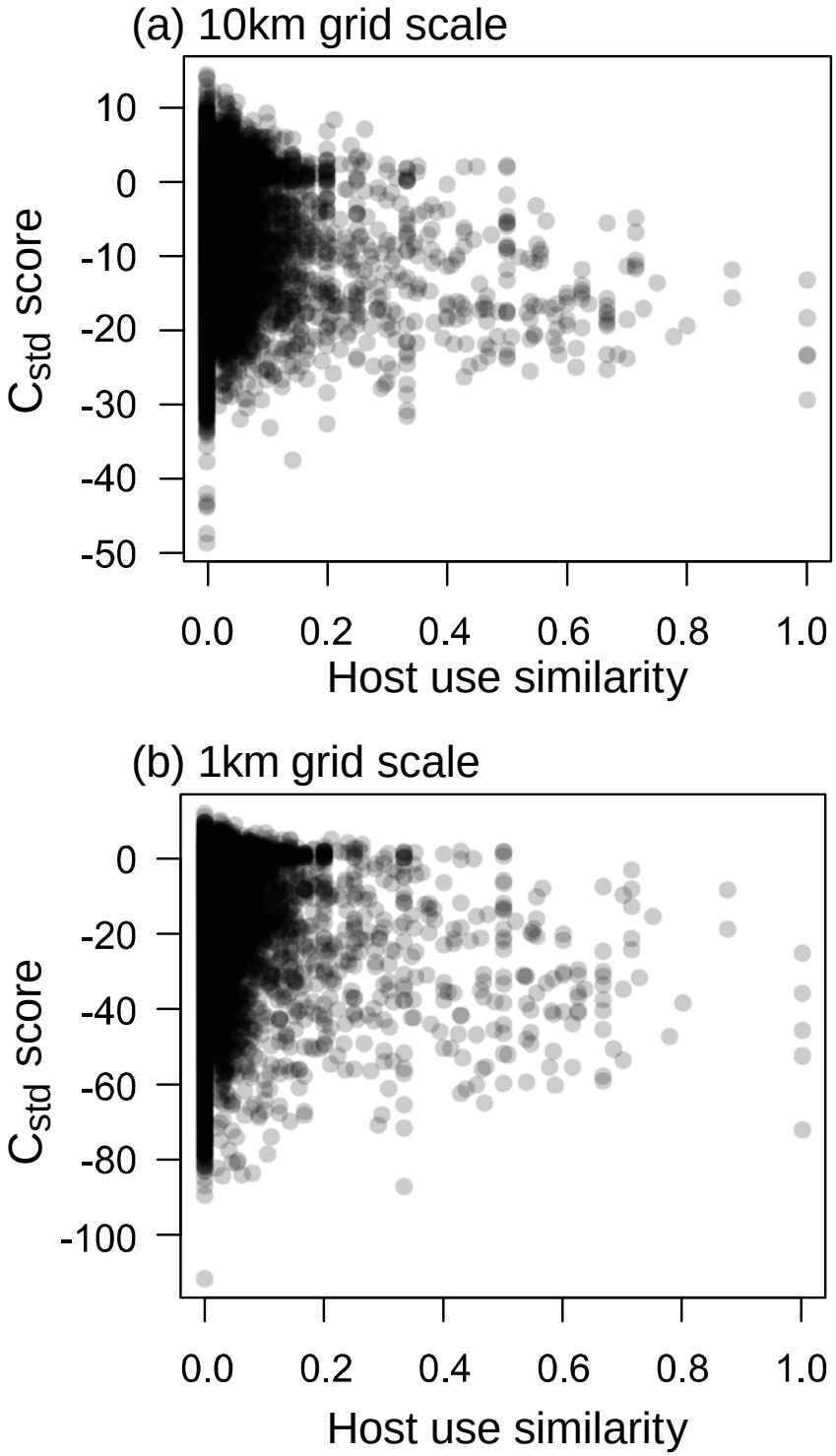
Appendix S2: Details of the methods used for ecological niche modeling.

Legend

Figure 1. The relationships between C_{std} scores and host use similarities (10-km grid scale: Spearman $\rho = -0.132$, $P = 0.0001$; 1-km grid scale: Spearman $\rho = -0.132$, $P = 0.0001$; Mantel test).

bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Figure 1.



bioRxiv preprint doi: https://doi.org/10.1101/132530; this version posted May 1, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Table 1. Correlations among host use similarity (Host), taxonomic relatedness (Taxon), climate niche similarity (Climate), and total dispersal ability (Dispersal), at two spatial scales. (a) Summary of Mantel test data on standardized C_{std} scores between pairs of butterfly species. (b) Summary of Mantel test data on pairwise correlations between host use similarity and the data of other explanatory matrices. (c) Summary of partial Mantel test data on standardized C_{std} scores between pairs of butterfly species. The "Host-Taxon" and "Host-Dispersal" data (b) were analyzed using the datasets of either grid mesh scale.

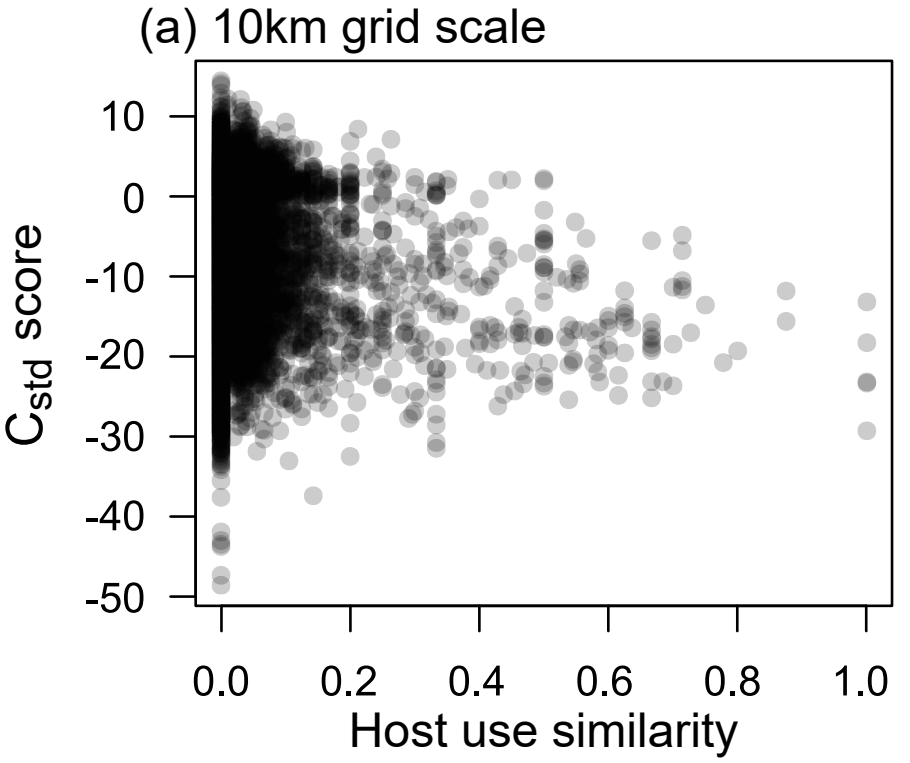
(a)	10-km grid		1-km grid	
Factor	Mantel ρ	*P*-values	Mantel ρ	*P*-values
Host	−0.126	**0.0001**	−0.126	**0.0001**
Taxon	−0.027	**0.0063**	−0.037	**0.0008**
Climate	−0.723	**0.0001**	−0.482	**0.0001**
Dispersal	−0.047	**0.0161**	−0.072	**0.0008**

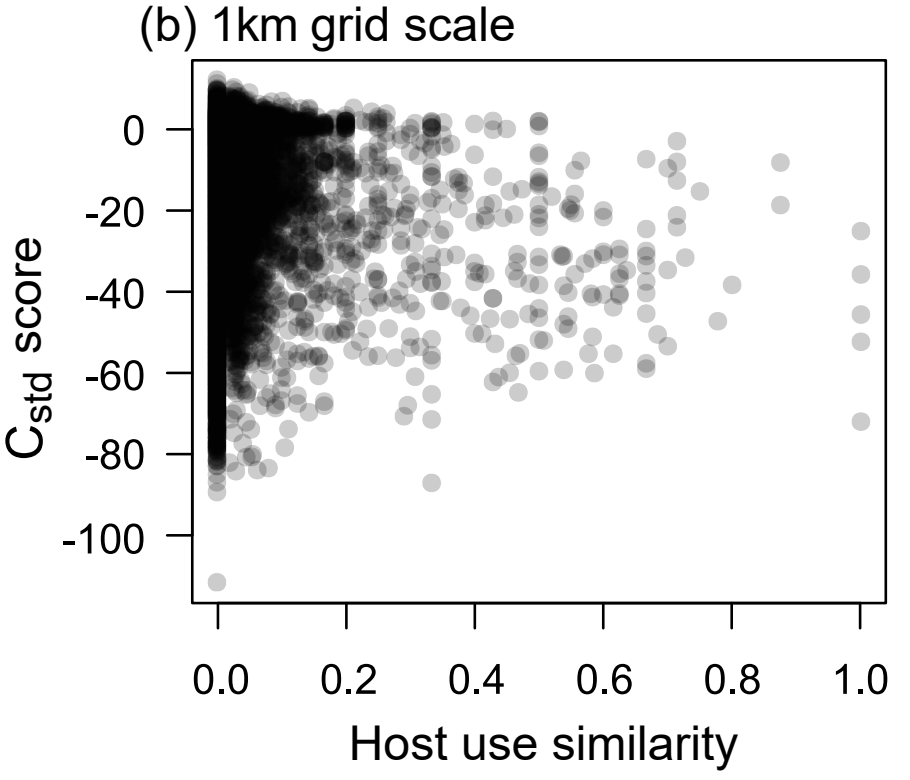
(b)	10-km grid		1-km grid	
Factor	Mantel ρ	*P*-values	Mantel ρ	*P*-values
Host-Taxon	0.097	**0.0001**	0.097	**0.0001**
Host-Climate	0.209	**0.0001**	0.240	**0.0001**
Host-Dispersal	0.067	0.0659	0.067	0.0659

(c)		10-km grid		1-km grid	
Factor	Covariate	Mantel ρ	*P*-values	Mantel ρ	*P*-values
Host	Taxon	−0.124	**0.0001**	−0.123	**0.0001**
Host	Climate	0.036	**0.0020**	−0.012	0.3660
Host	Dispersal	−0.124	**0.0001**	−0.121	**0.0001**

Spearman's correlation coefficients (ρ values) are shown for all four factors.

Bold: $P < 0.05$; Underlined: $0.05 < P < 0.1$ after 9,999 permutations.


(a) 10km grid scale
10
0
-10
-20
-30
-40
-50
C_{std} score
0.0
0.2
0.4
0.6
0.8
1.0
Host use similarity


(b) 1km grid scale
0
-20
-40
-60
-80
-100
C_{std} score
0.0
0.2
0.4
0.6
0.8
1.0
Host use similarity