Climate, species richness, and body size drive geographical variation in resource specialization of herbivorous butterflies

Running title: Drivers of resource specialization

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Type of article: Letters

Number of words in the abstract: 149

Number of words in the main text: 4850

Number of references: 76

Number of figures: 2

Number of tables: 3

Number of text boxes: 0

Acknowledgements

We are particularly grateful to local entomologists, and naturalists who accumulated the background information on butterflies compiled for the dataset in this study. We also thank Dr. Matthew Forister, who provided R code associated with the alpha shape parameter. The Biodiversity Center of Japan and the Japanese Ministry of the Environment kindly provided us with datasets on butterfly distributions. Dr. Yasuhiro Sato gave us insightful comments for an early version of the manuscript. Financial support was provided by the Japan Society for the Promotion of Science (grants 15J00601, 18J00093 to R.N.) and Academy of Finland (grant 324392 to A.V.).

Authorship

R.N. conceived the idea, designed the study, and analyzed the data; R.N. and T.N. constructed the figures; K.H., R.N., T.I. constructed the butterfly dataset; R.N. and A.V. wrote the first draft; all the authors significantly contributed to the final text.

Data accessibility statement

The calculated indices related to butterfly species and the environmental variables used in this study for each 10-km grid cell are in Supplementary Table S7.

Abstract

Revealing drivers of variation in resource specialization is a long-standing goal in ecological and evolutionary research. As a general prediction, the degree of resource specialization increases towards lower latitudes. Although herbivorous insects are one of the best-studied consumer groups, factors determining the degree of specialization on large spatial scales are poorly understood. Herein, we focused on the fundamental host breadth of 246 herbivorous butterfly species distributed across the Japanese archipelago. Using Bayesian Structural Equation Modeling based on information of pooled geographical occurrence and host use, we show that local butterfly communities tend to become more specialized towards higher latitudes, a pattern that is opposite to predictions from classical hypotheses. We also found that the pattern is mainly driven by factors related to climate, butterfly diversity, and body size in each community. Our results re-emphasize the importance of current climate as a regulating factor for butterfly host breadth and morphology.

Keywords: Bayesian structural equation modeling, community assembly, continental islands, host breadth, Pareto distribution, latitudinal gradient, macroecology, trait-based approach

Introduction

Understanding the processes structuring communities across space and time is a central subject in ecology (Cavender-Bares *et al.* 2009). Resource specialization is a major factor shaping interspecific interactions and, therefore, community composition (Nylin *et al.* 2017; Volf *et al.* 2017; Dyer & Forister 2018). Drivers of variation in the degree of specialization has therefore been investigated intensively in the context of community ecology (Novotny & Basset 2005; Forister *et al.* 2015). Such studies have generally pointed out that species tend to be more specialized in the tropics than in the

temperate zone (MacArthur's latitude–niche breadth hypothesis; MacArthur 1972; Vázquez & Stevens 2004; Dyer *et al.* 2007; reviewed by Dyer & Forister 2018). Using a global dataset, Forister *et al.* (2015) addressed variation in resource specialization in herbivorous insects along a geographical gradient, and showed that the mean and variance of diet breadth in local communities indeed decreases toward the equator.

Resource specialization is driven by not only geographical and climatic gradients, but also many other factors. Specifically, the higher number of species in the tropics (Loder *et al.* 1998; Dyer & Forister 2018) could intensify interspecific competition ("species packing"; Dobzhansky 1950; MacArthur 1972) and thereby favor specialization (Coley & Kursar 2014). Also, the importance of body size and physiological constraints imposed by climatic conditions are often argued (Bergman's rule; Bergmann 1947). For example, there is evidence that average consumer body size, and its variation, increases towards lower latitudes (Loder *et al.* 1998), although body size is generally thought to be positively correlated with host breadth (Lindström *et al.* 1994; Pöyry *et al.* 2017). However, inferring the drivers of specialization is complicated by the fact that numerous potentially important factors change in parallel along the latitudinal and climatic gradient (Loder *et al.* 1998).

On the other hand, some studies have found no difference in the degree of specialization between temperate and tropical regions (e.g., Novotny *et al.* 2006), and the hypothesis has even been called a "zombie idea" that "still wanders the world feasting on scientists' brains" after having been killed by data and/or theory (Fox 2011; Moles & Ollerton 2016). Thus far, most studies on variation in resource specialization have relied on information on local communities. However, resource use within local communities can be shaped by interspecific interactions (Connell 1980). Local processes in community assembly (interspecific interactions), can produce "realized" resource specialization, which could mask underlying fundamental resource specialization. In this work, we aim to understand processes determining spatial

variation in “fundamental” resource specialization, which we defined as the host breadth not limited by interspecific interactions at the same trophic level. More specifically, we aim to reveal the drivers of geographical variation in fundamental resource specialization through macroecological approaches.

Herein, we focused on angiosperm-feeding butterflies across the Japanese archipelago to reveal the drivers of spatial variation in resource specialization. We calculated species-specific fundamental host breadth based on information on both pooled geographical occurrence and host-use records rather than on accumulation of local, site-specific data on host use for each species. The latitudinal range of the archipelago (22°N–45°N) comprises hemiboreal, temperate, and subtropical zones, making it a useful system for assessing spatially continuous change in resource specialization, i.e., not just providing a comparison between disconnected areas. In fact, most previous studies have simply compared resource specialization between tropical and temperate regions, which Dyer & Forister (2018) pointed out as a major methodological problem. We focused on the latitudinal pattern and aimed to reveal significant drivers of the level of specialization in regional species pools. As potential drivers, we focused on geography, current climate, diversity and body size of butterflies themselves, and their change along geographical gradients (Table 1). By using Bayesian Structural Equation Modeling (Bayesian SEM), which has received increasing attention in ecology and evolution (e.g., Arhonditsis *et al.* 2007; Read *et al.* 2018; reviewed in Grace *et al.* 2012), we investigated the complicated relationships between these variables and resource specialization in comprehensive models fitted for one index reflecting the distribution of host breadths and two indices of phylogenetic host breadth within each community.

Materials and methods

Study area

The Japanese archipelago forms a long chain of continental islands lying off the eastern coast of Asia, and is recognized as a hotspot of biodiversity (Mittermeier *et al.* 2011). The mean temperatures of the coldest months range from –18.4 to 22.3 °C, mean temperatures of the warmest months from 6.2 to 29.2 °C, and annual precipitation from 700.4 to 4477.2 mm (Fig. S1a, b: Japan Meteorological Agency, 1981–2010; http://www.jma.go.jp/jma/indexe.html). Also, the Japan Sea side of the archipelago typically receives more snow than does the Pacific Ocean side (Fig. S1c). The Japanese archipelago belongs to a transient region between the Palaeotropical or Indo-Pacific and the Holarctic regions (Cox 2001), and harbours relictual plants that were distributed throughout a large portion of the Northern Hemisphere during much of the Tertiary (Milne & Abbott 2002). Over 280 species of butterflies of five families are found in the region (Shiro□zu 2006). With the exception of three lycaenid species, larvae of Japanese butterfly species feed exclusively on plants (Honda 2005). The host plants are diverse and include both dicot and monocot angiosperms as well as gymnosperms (Saito *et al.* 2016).

Evaluation of butterfly host breadth and body size

Our analyses were based on butterfly census data, which includes records of 273 species/subspecies of butterflies from the entire Japanese archipelago, available on the website of the Biodiversity Center of Japan, Ministry of the Environment (http://www.biodic.go.jp/index_e.html), in grid cells of latitude 5 min and longitude 7.5 min (about 10 km × 10 km). For each species, the records were then used, in conjunction with relevant climate data, to predict their potential distribution in Japan using Maxent ver. 3.3.3e (Phillips *et al.* 2006; published in Nakadai *et al.* 2018; for details see Supplementary text 1). As an exception, due to difficulties in estimating the potential distribution by Maxent for rare species (Vaughan & Ormerod 2005; Breiner *et*

al. 2015), the presence records of eighteen butterfly species having four or fewer records each were used as such for the following analyses.

Information on host plants of each studied butterfly species was compiled in order to evaluate their diet breadth. The host plants of 278 butterfly species/subspecies (3,573 records in total, after excluding duplicates) were obtained from Saito *et al.* (2016). We used adult forewing length as a proxy for body size of each butterfly species. The forewing lengths of 284 species were derived from Shiro□zu (2006; earlier published in Nakadai *et al.* 2018). For a total of 246 butterfly species, we were able to assemble data on predicted distribution, host plants and body size. However, ten species were excluded from the analyses, for the following reasons: First, the taxonomic status of three species 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 non-herbivorous and four gymnosperm-feeding species (for details, see Table S1). After non-target species (those with taxonomic changes and non-angiosperm feeders) were removed, the remaining 3,358 records of host plants were selected and converted to plant-genus resolution for further analyses.

To describe the overall degree to which species are specialized to their hosts, for each grid cell, we estimated the alpha parameter of the discrete truncated Pareto distribution fitted to numbers of host genera for all butterfly species occurring within the cell (Forister *et al.* 2015; Kozubowski *et al.* 2015). Higher values of the Pareto alpha indicate higher incidence of species with relatively narrow host breadth in the community.

For each cell, we also calculated the community mean and divergence (based on Rao's Quadratic Entropy; RaoQ) for both phylogenetic host breadth and butterfly body size by using the ade4 package (Chessel *et al.* 2013) in R (R Development Core Team 2017). The community mean indicates the dominant trait value within an assemblage

(Violle *et al*. 2007), while community divergence represents the degree of dissimilarity between all possible pairs of species within the assemblage (Mouchet *et al.* 2010). To describe the genus-level phylogenetic host breadth of butterfly species, we applied the widely-used Faith's phylogenetic diversity index (cf., Davis *et al.* 2013). We calculated this index with the R package picante (Kembel *et al.* 2010), based on a genus-level angiosperm phylogeny derived from Zanne *et al.* (2014) using Phylomatic (Webb & Donoghue 2005). The methods for estimating phylogenetic host breadth and the distribution of host breadth follow Forister *et al.* (2015), which provides detailed descriptions and statistical background.

To determine whether the observed mean and divergence of each trait in each grid were greater or less than the values when drawing butterfly species at random from the regional species pool, we calculated standardized effect sizes (SES) using two types of null models (i.e., null model 1 and 2; for details Supplementary text 2). The randomization procedures for both types of null models were repeated 1,000 times to generate simulated datasets that were then used to compute cell-specific expected values for mean and divergence of host breadth and body size. We calculated SES values for each grid cell as the observed value minus the mean of the null distribution, with the result divided by the standard deviation of the null distribution. Therefore, a negative RaoQ value indicates that trait values within the cell are more similar than expected based on the null model (i.e., convergence within the community), whereas a positive value indicates that species in the assemblage are more dissimilar than expected (i.e., divergence within the community). In the main analysis, we used the datasets based on the simpler null model 1, but re-fitted the final models using null model 2, to explore the robustness of our results.

Climatic variables

We used annual mean temperature and precipitation at the 1-km grid scale from Mesh Climate Data 2010 (Japan Meteorological Agency, http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html). We also included annual maximum depth of snow cover (Mesh Climate Data 2010), and altitudinal data from the National Land Numerical Information database (Geospatial Information Authority of Japan). All of these variables were downloaded at the 1-km grid scale. Finally, for all variables, we calculated averages at the 10-km grid scale using ArcGIS Pro ver. 2.3.3 software (Environmental Systems Resource Institute, Redlands, CA, USA).

Driver analysis for host breadth and body size

To reveal the drivers of resource specialization, we compiled two Bayesian SEMs in which (1) the alpha parameter of the discrete truncated Pareto distribution and (2) the two indices of phylogenetic host breadth were explained by butterfly species richness, two indices of body size (i.e., mean and divergence) and six environmental factors. In this study, the highest correlation ($r = -0.901$) occurred between the alpha parameter of the discrete truncated Pareto distribution and the mean of phylogenetic host breadth (Table S6), so we separated those two models to reduce the risk of multicollinearity problems. The environmental factors included as explanatory variables were latitude and elevation as geographical factors, and annual precipitation, mean temperature and annual maximum depth of snow cover as climatic factors. Although climatic and geographical factors are correlated (Table S6), including both of these correlated variables may be informative (see justification with respect to multicollinearity in Supplementary text 3). For example, there is a strong negative correlation between latitude and annual mean temperature, but the ingredient of the partial effect of latitude may include other ecological factors that were not considered in this study, such as variation in day length and length of active season. Prior to analyses, two types of grid cells were excluded from the dataset: (1) cells with $p < 0.05$ according to a chi-square

goodness-of-fit test contrasting observed values of the host breadth distribution to the expectation from the fitted discrete truncated Pareto distribution, and (2) cells with fewer than twenty butterfly species. These cells (N = 1,291 and N = 1,209, respectively: N = 2,069 in total) were excluded because their values were considered less reliable and due to difficulties in correctly estimating alpha of the discrete truncated Pareto distribution (Forister *et al.* 2015; see Supplementary text 5). Regarding the second criterion, we also repeated the analysis with the minimum number of species set to ten or thirty, to check the robustness of the main results.

We fitted the full Bayesian structural equation models in Mplus version 8.4 (Muthén & Muthén 1998-2017). We evaluated model fit based on a Bayesian variant of root mean square error of approximation (BRMSEA), the Bayesian comparative fit index (BCFI), and the Bayesian Tuchr—Lewis index (BTLI) (Hoofs *et al.* 2018, Garnier-Villarreal & Jorgensen 2019, Asparouhov & Muthén 2019; for details see Supplementary text 4). Hoofs *et al.* (2018) suggested cutoff values for the lower (<0.05) and upper limit (<0.08) in the 90% posterior probability interval of the BRMSEA as a valid criterion for good model fit, and Asparouhov & Muthén (2019) proposed three possible conclusions: the fit index is inconclusive (lower limit <0.06< upper limit), the index suggests that the model fits reasonably well (both lower and upper limits <0.06), and the fit index suggests poor fit between model and data (0.06 < both lower and upper limits). For BCFI and BTLI, Asparouhov & Muthén (2019) suggested similar criteria, but so that the cuttoff values need to be beyond 0.95 for adequate fit.

After fitting the full model, we trimmed non-significant paths from the model until only significant paths remained (Kline *et al.* 2011). Also, we explored the robustness of the results of the main analysis by re-fitting the final models for each response variable using datasets of observed distributions instead of fundamental distributions estimated by Maxent, null model 2, and the aforementioned two minimum numbers of butterfly species (i.e., ten and thirty) within each grid cell.

Results

Across the Japanese archipelago, butterfly species richness increased towards lower latitudes (south) and higher elevations, and both mean and divergence of butterfly body size increased toward lower latitudes (Fig. 1). Pareto alpha, which indicates the degree of concentration of species having narrower host breadth, increased towards higher latitudes (north), and phylogenetic host breadth mean and divergence decreased towards higher latitudes (Table S6).

Of the total of 4673 grid cells of the Japanese archipelago, 2542 passed our filtering criteria and were included in the Bayesian SEM models (Tables 2, 3). Both final models satisfied the criteria of good fit measured by BRMSEA, BCFI and BLTI. Four of the 33 paths in the model of the Pareto alpha and five of the 42 paths in the model of phylogenetic host breadth were non-significant and therefore removed during the processes of model simplification (Tables 2, 3).

Of the many factors affecting host breadth, annual mean temperature was most strongly associated with host breadth in both SEM models (Tables 2, 3, Fig. 2). Specifically, communities with low concentration of narrower host breadth species (i.e., having low pareto alpha) as well as high community-level phylogenetic host breadth mean and divergence increased along with annual mean temperature (Tables 2, 3, Fig. 2). There were negative correlations between Pareto alpha and mean and divergence of body size (Table 2, Fig. 2a). Also, there was a positive correlation between phylogenetic host breadth mean and body size mean; phylogenetic host breadth mean and body size divergence; and phylogenetic host breadth divergence and body size divergence (Table 3, Fig. 2b).

Butterfly species richness was driven by annual precipitation, annual maximum depth of snow cover, latitude, and elevation. Based on standardized estimates, elevation was

the strongest (positive) driver of butterfly species richness, while latitude was the second most effective (negative) predictor (Table 2, 3).

Mean of butterfly body size was strongly driven by annual mean temperature (positively) and latitude (negatively), while the effects of annual precipitation, annual maximum depth of snow cover and butterfly species richness were relatively weak (Tables 2, 3, Fig. 2). Butterfly body size divergence was driven by latitude, annual mean temperature, annual precipitation, and butterfly species richness. Of these, latitude strongly and negatively influenced body size divergence (Tables 2, 3, Fig. 2). Furthermore, there was a positive correlation between butterfly body size mean and divergence (Table 2, 3, Fig. 2).

The significances and the strengths of major paths that were associated with host breadth and butterfly body size were consistent when re-running the final models with datasets of observed distributions (Table S3), null model 2 (Table S4), and the two alternative criteria for minimum number of butterfly species per grid cell (Table S5).

Discussion

Latitudinal pattern of fundamental host breadth is opposite to classical understanding

One of the most widespread assumptions in ecology is the increase in degree of resource specialization towards lower latitudes (i.e., towards the tropics) (Moles & Ollerton 2016; Dyer & Forister 2018). By contrast, our results show that the host breadth of butterfly communities becomes more specialized towards higher latitudes (i.e., towards the north) across the Japanese archipelago. Our finding therefore apparently contradicts the widespread assumption of how species accumulate to local communities. According to our results, host breadth of butterfly communities was most strongly associated with climatic factors (i.e., annual mean temperature, annual precipitation, annual maximum depth of snow cover), a geographic factor (latitude), and butterfly species richness. Specifically, the mean and divergence of host breadth of

butterfly communities were higher where temperatures were higher. Furthermore, grid cells having high butterfly diversity showed broader and more divergent host breadths.

The trend of broader and more divergent host breadths within communities towards lower latitudes could be produced by relaxing of physiological constraints by increasing the amount of energy, thus reducing the relative importance of abiotic environmental filters and allowing for wider variation in niches (Park 1949, Fisher 1960). Read *et al.* (2018) suggested that relaxing of physiological constraints together with stronger biotic interactions among species towards the tropics leads to increased resource specialization, which is opposite to our finding. We note that the existence of strong interspecific resource competition among herbivorous insects, causing niche partitioning, has been generally questioned (Lawton & Strong 1981; Strong *et al.* 1984; Nakadai & Kawakita 2017). In fact, Nakadai *et al.* (2018) showed that butterfly species pairs that use similar host-plant taxa tend to overlap in their distribution across the Japanese archipelago. Evidently, the relaxation of abiotic regulation towards lower latitudes allows the occurrence of butterfly species having broader host breadths because of the weak influence of interspecific competition.

Along the focal latitudinal and climatic gradients, many other variables than host breadth also change jointly or independently (e.g., both body size and diversity of butterflies). Teasing apart the directionality of causalities among these patterns constitute long-standing subjects in ecology (Wasserman & Mitter 1978; Loder *et al.* 1998). Consistent with previous studies on plant-feeding insects (Brown and Maurer 1989; Pöyry *et al.* 2017), we found a strong positive relationship between body size and host breadth. Lindström *et al.* (1994) argued that larger body size in Lepidoptera allows a larger "home range", and, thus, encounters with a wider range of host plants, but also requires more energy which is easier to acquire if the species is a broad generalist. In our dataset, both mean and divergence of body size increased toward lower latitudes and higher temperatures (Tables 2, 3). Such a pattern of increasingly smaller body sizes

towards higher latitudes is called a converse Bergmann cline (although most interspecific studies on insects have found no clines; Shelomi 2012). The southward increases in both mean and divergence of body size are also consistent with the hypothesis based on relaxing physiological constraints (Table 1). Furthermore, mean body size positively correlated with mean phylogenetic host breadth. Increasing mean body size within a community could therefore be one of the enhancers of the diet generalization in the communities of herbivorous insects (Table 1). Towards higher latitudes or elevations, increasingly shorter growing seasons also limit the duration of the larval stage, which would restrict the distributions of large-bodied or slow-developing insects (Blanckenhorn & Demont 2004; Shelomi 2012). For example, Zeuss *et al.* (2017) found that among European lepidopteran species, average body size and the average number of generations per year decreases with latitude.

Methodological considerations

In order to elucidate the detailed drivers of host breadth in Japanese butterflies, we attempted to include as many factors as possible in our analyses, but our results also reveal several important limitations of current methods that need to be addressed in future studies. The largest difference from previous studies concerns the properties of the herbivore community dataset. The analyses of Forister *et al*. (2015) and many others (e.g., Novotny *et al.* 2006) have been based on direct observations of local insect–plant associations in communities. By contrast, our 'species-pool' approach based on modeled distributions can stack the distributions also of some species pairs that would typically not occur at the same site at the same time due to, for example, phenological niche division. In our analyses, we did not focus on phenological patterns along the latitudinal gradient, because our main focus was on "fundamental" patterns on a large spatial scale. Differences in the results between previous studies and our results could partly reflect the phenology and the length of active time for butterfly species.

In addition, we mainly focused on the transient region between the hemiboreal and subtropical zones, so the pattern found cannot necessarily directly be generalized to global scale. Regional studies focusing on narrower latitudinal gradients should consider geohistorical effects (e.g., where the region was colonized by species at different times or where the hotspots of endemism are located). However, most of the butterfly species of the Japanese archipelago are not endemics, but rather widely-distributed species shared with the Eurasian continent. This is largely explained by the fact that the Japanese archipelago was repeatedly connected with the continent by land bridges throughout glacial episodes of the Pliocene and Pleistocene periods, allowing for butterfly dispersal (details reviewed in Tojo *et al.* 2017). On the other hand, detailed regional studies have the advantage that it is possible to extensively correct information on host use. Previous studies have suggested that sampling effort directly affects the inferred degree of host specialization (Dixon *et al.* 1987), but such effects are difficult if not impossible to address in large-scale meta-analyses.

Unfortunately, we were not able to directly study the effect of regional plant diversity on the geographic distribution of resource specialization. In general, however, the proportion of rare plant species increases towards the tropics (e.g., Ulrich *et al.* 2016), possibly due to negatively density-dependent survival (Janzen–Connell hypothesis; Janzen 1970). Such a process was suggested as a fundamental explanation for the opposed latitudinal pattern (i.e., more generalists toward lower latitudes) of resource specialization found in the simulation study by Forister & Jenkins (2017). Specifically, a high proportion of rare plants would favor the evolution of broader host breadth in insects, meaning that the mean and divergence of host breadth would increase toward lower latitudes (Ghazoul & Sheil 2010). However, even if the evenness of plant abundance would drive resource specialization, such patterns should be driven by resource biomass in a strict sense, but data on available plant biomass were lacking in our and previous studies. Therefore, studies focusing on the biomass of available

alternative resources are needed in the future, in order to reveal more detailed effects of floral composition on herbivore host breadth.

Historical and evolutionary perspectives

We did not address evolutionary processes in this study, because phylogenetic information on all the studied butterfly species was not available. However, our findings should be generalizable to other regions and broader spatial patterns by including evolutionary processes. For example, we could expand the recently proposed evolutionary ideas on species association dynamics proposed by Nylin *et al.* (2017) and the oscillation hypothesis proposed by Janz *et al.* (2001, 2006), which espcially focused on speciation and species distributions, into specific ideas from spatial perspectives, by adding a latitudinal direction to the oscillation dynamics. The oscillation hypothesis proposed by Janz *et al.* (2001, 2006) postulates that, over time, herbivorous insect lineages oscillate between a generalist state, during which they may expand their geographical ranges, and various specialist states presenting opportunities for local adaptation of individual populations; speciation occurs after host specialization. To explore this issue further, we plotted minimum and maximum values of phylogenetic host breadth and body size within butterfly communities against latitude (Fig. S3), and confirmed that the ranges of these trait values become increasingly narrow toward higher latitudes. If physical constraints on host breadth and/or body size in insect herbivores exist (Fig. S3), very large or very small butterfly species should have difficulties in extending their distribution ranges from the south to the north, and therefore such large or small species could be filtered out. Our finding is consistent with the proposal of Fisher (1960), who argued that the stable climate in the tropics allowed for a wider range of morphological and physiological adaptations than in the temperate region. On the other hand, the spread of butterfly species with broader host breadth from south to north might be hindered by biogeographic limitations (Kimura 2004;

Hirao *et al*. 2015). Therefore, we propose a novel prediction: butterfly species having a wide host breadth could have more likely expanded their distribution to south, and specialized and diversified there via oscillation processes, and only descendant species with narrower host breadth could return in the northward direction. Although biogeographic limitations and abiotic variables (e.g., temperature, precipitation, and snow) are important determinants of butterfly distributions, our above predictions would provide further insight into the importance of geographical and morphological constraints for species association dynamics and the oscillation hypothesis. These also provide a possibility to cross with other general ecological rules like Rapoport's rule (Rapoport 1982), which is related to latitudinal distribution range and global history that dramatically have changed the species distributions (Nyman *et al.* 2012).

Conclusions

Butterfly communities became more specialized in their host use towards higher latitudes (i.e., towards the north) across the Japanese archipelago, a pattern that is opposite to predictions from classical hypotheses. Our results clearly revealed not only how the variation in resource specialization is distributed, but also the potential influence of physiological constraints resulting from variation in body size along the same geographical gradient. Since Ehrlich & Raven (1964), coevolutionary interactions between plants and herbivores have been considered the main determinant of host breadth. However, our results re-emphasize the importance of current climate as a regulating factor for butterfly host breadth and morphology (Fisher 1960). Future studies should explore how latitudinal gradients in butterfly and plant phylodiversity and evenness of resources modify host breadth at a global scale. As the number of related variables would necessarily increase, the analyses would become more complex, which would make finding simple answers more difficult. However, it should be remembered that ecosystems are not simple, and novel analytical approaches such as

using Bayesian structural equation modeling provide a way for accepting the complexity of nature. This should be one of the starting points when striving to understand hidden eco-evolutionary patterns and processes driving the origin and maintenance of biological diversity.

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Figure legends

Figure 1 Patterns of (a) butterfly species richness based on stacked predicted species distribution data (Nakadai et al. 2018), (b) butterfly body size mean, (c) body size divergence, (d) alpha parameter of the discrete truncated Pareto distribution, (e) phylogenetic host breadth mean, and (f) phylogenetic host breadth divergence across the Japanese archipelago. Only grids that satisfied the criteria (see text) are shown in (d), (e), and (f). Values except (a) represent standardized effect sizes (SES) estimated based on null model 1.

Figure 2 Path diagrams of the Bayesian SEMs explaining host-breadth parameters. Parameter estimates are shown in Tables 2, 3, and Table S2. Red arrows indicate positive effects or correlations, and blue arrows indicate negative ones. Dashed lines indicate paths removed through the modification process in the analysis. The abbreviations indicate LAT: Latitude, ELV: Elevation, AP: Annual precipitation, AMT: Annual mean temperature, SNW: annual maximum depths of snow cover, BSR: Butterfly species richness, BSM: Body size mean, BSD Body size divergence, PAL: The alpha parameter of the discrete truncated Pareto distribution, PHBM: Phylogenetic host breadth mean, and PHBD: Phylogenetic host breadth divergence.

Figure 1

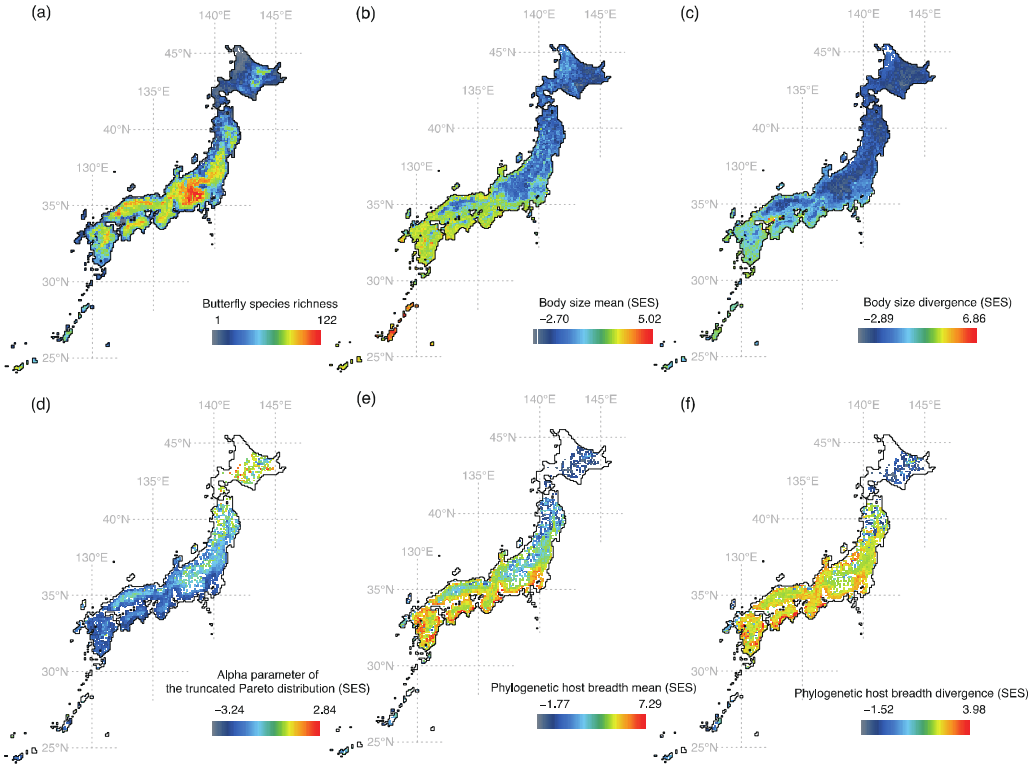

(a)
Butterfly species richness
1
122
(b)
Body size mean (SES)
−2.70
5.02
(c)
Body size divergence (SES)
−2.89
6.86
(d)
Alpha parameter of
the truncated Pareto distribution (SES)
−3.24
2.84
(e)
Phylogenetic host breadth mean (SES)
−1.77
7.29
(f)
Phylogenetic host breadth divergence (SES)
−1.52
3.98
140°E
145°E
45°N
135°E
40°N
130°E
35°N
30°N
25°N

Figure 2

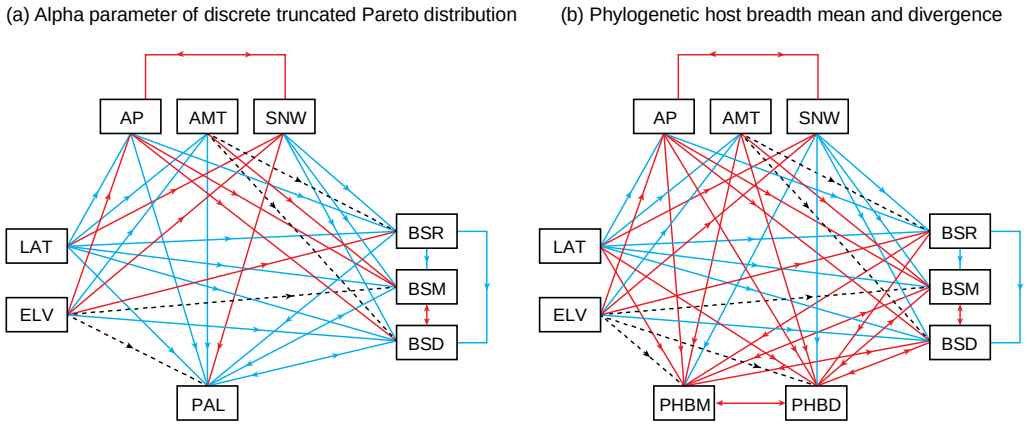

(a) Alpha parameter of discrete truncated Pareto distribution
AP
AMT
SNW
LAT
ELV
BSR
BSM
BSD
PAL
(b) Phylogenetic host breadth mean and divergence
AP
AMT
SNW
LAT
ELV
BSR
BSM
BSD
PHBM
PHBD

Table 1 Hypothetical paths from previous studies, which are considered in this study

Hypothetical path				References
Response	Predictor		Explanation	
Climate	Geography	(a)	Temperature, precipitation, and snow change along latitude and elevation gradients (+/–).	Romero *et al.* 2018
Butterfly diversity	Geography	(b)	Butterfly diversity changes along latitude (+/–) and elevation (+/–).	Sutton & Collins 1991, Gutiérrez 2009, Owens et al. 2017
Butterfly diversity	Climate	(c)	Butterfly diversity change along climatic conditions (+/–).	Currie et al. 2004, Owens et al. 2017
Butterfly body size	Geography	(d)	Butterfly body size changes along latitudes and elevations (+/–).	Bergmann 1947; Park 1949; Fisher *et al.* 1960
Butterfly body size	Climate	(e)	Butterfly body size and divergence change along with climatic conditions (+/–)	Bergmann 1947; Park 1949; Zeuss *et al.* 2017
Butterfly body size	Butterfly diversity	(f)	Body size increases toward regions that have lower butterfly diversity (+)	Hutchinson & MacArthur 1959
Host	Geography	(g)	Mean and divergence of host breadth decreases towards lower	Scriber 1995;

breadth				latitudes (–)	Forister *et al.* 2015
Host breadth	Climate		(h)	Mean and divergence of host breadth decrease towards regions that have higher amount of energy (+)	Schemske *et al.* 2009; Read *et al.* 2018
Host breadth	Butterfly diversity		(i)	Higher butterfly diversity intensifies competition and as consequence the host breadths become more narrow (–).	Dobzhansky 1950 ; MacArthur 1972; Coley & Kursar 2014
Host breadth	Butterfly body size	*	(j)	There is a positive correlation between host breadth and butterfly body size (possibly related to effectiveness of resource exploitation) (+)	Brown & Maurer 1989; Lindström 1994; Gaston *et al.* 1997; Davis *et al.* 2013

The asterisk indicates a correlational relationship

We also hypothesized a correlation within each factor (e.g., mean and divergence of body size)

Table 2 The final Bayesian structural equation model (SEM) focusing on the alpha parameter of the discrete truncated Pareto distribution fitted to butterfly host breadth. The abbreviations indicate LAT: Latitude, ELV: Elevation, AP: Annual precipitation, AMT: Annual mean temperature, SNW: annual maximum depth of snow cover, BSR: Butterfly species richness, BSM: Body size mean, BSD: Body size divergence, PAL: The alpha parameter of the discrete truncated Pareto distribution.

				95% C.I.		
				Lower	Upper	
	Response	Explanation	Estimate	2.5%	2.5%	Significance
Causal effect	AMT	LAT	-0.836	-0.846	-0.826	*
		ELV	-0.525	-0.541	-0.510	*
	AP	LAT	-0.549	-0.574	-0.523	*
		ELV	0.305	0.276	0.333	*
	SNW	LAT	0.470	0.440	0.499	*
		ELV	0.339	0.307	0.370	*
	BSR	AMT	–	–	–	
		AP	-0.191	-0.230	-0.151	*
		SNW	-0.220	-0.257	-0.182	*
		LAT	-0.316	-0.359	-0.273	*
		ELV	0.646	0.618	0.673	*
	BSM	AMT	0.397	0.351	0.443	*
		AP	0.238	0.210	0.266	*
		SNW	-0.180	-0.206	-0.153	*
		LAT	-0.274	-0.328	-0.220	*
		ELV	–	–	–	
		BSR	-0.135	-0.160	-0.109	*
	BSD	AMT	–	–	–	
		AP	0.305	0.279	0.329	*
		SNW	-0.213	-0.237	-0.189	*
		LAT	-0.548	-0.575	-0.521	*
		ELV	-0.281	-0.306	-0.257	*
		BSR	-0.230	-0.253	-0.206	*

	PAL	AMT	-0.885	-0.943	-0.826	*
		AP	-0.263	-0.298	-0.229	*
		SNW	0.160	0.127	0.193	*
		LAT	-0.405	-0.476	-0.336	*
		ELV	–	–	–	
		BSR	-0.257	-0.288	-0.225	*
Co-variate	PAL	BSM	-0.212	-0.249	-0.175	*
		BSD	-0.287	-0.323	-0.251	*
	BSM	BSD	0.729	0.711	0.747	*
	AMP	SNW	0.335	0.299	0.369	*

	Model fit (N=2542)		
	Lower 5.0%	Upper 5.0%	
BRMSEA	0.045	0.062	†
BCFI	0.997	0.999	††
BTLI	0.987	0.993	††
BIC		95188.085	

† Satisfied only the criteria of good model fit of BRMSEA (Lower 5.0% <0.05, Upper 5.0% < 0.08: Hoof et al. 2018).

†† Satisfied the criteria of good model fit of BRMSEA (both Lower 5.0% and Upper 5.0% <0.06: Asparouhov & Muthén 2019), BCFI and BTLI (both Lower 5.0% and Upper 5.0% >0.95: Asparouhov & Muthén 2019).

*Credible interval (C.I.) did not overlap zero

–Paths trimmed through model modification (The original full model is in Table S2)

Table 3 Results of the Bayesian structural equation model (SEM) focusing on mean and divergence (RaoQ) of phylogenetic host breadth. The abbreviations indicate LAT: Latitude, ELV: Elevation, AP: Annual precipitation, AMT: Annual mean temperature, SNW: annual maximum depth of snow cover, BSR: Butterfly species richness, BSM: Body size mean, BSD: Body size divergence, PHBM: Phylogenetic host breadth mean, and PHBD: Phylogenetic host breadth divergence.

				95% C.I.		
				Lower	Upper	
	Response	Explanation	Estimate	2.5%	2.5%	Significance
Causal effect	AMT	LAT	-0.836	-0.846	-0.826	*
		ELV	-0.525	-0.541	-0.509	*
	AP	LAT	-0.549	-0.574	-0.523	*
		ELV	0.305	0.275	0.334	*
	SNW	LAT	0.470	0.440	0.499	*
		ELV	0.339	0.307	0.370	*
	BSR	AMT	–	–	–	
		AP	-0.191	-0.231	-0.151	*
		SNW	-0.220	-0.258	-0.181	*
		LAT	-0.316	-0.360	-0.272	*
		ELV	0.646	0.618	0.673	*
	BSM	AMT	0.395	0.349	0.441	*
		AP	0.238	0.210	0.266	*
		SNW	-0.180	-0.207	-0.154	*
		LAT	-0.275	-0.330	-0.221	*
		ELV	–	–	–	
		BSR	-0.135	-0.161	-0.109	*
	BSD	AMT	–	–	–	
		AP	0.304	0.279	0.329	*
		SNW	-0.214	-0.237	-0.190	*
		LAT	-0.549	-0.576	-0.521	*
		ELV	-0.280	-0.304	-0.256	*
		BSR	-0.230	-0.254	-0.207	*

	PHBM	AMT	0.823	0.762	0.882	*
		AP	0.265	0.230	0.300	*
		SNW	-0.243	-0.277	-0.210	*
		LAT	0.471	0.399	0.542	*
		ELV	–	–	–	
		BSR	0.381	0.349	0.413	*
	PHBD	AMT	0.881	0.813	0.951	*
		AP	0.324	0.284	0.363	*
		SNW	-0.042	-0.081	-0.004	*
		LAT	0.645	0.563	0.728	*
		ELV	–	–	–	
		BSR	0.558	0.523	0.593	*
Co-variate	PHBM	BSM	0.245	0.207	0.282	*
		BSD	0.332	0.297	0.366	*
		PHBD	0.855	0.844	0.865	*
	PHBD	BSM	0.128	0.089	0.167	*
		BSD	0.195	0.157	0.232	*
	BSM	BSD	0.729	0.71	0.747	*
	AMP	SNW	0.335	0.301	0.369	*

	Model fit (N=2542)		
	Lower 5.0%	Upper 5.0%	
BRMSEA	0.043	0.060	†
BCFI	0.998	0.999	††
BTLI	0.987	0.993	††
BIC		102244.105	

† Satisfied only the criteria of good model fit of BRMSEA (Lower 5.0% <0.05, Upper 5.0% < 0.08: Hoof et al. 2018).

†† Satisfied the criteria of good model fit of BRMSEA (both Lower 5.0% and Upper 5.0% <0.06: Asparouhov & Muthén 2019), BCFI and BTLI (both Lower 5.0% and Upper 5.0% >0.95; Asparouhov & Muthén 2019).

*Credible interval (C.I.) did not overlap zero

–Paths trimmed through model modification (The original full model is in Table S2)

Appendix

Figure S1 Geographical patterns of climatic variables and elevation. (a) annual mean temperature, (b) annual precipitation, (c) annual maximum depth of snow cover, (d) elevation.

Figure S2 Latitudinal patterns in (a) phylogenetic host breadth minimum ($r=-0.014$, $p<0.001$), (b) phylogenetic host breadth maximum ($r=-0.059$, $p<0.001$), (c) body size minimum ($r=-0.130$, $p<0.001$), and (d) body size maximum ($r=0.071$, $p<0.001$). Values represent standardized effect sizes (SES) estimated based on null model 1

Figure S3 Latitudinal patterns in (a) alpha parameter of the discrete truncated Pareto distribution by using predicted occurrence data ($r=0.020$, $p<0.001$), (b) alpha parameter of the discrete truncated Pareto distribution by using observed occurrence data ($r=0.008$, $p<0.001$). Values represent non-standardized trends which are comparative with Forister et al. (2015).

Figure S4 The relationships between body size and diet breadth across Japanese butterfly species. There were no significant correlations ((a) $r=-0.021$, $p=0.745$; (b) $r=-0.071$, $p=0.268$).

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

Table S2 Comparison between the results based on the full model and final model for (a) discrete truncated Pareto alpha and (b) phylogenetic host breadth.

Table S3 Comparison between the results based on predicted and observed distribution datasets for (a) discrete truncated Pareto alpha and (b) phylogenetic host breadth. The model structures are as in Tables 2, 3.

Table S4 Comparison between the results based on null model 1 and null model 2 for (a) discrete truncated Pareto alpha and (b) phylogenetic host breadth. The model structures are as in Tables 2, 3.

Table S5 Comparison between the results based on different criteria of minimum butterfly species richness for (a) discrete truncated Pareto alpha and (b) phylogenetic host breadth. The model structures are as in Tables 2, 3.

Table S6 The correlations among the environmental variables and the calculated indices.

Table S7 The environmental variables and the calculated indices that were used in this study for all 10-km grids.

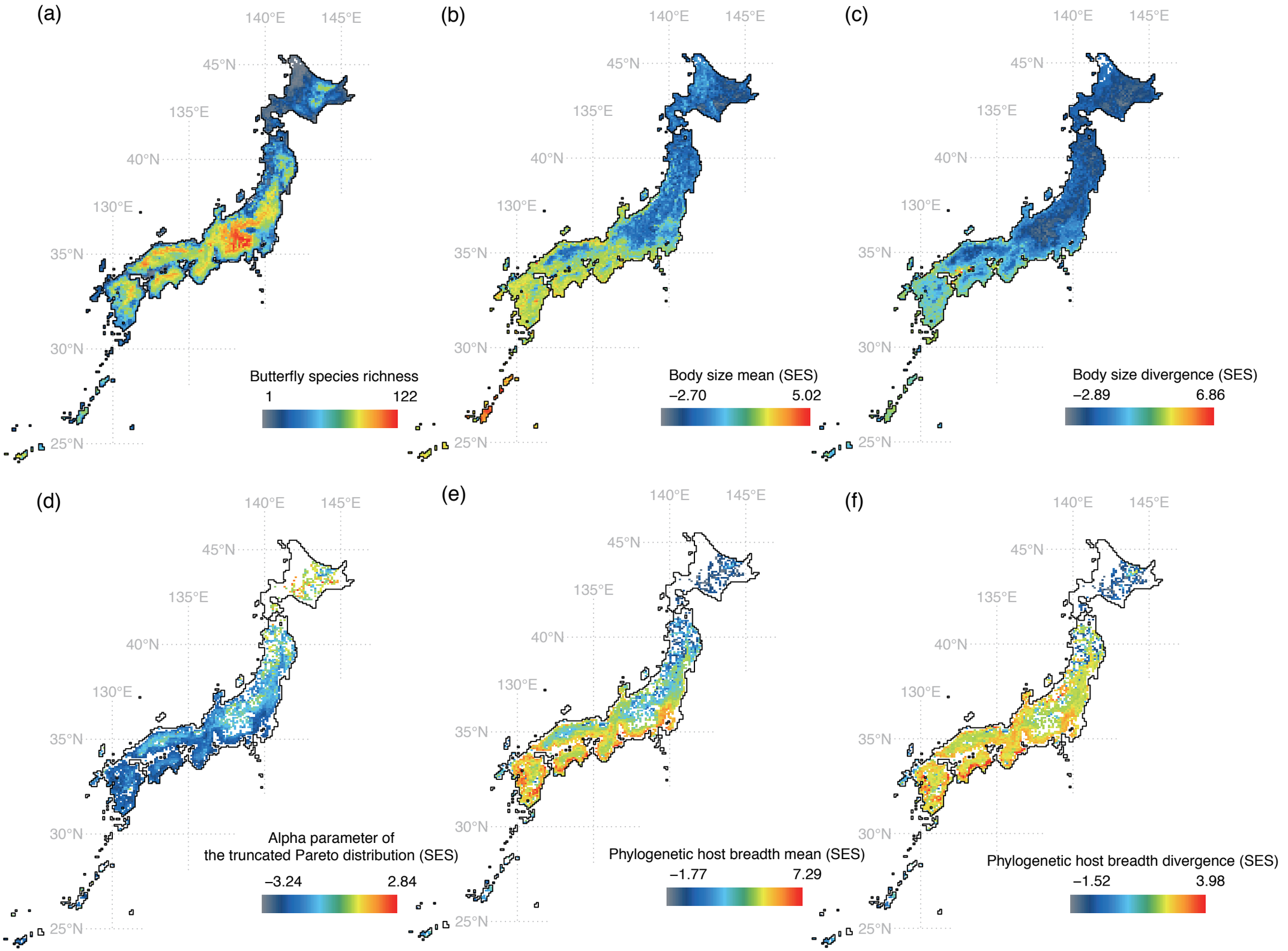
Supplementary text 1 Detailed description of butterfly distribution data.

Supplementary text 2 Detailed description of null models.

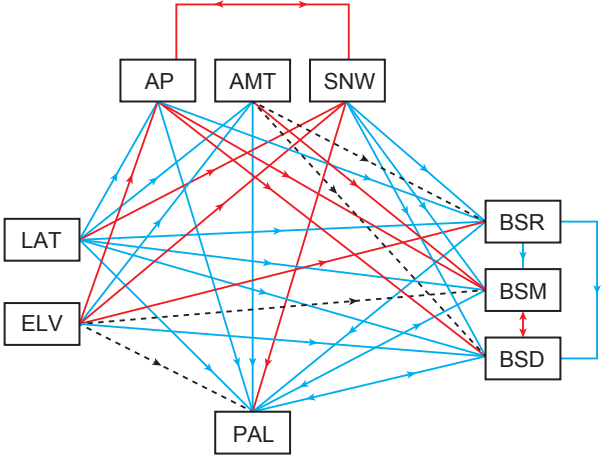
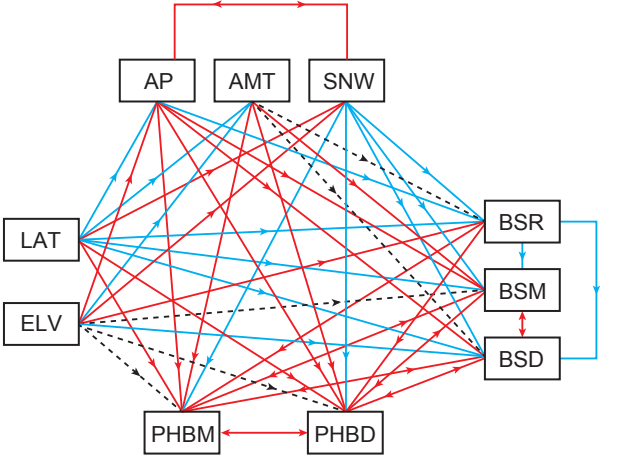
Supplementary text 3 Treatment of multicollinearity problems in Structural Equation Modeling.

Supplementary text 4 Detailed explanation of Bayesian SEM.

Supplementary text 5 Sampling size dependency in the chi-square test.


(a)
140°E
145°E
45°N
135°E
40°N
130°E
35°N
30°N
25°N
Butterfly species richness
1
122
(b)
Body size mean (SES)
−2.70
5.02
(c)
Body size divergence (SES)
−2.89
6.86
(d)
Alpha parameter of
the truncated Pareto distribution (SES)
−3.24
2.84
(e)
Phylogenetic host breadth mean (SES)
−1.77
7.29
(f)
Phylogenetic host breadth divergence (SES)
−1.52
3.98

(a) Alpha parameter of discrete truncated Pareto distribution



(b) Phylogenetic host breadth mean and divergence