Title: Why species richness of plants and herbivorous insects do or do not correlate

Authors: Naoto Shinohara^{1*}, Takehito Yoshida^{2,3}

¹Department of Agricultural and Life Sciences, University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan

²Research Institute for Humanity and Nature, 457-4 Motoyama, Kamigamo, Kita-ku, Kyoto 603-8047, Japan

³Department of General Systems Studies, University of Tokyo, 3-8-1 Komaba, Meguro, Tokyo 135-8902, Japan

*Corresponding author

Department of Agricultural and Life Sciences, University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan

Email: naotos.biod@gmail.com

ORCID id: <https://orcid.org/0000-0002-0816-2536>

Author contributions

NS and TY conceived the study; NS conducted fieldwork; NS analysed the data; and NS led the writing of the manuscript. All authors actively contributed to the manuscript's results and discussion and approved the final manuscript for publication.

20

21

Abstract

Unraveling the determinants of herbivorous insect diversity has been a major challenge in ecology. Despite the strong association between insect and plant species, previous studies conducted in natural systems have shown great variation in the strength of the correlation between their species richness. Such variation can be attributed to the proportion of generalist insect species (generality), though both higher and lower generality may weaken the correlation because 1) generalist insect species are less dependent on the number of plant species and 2) specialist insect species utilize only a part of the total plant species. To explore these opposing effects, we studied plant and herbivorous insect communities in semi-natural grasslands in Japan. Plant–insect interactions were evaluated in a unique way with a particular focus on the staying and herbivory behaviors of insects, which reflect their habitat use as well as host use. We found that generality of insect communities negatively affected the correlation between species richness of plants and insects. However, such negative effect was significant only when the insect species richness was related with the number of plant species interacted with some insect species, instead of with that of total plant species. The results suggest that considering either of the opposing effects of insect generality is insufficient and they should be inclusively interpreted to understand the relationship between plant and insect species richness.

40 **Keywords:** Herbivory network; insect species richness; plant–insect interaction; plant
41 species richness; semi-natural grassland

Introduction

Understanding the factors determining and regulating species diversity has been a major challenge in ecology (Hutchinson 1959) and several studies have focused on herbivorous insect species, which account for a major fraction of global biodiversity (Novotny et al. 2006; Lewinsohn and Roslin 2008). Due to the strong dependence of herbivorous insects on plants as resources and habitats, herbivorous insect species diversity has been commonly related to plant species diversity (Southwood et al. 1979; Erwin 1982). As expected, studies in experimental grasslands, where plant species richness was manipulated, consistently demonstrated a significant correlation between plant and insect species richness (Haddad et al. 2009; Hertzog et al. 2016). However, contrary to the findings of the experiments, observation studies in natural systems have shown inconsistent patterns about the correlation. Some studies concluded that plant species richness is a good predictor of insect species richness even after accounting for the effects of environmental conditions (Pellissier et al. 2013; Kemp and Ellis 2017; Miller et al. 2017), while others concluded that that was not the case (Hawkins and Porter 2003; Axmacher et al. 2009). Therefore, the relevance of plant species richness to that of insect species is still debatable (Vessby et al. 2002; Castagneyrol and Jactel. 2012).

The variation in the correlation between plant and insect species richness can be attributed to the proportion of generalist insect species (generality), though its effect has been interpreted in opposing directions. As discussed in some studies (Petermann et al. 2010; Kemp and Ellis

2017), lower generality of insect species may weaken the correlation because their limited diet breadth would result in larger part of plant species having no relationship with any insect species. In contrast, other studies (Koricheva et al. 2000; Axmacher et al. 2009; de Araujo et al. 2013) pointed out that a higher proportion of generalist insect species can lead to a weaker correlation because generalist insect species are less dependent on the number of plant species. Although these opposing effects are straightforward, they have been rarely inclusively discussed in previous studies. Therefore, it remains unclear whether higher insect generality dampens or strengthens the correlation of plant and insect species richness in natural systems and few empirical tests were conducted.

To explore the effects of herbivorous insect generality on the correlation between plant and insect species richness, we tested the three hypotheses: (1) if a higher proportion of plant species are not utilized by any insect species, the correlation would be weaker (unutilized plant species hypothesis). This predicts that the herbivorous insect species richness is better explained by utilized plant species richness than by the total plant species richness. (2) Higher proportion of generalist insect species would result in the weaker correlation (higher generality hypothesis), (3) but such pattern would be observed only when the utilized plant species was considered because of the opposing effects of the generality. These hypotheses were tested in a study on plant-herbivorous insect communities in Japanese semi-natural grasslands.

Materials and Methods

Study site

The study was conducted in an agricultural area (about 4 km², Fig. S1) located in suburban Tokyo, central Japan (35°35'39.6"N, 139°25'50.9"E). This area has a temperate climate with a mean annual temperature of 15.0 °C, and a mean annual precipitation of 1529.7 mm (data averaged across 1981–2010). The landscape represents the traditional Japanese agricultural landscapes, which comprises a mosaic ensemble of agricultural landscapes, secondary forests, and residential areas in a limited area (Kadoya and Washitani 2011). In this area, semi-natural grasslands are maintained in the form of strips on the edges of rice fields (Fig. S2) by periodic mowing. Although such semi-natural grasslands harbor a great number of plant and insect species (Kitazawa and Ohsawa 2002), changes in local agricultural management (e.g., mowing frequency) affect the diversity of plant and herbivorous insect species (Uchida and Ushimaru 2014). Therefore, a great variation in plant and herbivorous insect species diversity can be observed even within a limited area.

Among this area, 19 transects (2 m × 20 m) were established on the grasslands (Fig. S1, referred to as “sites” hereafter) for the plant and herbivorous insect surveys.

Data collection

Each site was surveyed in three seasons when plants and herbivorous insects were abundant:

early summer (15 June–11 August); late summer (22 August– 5 September); and autumn (19 September –5 October) in 2017. We could not survey every site for every season, because mowing by local farmers often reduced the aboveground vegetation. Therefore, the surveys were restricted to the sites where the vegetational structure seemingly recovered enough after mowing (at least two weeks after mowing) in each season, resulting in 31 surveys in total (9 sites in early summer, 14 sites in late summer, and 8 sites in autumn).

We conducted two types of survey. First, to obtain plant–insect interactions data, we walked along the transect slowly (ca. 20 m/h), while carefully and exhaustively counting the number of herbivorous insect individuals exhibiting either of the two types of the behavior: “herbivory” or “staying”. The behavior was deemed “herbivory” when we observed an insect individual actually feeding on a part of the plant body (i.e., leaf, stem, or petal). The behavior was deemed “staying” when the insect individual just stayed on a part of the plant body. Therefore, the observations of these behaviors were recorded as the interaction data (i.e. what insect species fed or stayed on what plant species). The surveys were conducted twice for each site within each season, resulting in the 2 h sampling effort for each site and each season. Second, to quantify the plant species composition, we established five quadrats (0.5 m × 0.5 m) on each transect and recorded the present plant species with their coverage percentage as an index of abundance.

Evaluation of plant–insect interactions

Plant–insect interactions were determined by two approaches based on the data collected from the behavior observation. First, we regarded a plant species to be utilized as host by an insect species if “herbivory” behavior was observed between them in any of the transect surveys. Second, we consider non-trophic plant–insect interactions, because architectural structure of plant individuals has been known as an important determinant of insect communities (Woodcock et al. 2007): Some insect species may prefer open microhabitats provided by tall grass species to facilitate thermoregulation (e.g. Joern 2005) and some may prefer particular plant species that attract less predators (“enemy free space hypothesis”; e.g. Price et al. 1980). To evaluate such non-trophic plant–insect interactions, we examined “preferred stays” with an assumption that insect species are dependent on plant species on which they preferably stay. Under this assumption, “preferred stays” of each insect species were determined by comparing “null stays” and observed “staying” behavior. First, the frequency of “null stays” of each insect species on each plant species were evaluated for each season separately. The total (across all sites in each season) number of observed individuals of an insect species were randomly distributed to all plant species proportional to their coverage summed across all sites surveyed in the season. These “null stays” represented the expected frequency of staying of the insect species on each plant species without any preference for plant species. The random distribution procedure was repeated 1,000 times for each insect species, to provide its frequency of “null

stays” on each plant species with a 95% confidence interval. Then, the frequency of observed stays on each plant species (unfilled points in Fig. 1) was compared to that of “null stays” and whether it significantly deviated from the expectation (i.e., greater than the upper bound of 95% confidence interval shown as a solid line in Fig. 1) was examined. The plant species, on which focal insect species stayed more frequently than expected (filled points in Fig. 1), were considered as interacted with the insect species. The procedure was conducted for each insect species, and for each season. Although it is interesting to investigate the congruence of trophic and non-trophic interactions, such analysis is beyond the scope of this study and we determined plant–insect interactions by summing up the interaction data obtained from both of the observational and null-model approaches.

Statistical analyses

All statistical analyses were performed using R 3.3.1 (R core team 2018). First, diet breadth of each insect species was defined as the number of plant species it interacted with. To represent the proportion of generalist insect species at site (community) level, we calculated the “generality” index that is the averaged diet breadth across insect species within the site.

To test the hypotheses, generalized linear mixed models (GLMMs) were performed using “lme4” package (Bates et al. 2015). First, models were developed to test the hypothesis that insect species richness is better explained by the number of interacted plant species, rather

than by that of total plant species. We used GLMMs (Poisson error distribution and log link function) with insect species richness as a response variable, either interacted or total plant species richness as an explanatory variable, and seasons as a random term. Here, the interacted plant species refer to those that were evaluated as interacted with at least one herbivorous insect species within each site.

Second, models were developed to test the second and third hypotheses. We used GLMMs (Poisson error distribution and log link function) with insect species richness as a response variable, either interacted or total plant species richness and its interactive term with generality index as explanatory variables, and season as a random term. The second and third hypotheses predict a negative coefficient for the interactive term, but only when interacted plant species richness was used as an explanatory variable. For the models, the significance of the partial regression coefficients of the explanatory variables were evaluated using Wald test.

Results

In total, we recorded 152 plant species and 116 herbivorous insect species (1803 individuals). We recorded 118 plant species and 70 insect species (375 individuals) in early summer (9 sites); 93 plant species and 58 insect species (788 individuals) in late summer (14 sites); 75 plant species and 52 insect species (640 individuals) in autumn (8 sites).

We obtained 144 and 1659 observations of herbivory and staying behavior respectively from the field survey. These observations resulted in the estimate of 388 interactions between plant and insect species, where 72 interactions were estimated from observation of herbivory and 328 were from the evaluation of preferred stays, and 12 were from both (Fig. 2a). Distributions of the number of interactions per insect species (Fig. 2b, c) were similar as the one previously known for niche breadth of herbivorous insects, such that specialist species predominate and generalist species are less common (Forister et al .2015).

We found that insect species richness was significantly explained by interacted plant species richness (GLMM: coefficient = 0.044, $z = 3.20$, $P = 0.001$) (Fig. 3a), but not by total plant species richness (coefficient = 0.007, $z = 0.978$, $P = 0.328$) (Fig. 3b). The GLMM including the interactive term between interacted plant species richness and generality index as an explanatory variable showed a marginally significant negative effect of the interactive term (coefficient = -0.012, $z = -1.76$, $P = 0.078$), as well as a significant positive effect of interacted plant species richness (coefficient = 0.089, $z = 3.12$, $P = 0.002$) (Fig. 4b). In contrast, when

188 total plant species richness was incorporated into the model, no significant effect of the
 189 interactive term (coefficient = -0.001, $z = -1.37$, $P = 0.170$) and marginally significant positive
 190 effect of total plant species richness (coefficient = 0.024, $z = 1.69$, $P = 0.091$) (Fig. 4a) on insect
 191 species richness were found.
 192

Discussion

Although experimental studies consistently reported that herbivorous species richness is well explained by plant species richness (Haddad et al. 2009; Hertzog et al. 2016), such correlation in natural systems is variable (e.g. Hawkins and Porter 2003; Kemp and Ellis 2017) and consistent explanation for the variation has been lacked. In the present study, we showed that the correlation was dampened by (1) the presence of plant species those were not utilized by any insect species (unutilized plant species hypothesis) and by (2) the high ratio of generalist insect species (higher generality hypothesis), though (3) such effect of higher generality was significant only when the interacted plant species were considered.

In light of the two hypotheses, we may explain the variation in the correlation between plant–insect species richness among previous studies. First, most previous studies have attempted to explain insect species richness by total plant species richness rather than by utilized plant species richness, and some of them have found no significant relationships between them (Vessby et al. 2002; Axmacher et al. 2009; Walcher et al. 2017). On the contrary, a study on plant and their associated insect species (collected from individuals of the focal plants) showed a significant relationship between their species richness even accounting for geographic and environmental variables (Kemp and Ellis 2017). Considering the limited diet breadth of herbivorous insect species (Fig. 2, Forister et al. 2015), distinguishing host plant species would be crucial for explaining insect species richness (but see Hawkins and Porter

2003). The proportion of unutilized plant species depends on the factors causing absence of some insect species independently of host plant species presence (e.g. dispersal limitation or top predator pressure [Koricheva et al. 2000; Schmitz and Suttle 2000]), and such factors may have caused the variation of the correlation between plant–insect species richness among different study systems.

Second, although the negative effect of insect generality on plant–insect species richness correlation may be frequently presumed, empirical evidence that explicitly showed the predicted pattern has been rare. We showed that the correlation between plant and herbivorous insect species richness was negatively affected by insect generality, which indicates that the possibility of colonization of specialist insect species was enhanced with increasing plant species richness, whereas generalist insect species occurred irrespective of plant species richness. It has been suggested that insect generality may vary among study systems that differ in time after disturbance (Piechnik et al. 2008), degree of land-use intensification (de Araujo et al. 2015, Shinohara et al. 2019), spatial scale (Hughes 2000), and taxonomical groups (Forister et al. 2015). Therefore, incorporating those factors in future studies may help explain the relationship between plant–insect species richness. For example, a meta-analysis approach to relate those factors with the variation in the correlation between plant and insect species richness among previous studies may be promising (e.g. Castagneyrol and Jactel. 2012).

More importantly, we found that such negative effect of insect generality on the correlation was not significant when unutilized plant species were also counted in addition to utilized plant species. So far, previous studies have appreciated only either of the opposing directions of the effect of insect generality on plant–insect relationship (unutilized plant species hypothesis and higher generality hypothesis), which has caused the contradictory situation where the weak correlation between plant and herbivorous insect can be associated with both lower (e.g. Kemp and Ellis 2017) and higher (e.g. Axmacher et al. 2009) generality of insects. However, our result suggests that consideration for only negative effect of insect generality may be insufficient to explain the correlation between plant and insect species richness. We conclude that the both mechanisms should be inclusively examined when attributing the strength of the correlation between plant–insect species richness to insect generality.

243 **Data accessibility**

244 The data used in this study are archived in figshare repository:

245 <https://doi.org/10.6084/m9.figshare.11876055.v1>

246

247 **Acknowledgements**

248 The study was supported by the Research Institute for Humanity and Nature (RIHN: a

249 constituent member of NIHU) Project No. 14200103. We thank Koichi Tagoku, Susumu

250 Yamada, and members of Yui-no-Sato for supporting and assisting our study in the field, and

251 Gaku Takimoto, Marc Johnson, and Yuya Fukano for their helpful comments. We also thank

252 Naoyuki Nakahama, Kazuhide Nakajima, and Takuya Yoshida for assisting field surveys and

253 taxonomic identification.

254

Literature cited

- Axmacher, J. C., G. Brehm, A. Hemp, H. Tünte, H. V. M. Lyaruu, K. Müller-Hohenstein, and K. Fiedler. 2009. Determinants of diversity in afrotropical herbivorous insects (Lepidoptera: Geometridae): Plant diversity, vegetation structure or abiotic factors? *Journal of Biogeography* 36:337-349 doi: 10.1111/j.1365-2699.2008.01997.x
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67(1):1-48 doi: 10.18637/jss.v067.i01
- Castagneyrol, B., and H. Jactel. 2012. Unraveling plant-animal diversity relationships: a meta-regression analysis. *Ecology* 93: 2115-2124 doi: 10.1890/11-1300.1
- de Araújo, W. S., M. C. Vieira, T. M. Lewinsohn, and M. Almeida-Neto. 2015. Contrasting Effects of Land Use Intensity and Exotic Host Plants on the Specialization of Interactions in Plant-Herbivore Networks. *PLoS ONE* 10(1): e0115606 doi: 10.1371/journal.pone.0115606
- Erwin, T. L. 1982. Tropical Forests: Their Richness in Coleóptera and Other Arthropod Species. *The Coleopterists Bulletin* 36:74-75
- Forister, M. L., V. Novotny, A. K. Panorska, L. Baje, Y. Basset, ..., L. A. Dyer. 2015. The global distribution of diet breadth in insect herbivores. *PNAS* 112:442-447 doi: 10.1073/pnas.1423042112
- Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009.

274 Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology*
275 *Letters* 12:1029-1039 doi: 10.1111/j.1461-0248.2009.01356.x

276 Hawkins, B. A., and E. E. Porter. 2003. Does Herbivore Diversity Depend on Plant Diversity?
277 The Case of California Butterflies. *The American Naturalist* 161:40-49 doi:
278 10.1086/345479

279 Helsen, K., M. Hermy, and O. Honnay. 2013. Spatial isolation slows down directional plant
280 functional group assembly in restored semi-natural grasslands. *Journal of Applied*
281 *Ecology* 50:404-413 doi: 10.1111/1365-2664.12037

282 Hertzog, L. R., S. T. Meyer, W. W. Weisser, and A. Ebeling. 2016. Experimental manipulation
283 of grassland plant diversity induces complex shifts in aboveground arthropod diversity.
284 *PLoS ONE* 11:1-16 doi: 10.1371/journal.pone.0148768

285 Hughes, J. B. 2000. The scale of resource specialization and the distribution and abundance of
286 lycaenid butterflies. *Oecologia* 123:375-383 doi: 10.1007/s004420051024

287 Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why Are There So Many Kinds of
288 Animals? *The American Naturalist* 93:145-159 doi: 10.1086/282070

289 Joern, A. 2005. DISTURBANCE BY FIRE FREQUENCY AND BISON GRAZING
290 MODULATE GRASSHOPPER ASSEMBLAGES IN TALLGRASS PRAIRIE.
291 *Ecology* 86:861–873 doi: 10.1890/04-0135

292 Kadoya, T., and I. Washitani. 2011. The Satoyama Index: A biodiversity indicator for

293 agricultural landscapes. *Agriculture, Ecosystems and Environment* 140:20-26 doi:
 294 10.1016/j.agee.2010.11.007

295 Kemp, J. E., and A. G. Ellis. 2017. Significant local-scale plant-insect species richness
 296 relationship independent of abiotic effects in the temperate cape floristic region
 297 biodiversity hotspot. *PLoS ONE* 12:1-16 doi: 10.1371/journal.pone.0168033

298 Kitazawa, T., and M. Ohsawa. 2002. Patterns of species diversity in rural herbaceous
 299 communities under different management regimes, Chiba, central Japan. *Biological*
 300 *Conservation* 104:239-249 doi: 10.1016/S0006-3207(01)00170-7

301 Koricheva, J., C. P. H. Mulder, B. Schmid, J. Joshi, and K. Huss-Danell. 2000. Numerical
 302 responses of different trophic groups of invertebrates to manipulations of plant diversity
 303 in grasslands. *Oecologia* 125:271-282 doi: 10.1007/s004420000450

304 Lewinsohn, T. M., and T. Roslin. 2008. Four ways towards tropical herbivore megadiversity.
 305 *Ecology Letters* 11:398-416 doi: 10.1111/j.1461-0248.2008.01155.x

306 Miller, J. E. D., P. G. Hahn, E. I. Damschen, and J. Brennan. 2017. Functional dependence
 307 underlies a positive plant-grasshopper richness relationship. *Basic and Applied Ecology*
 308 21:94-100 doi: 10.1016/j.baae.2017.06.001Get rights and content

309 Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006.
 310 Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests?
 311 *Science* 738:2003-2006 doi: 10.1126/science.1129237

312 Pellissier, L., C. Ndiribe, A. Dubuis, J. Pradervand, N. Salamin, A. Guisa, and S. Rasmann.
313 2013 Turnover of plant lineages shapes herbivore phylogenetic beta diversity along
314 ecological gradients. *Ecology Letters* 16:600-608 doi: 10.1111/ele.12083

315 Petermann, J. S., C. B. Müller, A. Weigelt, W. W. Weisser, and B. Schmid. 2010. Effect of plant
316 species loss on aphid-parasitoid communities. *Journal of Animal Ecology* 79:709–720
317 doi: 10.1111/j.1365-2656.2010.01674.x

318 Piechnik, D. A., S. P. Lawler, and N. D. Martinez. 2008. Food-web assembly during a classic
319 biogeographic study: species’ “trophic breadth” corresponds to colonization order. *Oikos*
320 117:665-674 doi: 10.1111/j.2008.0030-1299.15915.x

321 Price, P. W., C. E. Bouton, P. Gross, A. Bruce, J. N. Thompson, and a E. Weis. 1980.
322 INTERACTIONS AMONG THREE TROPHIC LEVELS: Influence of Plants on
323 Invertebrates Between Insect Herbivores and Natural Enemies. *Annual Review of*
324 *Ecology and Systematics* 11:41–65 doi: 10.1146/annurev.es.11.110180.000353

325 R Core Team 2018. R: A language and environment for statistical computing. R Foundation for
326 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

327 Schmitz, O. J., and K. B. Suttle. 2001. Effects of Top Predator Species on Direct. *Ecology*
328 82:2072-2081 doi: 10.1890/0012-9658(2001)082[2072:EOTPSO]2.0.CO;2

329 Shinohara, N., K. Uchida, and T. Yoshida. 2019. Contrasting effects of land-use changes on
330 herbivory and pollination networks. *Ecology and Evolution* 9:13585–13595 doi:

331 10.1002/ece3.5814

332 Southwood, T. R. E., V. K. Brown, and P. M. Reader. 1979. The relationships of plant and insect
333 diversities in succession. *Biological Journal of the Linnean Society* 12:327-348 doi:
334 10.1111/j.1095-8312.1979.tb00063.x

335 Uchida, K., and A. Ushimaru. 2014. Biodiversity declines due to abandonment and
336 intensification of agricultural lands: Patterns and mechanisms. *Ecological Monographs*
337 84:637-658 doi: 10.1890/13-2170.1

338 Vessby, K., B. Söderström, A. Glimskär, and B. Svensson. 2002. Species-Richness Correlations
339 of Six Different Taxa in Swedish Seminatural Grasslands. *Conservation Biology* 16:430-
340 439 doi: 10.1046/j.1523-1739.2002.00198.x

341 Walcher, R., J. Karrer, L. Sachslehner, A. Böhner, B. Pachinger, D. Brandl, J. G. Zaller, et al.
342 2017. Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both:
343 abandonment and extensive management of mountain meadows in three regions across
344 the Austrian and Swiss Alps. *Landscape Ecology* 32:1937-1951 doi: 10.1007/s10980-
345 017-0556-1

346 Woodcock, B. A., S. G. Potts, T. Tscheulin, E. Pilgrim, A. J. Ramsey, J. Harrison-cripps, V. K.
347 Brown, et al. 2009. Responses of invertebrate trophic level, feeding guild and body size
348 to the management of improved grassland field margins. *Journal of Applied Ecology*
349 46:920–929 doi: 10.1111/j.1365-2664.2009.01675.x

Figures

Figure 1. An illustration of the null-model approach for evaluating the preferred stays of a herbivorous insect species (*Proboscidoecoris varicornis*), as an example, on all plant species observed. The horizontal axis represents plant species in order of the coverage summed across all sites in each season, and the vertical axis represents the frequency of stays of the herbivorous insect species on each plant species. Dashed and solid lines represent the expected (null) frequency of stays (mean and the upper bound of 95% confidence interval, respectively) calculated based on the total coverage of each plant species summed across all sites in each season. Points represent the frequency of observed stays on each plant species. Filled red points represent that they significantly deviated from the expectation (above the solid line), which we considered the plant and the herbivorous insect species having interacted.

Figure 2. A plant–herbivorous insect interaction network determined by the observational and null-model approaches. Upper and lower bars represent insect and plant species respectively, with their relative frequency of interactions shown by the bar width. Links represent the plant–insect interactions determined by observation of herbivory (black), evaluation of preferred stays (gray), or both (red). The network shown is based on early-summer data as an example (a). Distribution of number of interacted

plant species for each insect species, in which interactions were determined by observation of herbivory (b) or evaluation of preferred stays (c).

Figure 3. Relationship between herbivorous insect species richness and total plant species richness (a), and relationship between herbivorous insect species richness and interacted plant species richness (b). Regression line is estimated based on the results of the GLMM.

Figure 4. Effects of herbivorous insect generality on the relationships between herbivorous insect species richness and total plant species richness (a), or interacted plant species richness (b). The color of the points represents the generality: reddish ones represent higher generality, and blueish ones represent lower generality. Regression lines are estimated based on the results of the GLMM. Red, dashed line represents the model with the highest generality (4.75), and blue, solid line represents one with the lowest generality (3.00).

386 Figure 1

387

Figure 2

Figure 3

Figure 4