

Scale-dependent contribution of biotic and abiotic factors to longhorn beetles (Cerambycidae) community composition variation at the Indo- Burma biodiversity hotspot

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Abstract

Despite centuries of exploration, our perception of potential mechanisms determining the species community assemblage is still in infancy. Longhorn beetle as an insect with larval stage feeds on the xylem of plants or trees, the relative importance of biotic (host-specificity) and abiotic (climate gradients) processes to determining their community compositional variation is unknown. In the aim of exploring the knot, we therefore designed the experiment throughout multiple spatial scales (macro/regional and micro/local) along tropical to temperate climate gradients at the Indo-Burma biodiversity hotspot, to examine to what extent biotic and abiotic factors may exert a significant influence on longhorn beetle species composition assembly, and whether this relationship is scale dependent. The relationships between longhorn beetles species composition variation and biotic and abiotic factors were examined using β -dissimilarity indices comparison, NMDS analysis, variation partitioning based on RDA, linear mixed-effect model and mantel test. We found a positive relationship between the species compositional variation of both beetle and plants, in which longhorn beetle species dissimilarity apparently track changes in plant dissimilarity both at macro/regional and micro/local scales. NMDS analysis showed that abiotic factors have prominent influence to the longhorn beetle community assemblage. Variation partitioning and linear mixed-effect model retained significantly correlated Environment and plant diversity metrics for beetle diversity. Thus, we concluded that: 1) biotic and abiotic factors collaboratively shaped longhorn beetle community composition along various spatial scales; 2) the relative importance of abiotic and biotic variation explaining the longhorn beetle community composition vary by spatial scale; and 3) biotic interactions have prominent effect to longhorn beetle community composition at local-scale while macroclimatic gradients impose the most control on it at macro-scale. Besides, our study showed that the influence of dispersal limitation in the species assembly of longhorn beetles from tropical to temperate area was minor compared with plant community.

Keywords:

Host specificity, plant-insect interaction, climate gradients, community assembly, β -diversity

Introduction

β -diversity (site-to-site variation in species composition) as a method to quantify the species assembly pattern has provide insights into the processes that create and maintain the compositional variation of natural communities (Whittaker, 1960, Moritz *et al.*, 2001; Graham *et al.*, 2006), β -diversity of biological communities

along biological gradients is a long debated focal topic for ecologists and bio-geographers (Routledge, 1977; Harrison *et al.* , 1992). Differences in β -diversity occurring along gradients are often used to infer variation in the processes of structuring communities. Recent studies suggested the driving forces of β -diversity was caused by a series of combined mechanisms that affect these local community assembly processes interactively with different relative contributions among bio-geographical regions (Mori & Seidl, 2018). Generally, Species relationships in the community can be conceived in terms of a multidimensional coordinate system, the axes of which are the various resource gradients, and those gradients usually can be categorized as focusing on two major components: biotic and abiotic processes (Sexton *et al.* ,2009).

In nature, the influence of biotic and abiotic factors shaping species community are often varying in time and spatial scale, and disentangling the relative influences of these factors is not always a straightforward process. Biotic interactions, which including interspecific competition, mutualism, and predation/host relationships, may modify either the resource availability or the local abiotic environment with potentially contrasting consequences on abundance, and both positive and negative interactions may affect species assemblage through inhibiting or facilitating species establishment, individual growth and population size (Holt 2009; Svenning *et al.* 2014). A good deal of examples from the ecological literatures documented that these interactions are not static in space and can be linked with the impacts of changing climate via different complicated ways (Braschler & Hill 2007; Gilman *et al.* , 2010). And a part of these cases were elaborated as follows. Whittaker proposed a conceptual framework in which abiotic factors (temperature and precipitation) explained the distribution of terrestrial biomes of the world (Whittaker 1975). Further more, the idea that climate is the dominant factor shaping species distributions at broad scale is conceived to explain the correlation of climate and species occurrence patterns observed at a comparable spatial resolution (Woodward 1987). Different with the broad spatial scale, Soberón & Nakamura claimed that the pattern of fine spatial resolution is created by biotic interactions (Soberón & Nakamura 2009). This idea is also verified by Pearson & Dawson (2003), who stated that biotic interactions are expected to play a role in shaping species distributions only over local extents. All of these perspectives imply that the key point of the comparative influence of biotic and abiotic process for species assembly rely on scale.

From the literature, approximately 500,000 known species on the earth is herbivorous insects, which represent nearly a quarter of all terrestrial macroscopic biodiversity (Daly, Doyen, & Purcell, 1998; Southwood, 1973;). The intimate association with land plants (especially angiosperms) might be the dominating driving force of herbivorous insects' extraordinary diversification (Farrell, 1998; Strong, Lawton, & Southwood, 1984; Marvaldi, Sequeira, O'Brien, & Farrell, 2002; Mitter, Farrell, & Wiegmann, 1988). There are a great deal of observations showing that most herbivorous insects only feed on one or few related plant species and showed narrow host range; adaptation towards different host-plant species can potentially generate ecological specialization in plant-feeding insects and, subsequently, species formation. If plant diversity influences insect speciation, we can expect that insect community composition will be strongly correlated with host-plant community composition. This should be observable at the level that insect community composition will co-vary with the host plant community composition.

For arthropod insect communities, substantial compositional change is prevalent between regions along abiotic gradients within regions (Hoisset *et al.* , 2012; Pellissier *et al.* , 2013) and between habitats differing in plant community composition under the conditions that evolved host specialization (Siemann *et al.* , 1998; Schaffers *et al.* , 2008). If insect speciation results from allopatric host shifts of specialized insect species, insect community composition variation should be associated with plant community composition variation in a predictable manner (Siemann *et al.* , 1998; Schaffers *et al.* , 2008; Pellissier *et al.* , 2013). However, although the matching patterns could indicate speciation through host shifts or allopatric insect speciation with subsequent host specialization, it could also indicate parallel responses to broad abiotic gradients. Therefore, patterns resulting from parallel responses to macroclimatic gradients are often difficult to distinguish from patterns resulting from evolutionary associations (Hawkins & Porter, 2003). A potential approach to tease these two factors apart is to examine patterns of association between plant and insect β -diversity at different spatial scales (Kemp *et al.* , 2017). If both patterns result from insect-host specialization, plant and insect β -diversity should be correlated at fine, as well as broad spatial scales. However, if patterns result from

parallel responses to broad abiotic gradients, β -diversity patterns should only be correlated at broad spatial scales (Kemp *et al.* , 2017).

Longhorn beetles belongs to the order Coleoptera of the class Insecta, presenting a period in their life cycle (mainly larval stage) feeds on the xylem of plants or trees. It is estimated that there are more than 26000 species of longhorn beetles in the world, the relationships between longhorn beetles and their host plants are often quite specific, but there is a great range in the breadth of host tree species that might be used by the larvae of different species (Hanks, 1999). Longhorn beetle is not only an important component of ecological biodiversity, but also has vital effects in the sustaining and balancing of forest ecosystem. They are not only the decomposer of organic matter such as wood residues during forest renewal, but also the pollinators of some plant species. Since the diet habits of the longhorn beetle display attributes of host specificity, exploring the β -diversity of insect communities in different climatic zones and habitats will not only be helpful to understand the regional geography and renewal process of forest vegetation, but also contributes to understand the mechanism of maintenance and cycling of natural forest vegetation (Arias *et al.* 2008; Strong *et al.* 1984; Wagner 2000).

The effect of plant diversity and structural heterogeneity of habitat on longhorn beetle assemblages within a local scale have been heavily studied (Meng *et al.* , 2013; Gatti *et al.* , 2018), but a cross regional comparison of β -diversity of longhorn beetle communities and their association with plant species along a broad environmental gradient has rarely been reported. Our specific goal of the study was to determine the contribution of tree species and phylogeny to the long horn beetle β -diversity distribution models along the increasing spatial extent and climatic gradient across Yunnan province in SW China, the Indo-Burma biodiversity hotspots of the eastern Himalayas (Myers *et al.* , 2000). We hypothesize that: (1) species β -diversity of the longhorn beetle community is comparable and scale dependent to that of plant species across spatial space from the tropical to temperate regions; (2) biotic (insect and host plant interaction) and abiotic (climatic gradients) factors collaboratively shaped longhorn beetle community composition along various spatial scales; (3) the relative importance of abiotic and biotic variation explaining the longhorn beetle community composition vary by spatial scale, and biotic interactions have prominent effect to longhorn beetle community composition at local scale while macroclimatic gradients impose the most control on it at macro-scale.

Materials and Methods

Study sites from tropical to temperate regions

The study was carried out in the Yunnan province of south-west China (Fig. 1). Owing to the effects of a tropical monsoonal climate and varied mountain hilly topography, this area is covered with various types of highly complex vegetation from tropical monsoonal rainforest to temperate coniferous forest. Our sampling design is located at tropical Bubeng (Xishuangbanna), subtropical Xujiaba (Ailaoshan), and the cold temperate Yulong mountain (Lijiang), respectively (Fig. 1). Three large permanent plots for long term ecological research with an area of 20 or 25 ha have been established in recent years and a standardized vegetation inventory has shown a hyper-diverse forest at Bubeng (468 woody species) (Lan *et al.* , 2008), median-diverse at Xujiaba (103 woody species) (Wen *et al.* , 2018), and a much lower diversified coniferous forest at the Yulong mountain (62 woody species) (Huan *et al.* , 2017).

Sampling design

A spatially nested sampling approach referring to the design described in Kemp & Ellis (2017) was followed. To compare the role of elevation effects on β -diversity of beetle species distribution within the three different regions, we established three elevation transects at each region close to the above mentioned large permanent plots with the same range of elevation gradient covering almost 400 m in height. Each transect included five forest plots with the intermediate grain size of 25×20 sq. m established for the installation of beetle collection devices. Anthropogenic and natural disturbances, such as large canopy gaps in the plots, were avoided. All five forest plots at each transect were oriented parallel to respective contour lines and arranged with the least distance being 40 m away from each other. Each sampled transect is described below.

The tropical transects were located in Bubeng, Xishuangbanna (21.61° N, 101.58° S). This area borders Myanmar on the south-west and Laos on the south-east. Mean annual temperature and rainfall are 22 °C and 1500 mm, respectively. The rainy season ranges from May to October and dry season ranges from November to April. Approximately 80% of annual precipitation occurs in the rainy season. Three transects at different elevations (600, 800, and 1000 m) were selected based on current vegetation and topography conditions. The shortest distance between the three transects was around 0.5 km.

The subtropical transects were located in Xujiaba of the Ailao mountains (24.53° N, 101.03° S), which was about 329 km away from Bubeng (Fig. 1). The mean annual temperature and rainfall are 11 °C and 1900 mm, respectively, with a dry season between December and April. This area encompasses a large tract of evergreen broad-leaved forests primarily dominated by *Lithocarpus* and *Castanopsis* at mid elevation (ca. 2200-2600 m a.s.l.) with dense or sparse understory of bamboo, and *Rhododendron* dwarf forests toward higher elevations. Three transects at different elevations (2200, 2400, and 2600 m) were selected based on the vegetation and topography conditions, with an average distance of around 1.7 km between the three transects.

The temperate transects were located in the Yulong mountains of Lijiang (27.14° N, 100.23° S). The climate of this area has an average temperature of 5.5 °C, with average annual rainfall around 1600 mm. This area encompasses a large tract of temperate coniferous forests primarily dominated by *Berberidaceae*, *Caprifoliaceae*, and *Rosaceae* as the understory. Both *Pinaceae* and *Fagaceae* plants dominate the canopy and have a relative higher importance value. Similar to the transects in tropical Bubeng and subtropical Xujiaba, three elevation bands (3200, 3400, and 3600 m) were selected for insect sampling and vegetation inventory, with an average of around 1.4 km between the three transects.

Insect sampling and tree sampling

Beetle sampling was conducted using modified aerial collectors in the canopy and understory area of each forest plot at all sites. Aerial collectors, also called flight intercept traps (FITs), were constructed with two pieces of hard, transparent, plastic plates (50 × 35 cm, height × width) which were arranged crosswise and fixed upon a red or blue plastic bowl (35 × 30 cm, diameter × height). A piece of round, transparent, soft plastic plate with a diameter of 45 cm roofed the top of each FIT to prevent entry of too much precipitation during the rainy season. Within each plot, one trap was installed on canopy tree branches at a height of 10-30 m above the ground, and the second one was placed at the understory at a height of 2 m. The collecting basins of the FITs were filled with a liquid mixture of 75% alcohol and blue colored anti-freeze (ethanol-glycol) at 1:2 v/v. Ten FITs were used in each transect, totaling 90 FITs installed in all three investigated regions.

Owing to the large differences in climatic conditions among the three regions, the start time of collection from traps in each region differed slightly. Field work at Bubeng started in April, 2018 to end in April, 2019, and in Xujiaba and the Yulong mountain in May, 2018 to the end of May, 2019. Our insects sampling work last for 1 year at all plots, traps were emptied every 10 days during the collection periods with few exceptions where traps were destroyed by strong wind or collection was impossible owing to heavy rains. Despite the strict protective measures, we had a total of seven FITs destroyed by accident and the replacements were installed within the following 10 days. The collected specimen preserved alcohol and anti-freeze mixture were filtered and preserved in 70% ethanol liquid, after the first step of specimen cleaning (remove the trash and untargeted insects), we started the morphological classification and recorded the abundance and richness of longhorn beetles from each trap. The identification work was conducted with taxonomists experienced in Cerambycidae identification. Voucher specimens of the collected beetles have been deposited temporarily at the laboratory in the Honghe University and they will finally be transferred to the National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, Beijing.

Collection of vegetation data was conducted in April and May of 2019. At each elevation transect, five 25 m × 20 m plots were set up and spaced around 40 m away from each other. These were the same as the plots mentioned above for insect sampling to install the FITs. Therefore, in all three regions, we censused woody plants in 0.25-ha plots using identical field methods at each elevation transect. All plots

were established outside of large canopy gaps created by recent anthropogenic and natural disturbances. In each plot, we measured the abundance of each tree species (or morpho-species) [?] 5.0 cm diameter at breast height (1.2 m). All sampling methods used in the present study comply with the instruction of the Center for Tropical Forest Science (<http://www.ctfs.si.edu/>) to assemble long term, large-scale forest data from the tropics (Condit, 1995) and the Chinese Forest Biodiversity Monitoring Network (<http://www.cfbiodiv.org/>). Voucher specimens were collected whenever necessary in the field for later identification with the help of experienced botanists. When establishing plots on slopes, we positioned the plot centerline perpendicular to slopes to minimize elevation gradients within plots. In addition, because sampling in all regions included a similar numbers of plots spanning small and large geographical distances, we were able to compare the potential influence of spatial limitation between regions at similar scales, including scales that encompass typical dispersal distances (seed shadows) from tropical to temperate vegetation (Clark *et al.*, 1999; Myers *et al.*, 2013).

Environmental factors

We recorded air temperature and humidity data at a half hour frequency using a thermo-logger (DS1923Hygrochron^(r)iButton^(t) Maxim, CA, USA) from April 2018 to May 2019, and the duration was the same as the period of insect collection. The environment data logger device was fixed along with the one of the five canopy FITs in each transect. In total, we used seven variables including annual mean temperature (AMT), annual mean humidity (AMH), annual temperature range (ATR), annual humidity range (AHR), maximum temperature of the warmest month (MTWM), minimum temperature of the coldest month (MTCM), and average elevation (ELE) of each transect as the main environmental filter factors. These data were assembled as a secondary environment matrix prepared for canonical redundancy analysis RDA and detailed data information is listed in Table S1.1.

Data analysis

Insect and tree diversity estimation

For beetles diversity, both canopy and understory FITs within each plot were combined as the smallest sampling unit for diversity estimation, and trees diversity were recorded for each plot. The analyses of α -diversity were the number of species recorded in each sampling unit (Appendix 1 and Appendix 2). Because observed species richness values in field studies are typically an underestimate of the actual number of species occurring at a plot (Colwell and Coddington 1994), sampling completeness and estimated species richness were also calculated using the Chao1 (Chao 1984), Shannon and Simpson diversity estimator based on sample units.

The β -diversity was calculated using the package ‘vegetarian’ (Charney & Record, 2012) in R. The Horn similarity index was used as recommended by Jost (2007) as the only overlap measure that is not disproportionately biased toward rare or common species. This index is considered a true overlap measure that quantifies the overlap of effective species between sampling units (Tuomisto, 2010). The Horn similarity index is defined as:

$$^1\Delta_{\beta} = (\ln 2 - H_{\beta\Sigma\eta\alpha\nu}) / \ln 2$$

where $H_{\beta\Sigma\eta\alpha\nu}$ is the Shannon entropy based on Hill numbers and β -diversity is thus independent of α -diversity (Jost, 2007). We visualized β -diversity as $1 - ^1\Delta_{\beta}$ (i.e., compositional dissimilarity), such that values of 1 indicate complete species turnover between sampling units.

A second similarity matrix was created treating transects as the unit of sampling using the function ‘sim.table’ in the R package ‘vegetarian’. Additionally, geographic distance matrices were constructed at the plot and transect levels using the function ‘earth.dist’ in the R package ‘fossil’ (Vavrek, 2011). Given that we were computing and comparing turnover between identical sampling units in all cases, it is not necessary to consider the species accumulation curve to check whether sampling is adequate (Kemp & Ellis, 2017).

For the plant phylogenetic α and β diversity, the family and genus names of all the enumerated species (215

species in total) in the APG III system were obtained with the R package ‘plantlist’ (Zhang, 2018). Then, their phylogenetic relationships were examined using the online phylomatic tool (Webb & Donoghue, 2005) (www.phylodiversity.net/phylomatic/) based on the Angiosperm consensus tree from Davies *et al.* (2004). Further, similarity matrices were constructed for plant phylogenetic β -diversity (PhyloSor Index, Bryant *et al.*, 2008) with the function ‘phylosor’ in ‘picante’ in R (Kembel *et al.*, 2010). PhyloSor is a modified Sørensen similarity index which quantifies phylogenetic similarity of communities as the proportion of shared phylogenetic branch-lengths between two samples. And the phylogenetic α diversity were calculated with ‘pd’ in ‘picante’ in R (Kembel *et al.*, 2010). ‘pd’ is the sum of the total phylogenetic branch length for the sample.

Spatial scale of species community assembly

To quantify species β -diversity in relation to spatial distance, regional differences, and elevation gradient, the grouped plot-level β -diversity matrix was calculated and then partitioned into various independent spatial components that reflect various β -diversity levels (β -dissimilarity between sampling plots within regions) and δ -diversity (δ -dissimilarity between regions). We thus calculated insect species dissimilarity of (1) plots within transects (β_1 : 40-100 m scale), (2) plots between two neighboring transects within a region (β_2 : 200-300 m scale), (3) plots between two transects covering the highest elevation gradient within a region (β_3 : 1-3 km scale), (4) plots between two neighboring regions (δ_1 : 250-300 km scale), and (5) plots between two regions covering the highest spatial distance (δ_2 : > 500 km scale). We firstly performed two-way ANOVAs to test for differences in Horn similarity values between insects and plants at various spatial scales, and the checking of residuals’ normality and homoscedasticity caused doubt about the robustness of the anova result, so we choose Nonparametric Kruskal–Wallis ANOVA, followed by Scheffe’s post hoc tests. The spatial component of turnover in tree species composition was investigated in an identical fashion. Next, Wilcoxon paired tests were used to assess whether β -diversity was similar for trees and beetles for each respective separation distance (i.e., β_1 , β_2 , β_3 , δ_1 and δ_2). *P*-values were adjusted accordingly (Bonferroni corrections).

Correlation of biotic and abiotic factors to insect community composition

We first used Mantel tests to assess the overall relationship between insect and tree (species and phylogenetic) β -diversity for plot and transect level matrices. Because Mantel tests perform poorly when accounting for the influence of geographic separation on patterns of association (Legendre *et al.*, 2015), we developed an ordination (redundancy analysis-RDA) approach to test tree and tree’s phylogeny combined with environmental variation and spatial distance to explain beetle composition. We used forward and backward selection in an RDA analysis assessing the influence of plant species (Hellinger transformed) and plant phylogenetic turnover on beetle composition (Hellinger transformed). The selection procedure was conducted using the ‘ordistep’ function in ‘vegan’. Variation partitioning analyses through redundancy analysis was used to assess the percentage contribution (both unique and shared) of each group of predictor variables (i.e., plant species composition/plant phylogenetic turnover, environmental, and spatial distance) to explain the variation in abundance-based longhorn beetle species composition. The environmental variables were converted to a distance matrix after log-normalization, while the spatial distance which was captured as latitude/longitude coordination was converted into the Cartesian coordination for the above calculation. Significance of testable fractions (*P* [?] 0.05) were based on 999 permutations. Variation partitioning analyses were performed in R using ‘vegan’ and ‘packfor’ packages.

To further explore the potential mechanism of beetles community assembly pattern, nonmetric multidimensional scaling (NMDS) was conducted to show how dissimilarity changed within and between each sampling transect. NMDS analysis was performed using ‘metaMDS’ in ‘vegan’. The multi response permutation procedure and mean dissimilarity matrix (MRPP) algorithm was employed to ascertain if the mean distance within each group, which was defined as mean elevation of the transect, was significantly different from the mean distance of all the plots based on 999 permutations. To quantify the homogeneity of dissimilarity variances within each transect, the variances of the dissimilarity matrix were compared using the ‘betadisper’ method (Anderson, 2006). This test is analogous to Levene’s test for homogeneity of ANOVA variances. Finally, we used analysis of similarities (ANOSIM) to test if there was a significant difference between transects

(Clark *et al.* , 1999; Warton *et al.* , 2012). The P -value was also obtained based on 999 permutations.

Finally, we introduced linear mixed-effect model to analyze the effect of plant α -diversity and phylogenetic α -diversity, environmental variability and geographical variability on beetle α -diversity, respectively. In total we considered 4 groups of datasets: set 1) beetles standardized Shannon diversity (BeeShannon_stdz); set 2) plant standardized α -diversity metrics, which including standardized Chao1 diversity (PlaChao1_stdz), standardized Simpson diversity (PlaSimpson_stdz), standardized Shannon diversity (PlaShannon_stdz) and standardized phylogenetic α -diversity (PlaPD_stdz); set 3) standardized environmental variability, which including standardized AMT (AMT_stdz), standardized ATR (ATR_stdz) , standardized AMH (AMH_stdz), standardized AHR (AHR_stdz), standardized MTWM (MTWM_stdz) and standardized MTCM (MTCM_stdz); set 4) standardized geographical variability, which including standardized ELE (ELE_stdz) and standardized Latitude (Latitude_stdz). Beetles standardized Shannon diversity were treated as response variable and site names were treated as random effect, and the remaining variables including set 2), set 3) and set 4) were treated as fixed effect. Moran's I correlograms were built to evaluate the degree of spatial autocorrelation of the variables in relation to geographic distances and we found no significant positive spatial autocorrelation for these variables. For each dataset, we first fitted one global model including all the fixed effects and either a random intercept and slope (BeeShannon_stdz ~ PlaPD_stdz + PlaChao1_stdz + PlaSimpson_stdz + PlaShannon_stdz + ELE_stdz + AMT_stdz + ATR_stdz + AMH_stdz + AHR_stdz + MTWM_stdz + MTCM_stdz + Latitude_stdz + (1|SiteName)). We then used the 'dredge' function in the 'MuMIn' R package to fit all the possible combinations of models nested in the global models. Model selection was performed using an Information-Theory approach (Burnham and Anderson, 2002), based on Akaike Information Criterion values corrected for small sample size (AICc). For each replication we fitted and ranked the global model and the submodels but only the top ranking model were chosen. We determined conditional and marginal R^2 following the method of Nakagawa and Holger (2013) to estimate the explained variance of the fixed and random effects in the LMM. Conditional R^2 represents the variance explained by both fixed and random effects, and marginal R^2 refers to the variance explained by fixed effects only. The difference between these two components gives the R^2 of the random effect. All candidate models with $\Delta < 2$ are presented (Burnham and Anderson, 2002). All analyses were performed in R 3.4.5 (R Core Team, 2018).

Results

Tree and beetle composition

A total of 3290 longhorn beetle singletons were collected and assigned to 296 species as determined by specialists (see Appendix file 1). It included 1409 individuals of 212 species in tropical Bubeng, 1630 individuals of 83 species in subtropical Xujiaba, and 251 individuals of 16 species in the cold temperate Yulong mountain. The five most abundant longhorn beetle species which accounted for 49% of total individuals collected, in order of importance, were *Demonax cf. testaceoannulatus* , *Perissus* spec. 10, *Demonax* spec. 40, *Parachlytus excellens*, and *Pidonia* spec. 3.

A total of 2184 trees individuals from 215 species were recorded (see Appendix file 2). This included 1180 individuals of 137 species in Bubeng (tropical), 795 individuals of 60 species in Xujiaba (subtropical), and 209 individuals of 18 species in the Yulong mountain (temperate).

Species community assembly change with different spatial scales

Beetles β -diversity between sampling unites was significantly lower at each successive spatial scale (i.e., as the spatial distance between sampled FITs increased) (KW chi-square = 797.10, $df = 4$, $P < 0.001$, Fig. 2-I) than that of the tree except at the second narrowest scales, i.e., β_2 (Fig. 2-I). The general pattern of tree species turnover between sampling squares was similar to that of the beetles (KW chi-square = 956.20, $df = 4$, $P < 0.001$, Fig. 2-I). For the beetles group, the largest increase in β -diversity was evident between the plot (i.e., β_2 : 200-300 m apart) and transect (β_3 : 1-3 km apart) scale (Fig. 2-I) and these two scales had no significant difference with each other ($P > 0.05$). However, the largest increase in β -diversity for the tree group was only evident at the transect (β_3 : 1-3 km apart) scale (Fig. 2-I). The Wilcoxon paired t -tests

showed that tree communities had a significantly higher β -diversity value than beetles at the scales of β_1 , β_3 , and δ_1 ($Z = 3.732, 6.275$, and 10.35 , respectively; $P < 0.001$), but significantly lower β -diversity value at the scale of β_2 ($Z = 6.275$; $P < 0.001$) (Fig. 2-I). Thus, trees and beetle compositional turnover showed a roughly similar trend with some small differences along the increased spatial distance.

At the regional scale, tree and beetle β -diversity showed an asynchronous decreasing pattern from the tropical to subtropical and cold temperate regions (Fig. 2-II). For both the tree and beetle groups, the β -diversity among the three regions had significant differences (trees: KW chi-square = 11.5, $df = 2$, $P < 0.01$; beetles: KW chi-square = 15.2, $df = 2$, $P < 0.001$) (Fig. 2-II). The Wilcoxon paired t -tests showed that the tree community β -diversity was significantly higher than that of beetles at all three regions ($Z = \text{Bubeng:}7.364$, $\text{Ailaoshan:}8.783$, $\text{Lijiang:}6.108$; $P < 0.001$) (Fig. 2-II). Furthermore, at the transect scale of each region, the β -diversity of both the tree and beetle groups showed a generally decreasing pattern with increasing elevation (trees: KW chi-square = 56.4, $df = 8$, $P < 0.001$; beetles: KW chi-square = 69.5, $df = 8$, $P < 0.001$) (Fig. 2-III). However, the pairwise comparison of β -diversity between the tree and beetle groups at each transect did not show a significant difference between each other ($P > 0.05$) (Fig. 2-III) except for all comparisons in the subtropical Yulong mountain and transects of 800 and 1000 m in tropical Bubeng.

Correlation of biotic and abiotic factors to insect community composition

The ordination of FIT plots in the beetle species community applying the NMDS method yielded a significant two convergent solution (stress value = 0.04) after 20 iterations through a Bray-Curtis distance measure and clearly separated the groups according to their respective elevation (Fig. 3). The plots within the tropical Bubeng category of low elevation were slightly scattered. However, the plots in the middle and higher elevation categories showed an obviously clustered pattern. Plots from different elevation classes could be very dissimilar and the ordination ellipses for each elevation class did not overlap much. Therefore, the beetle species composition of the different elevations does not converge to the same scores (Fig. 3).

The results of a PERMANOVA model showed that major variations were distributed across the three most important environmental explanatory variables, including ELE, MTCM, and AMT, which together explained 45% of the variation in beetle species composition space.

The Mantel tests showed that β -diversity of beetles was significantly associated with tree species composition at all sampling plots at the macro scale (Table S1.2). Variation partitioning of RDA revealed that selected tree species and tree phylogenetic β -diversity separately explained 64% and 62% of the variation, respectively, with the joint effect of geographical distance and environment in beetle species composition at the macro scale. The pure effect of tree species and tree phylogenetic β -diversity was 10% and 6%, respectively, while the pure effect of the environment was 5% (Fig. 4-II) and 3% (Fig. 4-I) separately. However, the pure effect of geographic distance was very small at 1% (Fig. 4-II) and 0 (Fig. 4-I). The remaining unexplained variation of the main matrix was 28% (Fig. 4-II) and 31% (Fig. 4-I), respectively.

Through analysis of linear-mixed effect model, we found that the best model (i.e., delta AIC is equal to 0) retained both plant diversity and environment variables with significant correlation. All residuals of the models showed no significant spatial patterns ($p = 0.8351$), indicating that our mixed model explicitly incorporated the spatial dependence between plots, transects and regions. The best model showed that Fixed effects (i.e., lakes nested in regions) explained considerable variations of the models, with 65.08% (Tables 1). And random effect explained 32.28% (Tables 2). For the environment metrics, beetles standardized Shannon diversity is positively correlated with AHR_stdz, AMH_stdz, MTCM_stdz and MTWM_stdz. But negatively correlated with ATR_stdz. And for the plant diversity metrics, beetles standardized Shannon diversity is negatively correlated with PlaSimpson_stdz and PlaPD_stdz, but positively correlated with PlaChao1_stdz and PlaShannon_stdz.

Discussion

Our results reveal that changes in the composition of insect herbivore communities track changes in plant species community composition and plant phylogenetic turnover at multiple spatial scales within the Yunnan

province. Three lines of evidence suggest that the positive association of plant and insect turnover partly results from insect host specialization. First, from Fig. 2-I we can see that both plant and insect communities exhibit high levels of β -diversity across remarkably short spatial scales (i.e., β_1 : 40-100 m). This is not a pattern that is expected if compositional co-variation of these groups results from shared bio-geographical histories or parallel responses to climatic gradients, but instead points to host specificity as the underlying process, suggesting this is the scale where biotic interaction plays an important role in the community assemblage through ecological processes (also see Chesson, 2000). Second, we can see that pure plant species composition as a general control on wood boring longhorn beetle community composition accounted for 10% percent of the explained variation (Fig. 4-II). This explanation rate means that after removing the effect of geographic distance and environment, the insects and plants are still positively correlated, indicating that host plant specificity of Cerambycidae is one of the driving factors of the presented pattern. Finally, from Table 2 we can see that beetles standardized Shannon diversity is significantly positively correlated with standardized plant Chao1 and Shannon diversity.

To further confirm the relationship between plants and insects, it is important to improve the estimation of host specificity and species richness through correction for plant phylogenetic relatedness (Ødegaard *et al.*, 2005). Our study demonstrates that the phylogenetic diversity of plant communities had a strong positive influence on the species richness of Cerambycidae communities, and the pure effect of this on the Cerambycidae distribution was 6% percent (Fig. 4-I). The strong influence of plant phylogenetic composition on insect community composition suggests that insects tend to either be specialized on plant hosts at a supra-specific level (Novotny *et al.*, 2002), or that insects are selecting host plants on the basis of phylogenetically conserved traits (Ødegaard, 2006; Whitfield *et al.*, 2012). There is growing appreciation that long-term co-evolutionary interaction across trophic levels plays a major role in driving the composition and structure of communities (Futuyma & Agrawal 2009; Dinnage *et al.*, 2012). Evidence of these reciprocal evolutionary pathways (Wheat *et al.*, 2007; Fordyce 2010; Wagner 2000) has supported the view that phylogenetic information is embedded in the way plant–insect interactions shape community structure and evolution (Agrawal, 2007). Our study provides the first evidence in a natural system that plant phylogenetic β -diversity is highly correlated with Cerambycidae β -diversity, suggesting that the turnover in host-plant lineage structures Cerambycidae assembly in space.

In addition to the plant species composition and phylogeny determining the community assemblage of wood boring longhorn beetles, the environment also played an important role in influencing wood boring longhorn beetle community assemblage. From Fig. 2-I we can see that the relationship between plant and insect β -diversity holds at both regional (i.e., δ_1 : 250-300 km, δ_2 : 500 km) and local (i.e., β_1 : 40-100 m) scales. The local scale co-occurrence pattern is not likely resulted from the environmental gradients cause it varied slightly, however, with the increase of the spatial extent, the matched pattern gradually disappeared but recurrent at macro-scale, which lurking with the mechanism that the effects of biotic interaction is gradually averaged out with the scale aggregation, however, the effect of macroclimatic gradient become more and more obvious, which revealed that the highly associated pattern at coarse-scale might be the result of parallel responses of insects and plants to macroclimatic gradients. Second, from the NMDS analysis (Fig. 3), ELE, MTCM, and AMT together explained 45% of the variation in beetle species composition. All of these suggested that climate gradients impose constraints on Cerambycidae species richness and abundance. Third, the isolated effect of environment to Cerambycidae distribution accounted for 5%, which had a distinct advantage compared with spatial distance and the latter only accounted for 1% as the pure effect (Fig. 4). Finally, the best linear mixed effect model showed that beetles standardized Shannon diversity is significantly positively correlated with standardized AHR, AMH, MTCM and MTWM. But negatively correlated with standardized ATR (Table 2).

From the above analysis, we can conclude that the dominating mechanisms of insects and tree distribution patterns are related differently at different spatial scales. On the macro/regional scale, the environmental factors, including AMT and MTCM, induced by elevation and latitudinal gradient are the major driving forces on longhorn beetle β -diversity. However, on the micro/local scale, tree diversity and phylogenetic relationship affect the β -diversity much more. Considering the huge possibility of β -diversity scaling rela-

tionships varying widely across disparate organisms with different dispersal ability (Soininen *et al.* , 2007), spatial scales are the most important prerequisites to quantify the relative effects of environmental factors on longhorn beetle species distribution in the present study. As the results showed (Fig. 2-II & III), β -diversity had no significant differences for trees between the tropics and subtropics, and for beetles between the subtropics and the temperate regions at the regional scale. When focusing on local scale comparisons, a completely different pattern emerged. Mechanistically, β -diversity at local and regional scales is typically ascribed to differing processes operating at different spatial scales. These mechanisms can help inform our a priori expectations of how β -diversity might vary among sampling units drawn at each of these scales. Usually, environmental filtering should dominate over dispersal limitation at larger spatial scales, and the local assemblages are mainly influenced by ecological processes such as species interactions, stochastic occupancy, resource specificity, and niche requirements (Whittaker *et al.* , 2001; Ricklefs, 2004; Hortal *et al.* , 2010). The climate gradients along the latitude are known to be generally unvarying and result in stabilized patterns, whereas the different ecological processes interact with each other at a local scale leading to the β -diversity of various organism exhibiting divergent distribution patterns. Secondly, the results showed that the dispersal capacity would affect the ability of organisms to colonize suitable environments. Trees, compared with insects, showed that low average rates of dispersal can be expected to show lower average geographic range sizes and higher rates of local endemism, resulting in higher rates of species turnover from local to regional scales (Qian, 2009; Baselga *et al.* , 2012). Compared with the highest β -diversity of tree organisms that disperse via seeds (Soininen *et al.* , 2007), short-lived insect assemblages, including wood boring beetles, would not be affected by dispersal limitation to some extent (Novotny *et al.* , 2007; Hulcr *et al.* , 2008).

In conclusion, we compared the β -diversity in wood boring longhorn beetles and plant communities from the tropics to the cold temperate regions. The prerequisites of insect and plant interaction for determining the wood boring longhorn beetles existence at any spatial scales are definite and clear. Irrespective of whether from a micro/local or macro/regional spatial scale, β -diversity of longhorn beetles was related to plant richness and phylogenetic diversity to some extent, while at micro/local scale, longhorn beetles exhibits its strongest biotic niche relations (in affecting /or being affected by plant species), but with the increase of spatial resolution, their relationship are expected to be averaged out at landscape scale, and macroclimatic heterogeneity will dominate the community assemblage processes. Besides, the relative lower β -diversity of beetles than that of the plant communities from the tropics to temperate regions was controlled by their stronger dispersal ability.

Data Accessibility:

Cerambycidae data files: Dryad doi:<https://doi.org/10.5061/dryad.s7h44j136>

Plant species data files: Dryad doi:<https://doi.org/10.5061/dryad.s7h44j136>

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Figure captions:

Fig. 1 : Geographical location of the three sampling regions of Yunnan province, Southwest China.

Fig. 2 : Insect species (dark grey) and plant species (light grey) turnover (1-Horn similarity) between FIT sampling plots (25 x 20 sq. m) at different distances in three regions of Yunnan province, SW China. **Fig. 2-I :** The 1-Horn similarity value was calculated as turnover within (1) plots within transects (β_1 : 40-100 m scale), (2) plots between two neighboring transects within a region (β_2 : 200-300 m scale), (3) plots between two transects covering the highest elevation gradient within a region (β_3 : 1-3 km scale), (4) plots between two neighboring regions (δ_1 : 250-300 km scale), and (5) plots between two regions covering the highest spatial distance (δ_2 : > 500 km scale). **Fig. 2-II :** Insect species and plant species β -diversity (1-Horn similarity) distribution at different sampling regions in the Yunnan province, which included Bubeng (tropical region), Ailaoshan (subtropical region), and Lijiang (temperate region). **Fig. 2-III:** Insect species and plant species β -diversity (1-Horn similarity) distribution at different transects of the study area in the Yunnan province.

White dots represent medians, thick black bars represent first quartiles, and thin black lines represent the range. The shape of each plot shows the frequency distribution of the data. Letters indicate significant differences between separation distances within a group (insects or plants). Nonparametric Kruskal–Wallis ANOVAs were conducted to test for differences in Horn similarity values between insects and plants at various spatial scales and different region. *, **, and *** indicate significant differences in Horn similarity between insects and plants at each spatial scale and region.

Fig. 3 : Non-metric multidimensional scaling (NMDS) ordinations for beetle assemblages in different sampling plots. The red points are sampling plots, different numbers in the square represent different transects (1: Bubeng 600 m; 2: Bubeng 800 m; 3: Bubeng 1000 m; 4: Ailaoshan 2200 m; 5: Ailaoshan 2400 m; 6: Ailaoshan 2600 m; 7: Lijiang 3200 m; 8: Lijiang 3400 m; 9: Lijiang 3600 m). ELE: elevation; MTCM: minimum temperature of the coldest month; MTWM: maximum temperature of the warmest month; AMT: annual mean temperature; AMH: annual mean humidity; AHR: annual humidity range; ATR: annual temperature range. The colored ellipses are 95% confidence intervals of species centroids for each treatment level [‘ordiellipses’ (Oksanen *et al.* , 2013)]. Variables with a Pearson’s correlation coefficient at $P < 0.05$ are shown. Two convergent solutions were found after 20 iterations with a stress value of 0.0452 for longhorn beetles using the Bray-Curtis distance calculation method.

Fig. 4 : Variation partitioning results of redundancy analyses testing for the influence of plant species composition and phylogenetic turnover on wood boring longhorn beetle composition in the Yunnan province, SW China. **Fig. 4-I** represents the plant phylogenetic β -diversity combined with environmental factors and spatial distance to explain beetle composition. **Fig. 4-II** represents the plant species β -diversity combined with environmental factors and spatial distance to explain beetle composition. The pure effect of each counterpart is represented by areas with the letters (A; B; C; a; b; c). The overlapping areas represent the joint effect of the corresponding factors (D; E; F; G; d; e; f; g).

Fig. 1

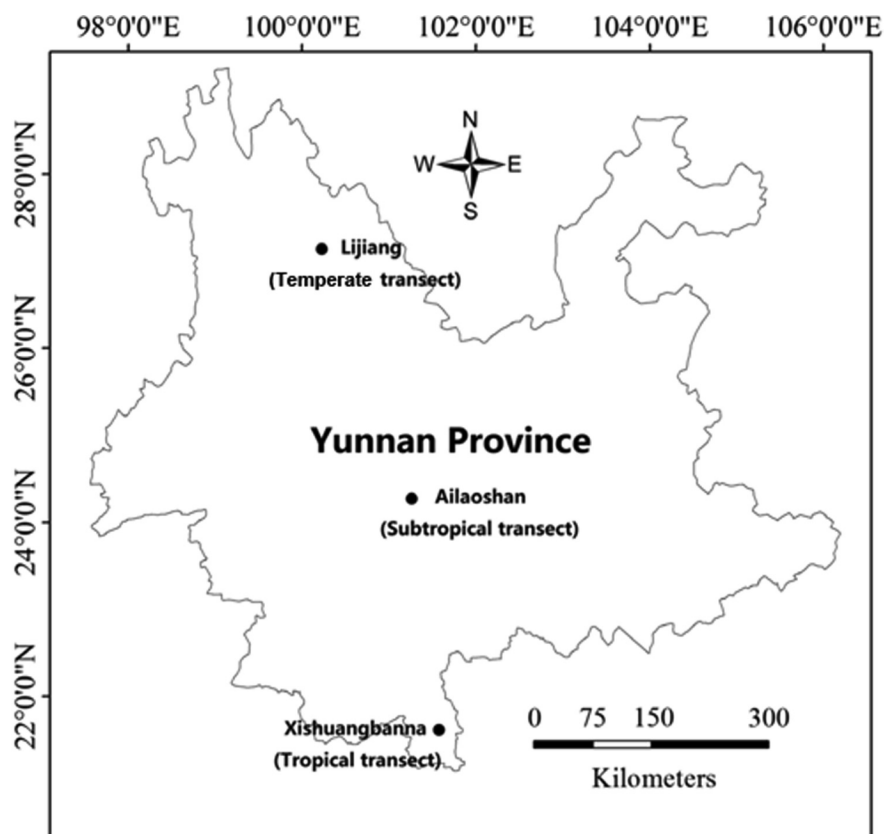


Fig. 2

Hosted file

image2.emf available at <https://authorea.com/users/308377/articles/439391-scale-dependent-contribution-of-biotic-and-abiotic-factors-to-longhorn-beetles-cerambycidae-community-composition-variation-at-the-indo-burma-biodiversity-hotspot>

2a

Fig. 3

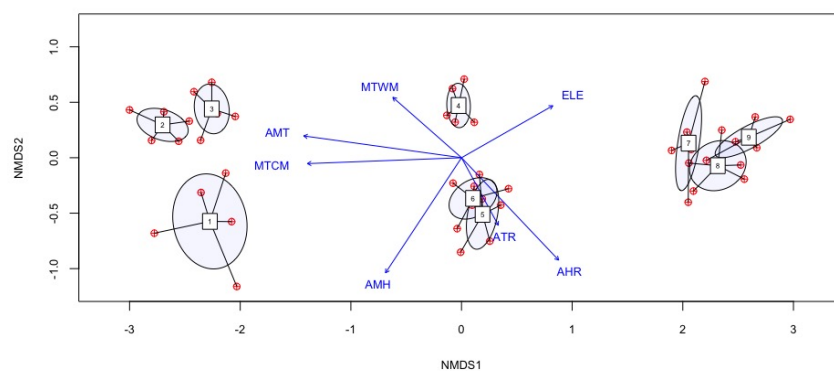


Fig. 4

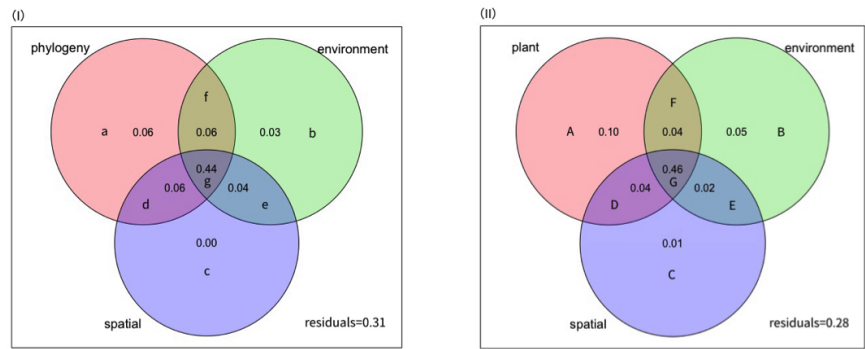


Table 1. Comparison of linear mixed-effect model fitted to the data on beetle Shannon diversity across 3 regions in Yunnan province, SW China. AICc means Akaike Information Criteria (Corrected). Delta means AICc Score differences. Weight refer to Akaike weights. Models with delta < 2 were presented and the top ranking model was the best. Conditional R^2 represents the variance explained by both fixed and random effects (total R^2), and marginal R^2 refers to the variance explained by fixed effects only (fixed R^2). The difference between these two components gives the R^2 of the random effect (random R^2). The full model was: BeeShannon_stdz ~ PlaPD_stdz + PlaChao1_stdz + PlaSimpson_stdz + PlaShannon_stdz + ELE_stdz + AMT_stdz + ATR_stdz + AMH_stdz + AHR_stdz + MTWM_stdz + MTCM_stdz + Latitude_stdz + (1|SiteName).

Model parameters	AICc	delta	weight	R^2	m	R^2 c
AHR_stdz + AMH_stdz + ATR_stdz + MTCM_stdz + MTWM_stdz + PlaChao1_stdz + PlaPD_stdz + PlaShannon_stdz + PlaSimpson_stdz + (1 SiteName)	53.46	0.00	0.22	0.6508	0.9736	
AHR_stdz + AMH_stdz + MTCM_stdz + MTWM_stdz + PlaChao1_stdz + PlaPD_stdz + PlaShannon_stdz + PlaSimpson_stdz + (1 SiteName)	54.10	0.64	0.16	0.6704	0.9711	

Model parameters	AICc	delta	weight	R ²	m	R ² c
AHR_stdz + AMH_stdz + ATR_stdz + Latitude_stdz +MTCM_stdz + MTWM_stdz + PlaChao1_stdz+ PlaPD_stdz + PlaShannon_stdz+ PlaSimpson_stdz + (1 SiteName)	54.27	0.82	0.15	0.6303	0.9571	
AHR_stdz + AMH_stdz + Latitude_stdz +MTCM_stdz + MTWM_stdz + PlaChao1_stdz+ PlaPD_stdz + PlaShannon_stdz+ PlaSimpson_stdz + (1 SiteName)	54.87	1.41	0.11	0.6467	0.9540	
AHR_stdz + AMH_stdz + ATR_stdz + AMT_stdz +MTCM_stdz + MTWM_stdz + PlaChao1_stdz+ PlaPD_stdz + PlaShannon_stdz+ PlaSimpson_stdz + (1 SiteName)	55.19	1.73	0.09	0.6447	0.9681	

Model parameters	AICc	delta	weight R ² m R ² c
AHR_stdz + AMH_stdz + ATR_stdz + MTCM_stdz + MTWM_stdz + PlaChao1_stdz + PlaShannon_stdz + PlaSimpson_stdz + (1 SiteName)	55.52 95.27 55.30	1.81 1.83 1.84	0.09 0.6508 0.9752 0.09 0.6681 0.9731 0.09 0.6687 0.9733
AHR_stdz + AMH_stdz + MTCM_stdz + MTWM_stdz + PlaChao1_stdz + PlaShannon_stdz + PlaSimpson_stdz + (1 SiteName)			
AHR_stdz + AMH_stdz + ATR_stdz + MTCM_stdz + MTWM_stdz + PlaChao1_stdz + PlaPD_stdz + PlaShannon_stdz + PlaSimpson_stdz + ELE_stdz + (1 SiteName)			

Table 2. Summary of best model explaining variation on beetle Shannon diversity across 3 regions in Yunnan province, SW China. The table presented Slope, t -value and p-value of fixed effects (Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1).

Fixed effects	slope	df t -value p-value
(Intercept)	0.3051	2.9209 0.619 0.5810
AHR_stdz	0.1284	863.3426 4.429 1.07e-05 (***)
AMH_stdz	0.3432	818.5499 5.389 9.26e-08 (***)
ATR_stdz	-0.1303	862.2722 -1.655 0.0984 (.)
MTCM_stdz	0.4908	861.4571 5.626 2.49e-08 (**)
MTWM_stdz	0.8436	833.4331 21.079 < 2e-16 (*)
PlaChao1_stdz PlaPD_stdz PlaShannon_stdz PlaSimpson_stdz	0.1712 -0.0285 0.5771 -0.4016	861.2401 11.864 < 2e-16 (*)

Table S1.1 Parameters of measured climatic variables of each FIT plot among the three sampled regions of Yunnan province, S China.

	Annual mean temperature	Annual mean temperature	Annual tempera- ture range	Annual mean humidity	Annual humidity range	Maximum tempera- ture of the warmest month	Minimum tempera- ture of the coldest month	Average elevation
Bubeng	Bubeng	Bubeng						
BB600	BB600	19.37938	27.245	93.716613	75.19	27.42	9.32	705.2
BB800	BB800	21.45051	28	86.773607	81.2	35.5	8.5	838.2
BB1000	BB1000	20.26883	23.5	87.333482	68.2	30	7.5	993.0
Ailaoshan	Ailaoshan	Ailaoshan						
ALS2200	ALS2200	14.33506	40.968	85.655087	84.996	40.653	-0.913	2368.2
ALS2400	ALS2400	13.00004	39.55	87.532566	91.187	34.637	-0.922	2501.0
ALS2600	ALS2600	11.69748	41.564	89.456637	97.278	32.128	-1.466	2692.2
Lijiang	Lijiang	Lijiang						
LJ3200	LJ3200	8.928336	27.18	68.33484	98.325	26.117	-1.327	3227.4
LJ3400	LJ3400	7.551954	30.29	73.91349	96.856	24.641	-4.593	3332.6
LJ3600	LJ3600	6.162154	39.73	76.384518	94.258	21.616	-7.497	3551.6

Table S1.2 Correlation coefficients and p -values from the Mantel tests exploring the association of insect and plant β -diversity (estimated as “1-Horn similarity”) in the Yunnan province, Southwest China. Insect β -diversity was significantly associated with plant species except in the temperate region but not for phylogenetic β -diversity in all three sampling subregions.

		FIT-level dataset (n_{FIT} = 45)	FIT-level dataset (n_{FIT} = 45)	Site-level dataset (n_{site} = 9)	Site-level dataset (n_{site} = 9)
		r	p	r	p
Macro	Macro	0.7944	0.001	0.9145	0.001
Beetles–Plant	Beetles–Plant				
species	species				
Beetles–Plant	Beetles–Plant				
phylogenetic	phylogenetic				
Tropics	Tropics				
(Bubeng)	(Bubeng)				
Beetles–Plant	Beetles–Plant				
species	species				
Beetles–Plant	Beetles–Plant				
phylogenetic	phylogenetic				
Subtropics	Subtropics				
(Ailaoshan)	(Ailaoshan)				
Beetles–Plant	Beetles–Plant				
species	species				
Beetles–Plant	Beetles–Plant				
phylogenetic	phylogenetic				
Temperate	Temperate				
(Lijiang)	(Lijiang)				
Beetles–Plant	Beetles–Plant				
species	species				
Beetles–Plant	Beetles–Plant				
phylogenetic	phylogenetic				

	FIT-level dataset (n_{FIT} = 45)	FIT-level dataset (n_{FIT} = 45)	Site-level dataset (n_{site} = 9)	Site-level dataset (n_{site} = 9)
	-0.7669	1	-0.9118	1
	0.5673	0.001		
	-0.4295	1		
	0.7915	0.001		
	-0.6318	1		
	0.1132	0.135		
	-0.2754	0.993		

Table S1.3 Results of redundancy analyses testing for the influence of plant species composition and phylogenetic turnover on wood boring longhorn beetle species composition in the Yunnan province, SW China. The results showed that the abundance of the 16 most important plant species explained 64% of variation in wood boring community composition, and 16 phylogenetic PC axes (accounting for 62% of variation in plant phylogenetic turnover between sampling units). F statistics to test the significance of variables were calculated using the iterative ‘anova.cca’ in ‘vegan’ using R.

		Number of species/phylogenetic PC axes included	F	P	Proportion explained
Insects	Plant species	16/45 (1,2,3,4,5,6,7,9,10,11,12,13,15,16,17,40)	2.349	0.001	0.64
Insects	Spatial	6/6 (1,2,3,4,5,6)	3.191	0.001	0.53
Insects	Environment	7/7 (1,2,3,4,5,6,7)	4.753	0.001	0.57
Insects	Plant phylogenetic	16/45 (1,2,3,22,29,30,31,33,35,37,38,40,41,42,43,45)	2.032	0.001	0.62
Insects	Spatial	6/6 (1,2,3,4,5,6)	3.191	0.001	0.57
Insects	Environment	7/7 (1,2,3,4,5,6,7)	4.753	0.001	0.57