# Habitat is More Important Than Climate and Animal Richness in Shaping Latitudinal

## **3 Variation in Plant Diversity**

4 Jie Gao<sup>1</sup>, Marc Bogonovich<sup>2</sup>, Xue Du<sup>1</sup>, Yanhong Liu<sup>1</sup>

5 <sup>1</sup>Forestry College of Beijing Forestry University, China.

6 <sup>2</sup> Indiana University, America.

7 Abstract: Species data of 249 National Nature Reserves in China was used to identify 8 potential underlying drivers of latitudinal gradients in plant diversity. We used generalized 9 linear models (GLMs) to assess the correlations between predictor and response variables. We also used SAM (Spatial Analysis in Macroecology) to eliminate 10 autocorrelation along each of the 249 studied locations. We used the Akaike information 11 12 criterion (AICc; Montoya et al. 2007) to select the independent variables were those included in the best models from different combinations of climate, habitat and animal 13 14 variables. Variance partitioning was used to decompose the variation in plant richness 15 across different taxonomic levels among the three groups of predictors. We found that: 16 Total plant species, gymnosperms, angiosperms and ferns showed significant latitudinal trends in richness (p < 0.001). Water-energy and habitat variables generally explained 17 18 more variation in richness across different plant groups than did animal richness. Annual 19 precipitation was selected as the best water-energy variable across different taxonomic 20 plants groups, soil PH and elevation range were selected as the best habitat variables across different taxonomic plant groups. The independent effects of habitatvariables were 21 22 higher than that of water-energy and animal variables across different taxonomic plants groups. Water-energy, habitat heterogeneity, and animal variables explain 48.8% of the 23 24 variation in total species richness, 28.2% in gymnosperm richness, 44.2% in angiosperm richness, and 38.9% in fern richness.Plants showed significant latitudinal trends in 25 26 richness (p < 0.001). Water-energy and habitat variables generally explained more 27 variation in richness across different taxonomic plants groups than did animal variables. 28 The independent effects of habitat variables were higher than those of water-energy and 29 animal variables across different taxonomic plants groups.

- 30 KEYWORDS
- 31 Species richness; Latitudinal gradients; water-energy; habitat; animal richness

32

### 33 1 Introduction

Understanding the processes governing variation in species diversity across space remains a fundamental challenge in ecology (Ricklefs, 2004; Lomolino et al., 2010; 36 Zellweger et al., 2017). In the past decades, hundreds of hypotheses have been proposed 37 to explain spatial variation in species diversity at broad scales (Palmer, 1994; Wiens & Donoghue, 2004; Dalby et al., 2014; Stein et al., 2014). Most of these efforts are focused 38 specifically on understanding the drivers of the latitudinal gradient in diversity (LGD), or 39 40 the observation that diversity peaks at the equator (Kreft, H., & Jetz, W. 2007). While much 41 attention has been given to the LGD, it is still not clear what the fundamental drivers of this 42 pattern are. This is a significant gap in our knowledge, since developing better models and 43 hypotheses for the LGD is essential for the management and preservation of biodiversity.



44

Fig. 2. Latitudinal gradient in species richness of total plant species, gymnosperms,
 angiosperms and ferns. The rs-values represents the correlation coefficient.

47

48 Many hypotheses related to the latitudinal gradient in diversity focus on the role of large scale climatic drivers. Annual precipitation and temperature, in particular, are highly 49 50 correlated with latitude (Gaston 2000), and are thus expected to underlie these relationships. This hypothesis assumes that the establishment and persistence of species 51 52 is dictated by species' physiological tolerances to stress. However, fractions of variation in species richness that remain unexplained after assessing climatic drivers suggest the 53 54 presence of additional drivers of the LGD. Niche-based processes relating to habitat filtering unrelated to continental climatic gradients are also important (CITE). Just as 55 56 species have different tolerances to climate, species may sort along gradients of soil productivity or light availability. This, in turn, results in spatial heterogeneity in community
composition (Chase & Myers, 2011; Zellweger et al., 2017).

59 Habitat heterogeneity should improve the probability of species coexistence, areas 60 with high heterogeneous habitat should be more capable for providing shelter and refuge during periods of extreme environmental conditions, and guarantee the persistence of 61 62 more species (Tews et al., 2004; Kallimanis et al., 2010; Fjeldså et al., 2012). Habitat 63 habitat may also increase speciation resulting from isolation or adaptation to complex 64 environmental conditions (Hughes, & Eastwood, 2006). Topographic factors influences 65 water availability and soil biogeochemical processes and should thus filter communities based on limiting soil water and nutrient availability (Baldeck et al., 2013). Soil pH is 66 related to the abundance of toxic elements and nutrients. Topography and soil pH should 67 68 thus primarily affect plant beta diversity (Baldeck et al., 2013; Zellweger et al., 2017). 69 Water-energy theory proposes increasing solar energy (with an abundance of water) at 70 low latitudes will causes increased net primary productivity and the higher the net primary 71 productivity, the more plant species there will be in an area (i.e. Evans et al., 2008). 72 However, the observed changes in species richness in an area along the latitude are 73 either too small or in the wrong direction to account for the observed changes (Cardillo et 74 al. 2005).

In general, climatic and topographical predictor variables are rather coarsely resolved when studying the effects of environment on species diversity, whereas effects of biotic interactions on beta diversity are often not considered (Zellweger et al., 2017). Ecological species interactions such as competition, predation, mutualism, and parasitism could significantly promote species coexistence (Carstensen, & Olesen, 2015; Zellweger et al., 2017).

81 In addition to the abiotic environment, biotic interactions, both within and among 82 trophic levels, are likely to be important factors driving diversity. In the process of long-term survival and development, animals and plants have formed complex 83 84 interdependencies and mutualistic relationships. Plants provide resources that many animals depend on (CITE). Likewise, many insects and birds provide essential pollination 85 services for plants (CITE). Thus, investigating whether plant species richness is related to 86 animal richness is important for teasing apart community assembly mechanisms in plant 87 communities (Lee & Rotenberry, 2005; Ponisio, M' Gonigle, & Kremen, 2016; Zellweger et 88 89 al., 2017).

The main purpose of our study was to elucidate the relationships between climate, habitat, and biotic variables, and to identify the critical factors affecting the distribution of plant diversity along latitudinal gradients. Analysis of different plant taxonomic groups allowed us to investigate how the effects of various predictors differ between taxa with different ecological requirements. We aim to answer the following questions relating to plant community assembly, and their involvement in driving latitudinal gradients in diversity. i) Are there important differences in latitudinal gradients in species richness
between angiosperms, gymnosperms, and ferns? ii) Are diversity patterns relating to
latitude correlated with climatic, habitat, and biotic variables? And iii) what are the
differences in the strength of correlations between these variables.

100

#### 101 2. Materials and Method

#### 102 2.1 Study site and Species data

We used data obtained from regional plant floras conducted within national nature reserves in China that cover a total latitudinal range of 40 degrees. Across this gradient, annual precipitation ranges from a low of 40 mm to a high of 3200 mm, and temperate ranges from a low of -12°C to a high of 27 °C. This sampling gradient also spans four major forest types, including temperate broadleaf forest, temperate coniferous forest, tropical/subtropical forest, and grasslands. Floras were conducted from 1984 to 2017, and included sampling of all vascular plant species.

We compiled data from regional plant floras of 249 national nature reserves (Fig.1) from 110 newly published Scientific Investigation Reports (Appendix Table. S1 and Fig. S1), and 111 are by far the most comprehensive documentation of plants in China in National Nature 112 Reserves. These reserves covered four types of forests according to the classification of 113 the World Wildlife Foundation (http://worldwildlife.org) (Gao et al. 2017): temperate 114 broadleaf and mixed forests, tropical and subtropical moist broadleaf forests, temperate 115 116 coniferous forests and grasslands, covering a latitudinal gradient of 40° from tropical rain forests to boreal forests and 166,327 km<sup>2</sup>. Species lists of all plant types (Gymnosperms, 117 Angiosperms, Ferns and all plant species) in a definite region are provided in these 118 reports. Species richness, animal richness (Mammals, birds, insects), area, longitude, 119 latitude and elevation range (Max elevation - Min elevation) were also obtained from these 120 publications (Table.S1). 121



123 Fig.1. Locations of the studied area.

124

#### 125 2.2 Environmental predictor variables

We used climate and habitat variables that we expected to be strongly correlated with 126 latitudinal variation in plant species richness. Climatic variables included mean annual 127 temperate and precipitation, which were obtained from the WorldClim database using a 128 10 km spatial resolution (Fick, S.E. & R.J. Hijmans, 2017). Local habitat variables included 129 elevation and soil pH, which were obtained from the scientific reports and the harmonized 130 world soil database, respectively. Biotic variables included mammal, insect, and bird 131 132 species richness, obtained from associated faunal surveys conducted at the same 249 locations mentioned above. Finally, sampling area was included to control for variability in 133 reserve size. This was important because species richness increases with sampling area. 134

135 Strong multicollinearity can result in the exclusion of causal ecological variables from examined models (Heikkinen et al. 2005). In order to avoid strong multicollinearity among 136 137 the environmental variables, we selected annual mean temperature, annual precipitation our water-energy variables, 138 as which obtained from WorldClim database 139 (http://www.worldclim.org/, Hijmans et al., 2005) at a spatial resolution of 10 km at the 140 midpoint of each national nature reserve. Habitat variables included area, elevation range, 141 and soil PH. Soil PH was obtained from the Harmonized World Soil Database. Mammal 142 richness, insect richness, bird richness were regarded animal factors. Latitude for 143 ecoregions was taken as the geographic midpoint between the northern and southern 144 boundary of each region.

#### 145 2.3 Analyses

Our primary interest was in determining which environmental gradients were most 146 147 correlated with variation in species richness across the 249 sampling locations in China. 148 We first tested the normality of all environmental variables and they were all normal. Then correlations between predictor and response variables were assessed using generalized 149 150 linear models (GLMs). Plant richness was regressed against latitude, and the GLM 151 models were chosen using AIC. To eliminate autocorrelation along each of the 249 studied locations, the Spatial Analysis in Macroecology (SAM) software package 152 153 (www.ecoevol.ufg.br/sam) was used with the method of geographically weighted regression (GWR). SAM correlograms for each variable in the dataset were used, 154 155 showing Moran's I and the correlogram. The explanatory power of the climate, habitat and 156 biotic variables were evaluated using multiple regression. The independent variables were those included in the best models as selected using the Akaike information criterion (AICc; 157 Montoya et al. 2007) from different combinations of climate, habitat and biotic variables. 158 The model with the lowest AICc value (Heikkinen et al. 2005) was selected as the best 159 160 one.

Next, we used variance partitioning analysis (VPA) to decompose plant richness 161 according to the three groups of predictors (i.e., climate, habitat, and biotic variables). 162 Variance partitioning uses partial multiple regression to assess units of unique versus 163 redundant variation in the response variable (Borcard et al. 1992, Peres-Neto et al. 2006, 164 Legendre 2008). In our analysis, partitioning led to seven individual fractions: (i) unique 165 climate; (ii) unique habitat; (iii) unique biotic; as well as shared variation due to redundant 166 explained variation for (iv) climate and habitat; (v) climate and biotic; (vi) habitat and biotic; 167 and (vii) all three groups together. As above, analyses were conducted for all vascular 168 plant life, as well as for gymnosperms, angiosperms, and ferns individually. This was done 169 170 using the 'varpart' function in the 'vegan' package in R (R Core Team, 2017).

#### 171 3 Results

We observed wide variation in species richness across the 249 study locations in China. For all species combined, species richness ranged from a low of 80 to a high of 4,880. Likewise, gymnosperm richness ranged from 1 to 89 species, angiosperms from 79 to 4200, and fern richness from 0 to 600. This variation in richness was strongly correlated with latitude. Latitude alone explained 27% of the variation in total plant species richness (r = - 0.52, *p* < 0.01). This relationship was stronger for angiosperms and ferns (r = -0.591 and -0.587, respectively) than for gymnosperms (r = -0.432).

179 The latitudinal variation in plant richness that we observed appears to be driven 180 largely by variation in climate. Richness was strongly correlated with both AMT (Annual mean temperature) and AP (Annual precipitation). These correlations were stronger for 181 182 angiosperms and ferns than for gymnosperms (Fig. 3). Variation in habitat (i.e., elevation 183 and soil pH) was also important. There was a strong positive correlation between 184 elevation and richness (r = 0.357, p < 0.001). In contrast, soil pH was negatively associated with richness (i.e., higher richness in more basic soils). As with latitude and 185 climate, correlations were stronger for angiosperms and ferns than for gymnosperms (Fig. 186 187 4).



Fig. 3. Relationships between the AMT (Annual mean temperature), AP (Annualprecipitation) and total plant species, gymnosperms, angiosperms and ferns.

Area showed no significant effects on richness across different taxonomic groups (p > 0.05) (Fig.4). Animal richness was positively correlated with richness (p < 0.01). The effects of bird and insect richness on gymnosperm richness is expected to be less than their effects on angiosperms and ferns, however, mammal richness and gymnosperm richness were more correlated than mammals and angiosperms and ferns (Fig.5). The correlation between plant richness was significantly higher than the correlation between 198 animal richness (Fig. S2).



199

Fig. 4. Relationships between insect, bird, and mammal richness and total plant species,
 gymnosperms, angiosperms and ferns. The r<sub>s</sub>-values represents correlation coefficient.

202

The selected explanatory variables for different plant taxonomic groups are presented in Table 1 for each of the three groups of variables. Water-energy and habitat variables generally explained more variation in richness across different taxonomic plants groups than did animal richness (Table. 1). Annual precipitation was selected as the best climate variable across all taxonomic plants groups, soil PH and elevation range were selected as the best habitat variables across different taxonomic plants groups. The explanatory power of the selected habitat variables and water-energy variables was much higher than that of the animal variables across different taxonomic plants groups. For ferns richness, the explanatory power of animals is smaller (4%) than for other plants groups (~ 10%).



213

Fig. 5. Relationships between elevation range, soil pH and Area and total plant species,
gymnosperms, angiosperms and ferns. The r<sub>s</sub>-values represents Spearman's correlation
coefficient

217

Table 1 Summary of the multiple regression models for water-energy, animal, and habitat hypotheses for total species richness, gymnosperm richness, angiosperm richness, and fern richness. The model with lowest AICc (Akaike information criterion corrected for spatial autocorrelation) was selected as the best one. The *P*-values were calculated after accounting for spatial autocorrelation using Dutilleul (1993)'s method.

Hypotheses	Predictors	Adjusted R <sup>2</sup>	P-value	AICc
Water-energy	Annual precipitation (+)	0.283	< 0.01	1498
Animal	Insect richness (+), Mammal richness (+)	0.100	< 0.01	1522
Habitat	Soil PH (—), Elevation range (+)	0.393	< 0.01	1485
Water-energy	Annual precipitation (+)	0.118	< 0.01	756
Animal	Insect richness (+), Mammal richness (+)	0.101	< 0.01	760
Habitat	Soil PH (—), Elevation range (+)	0.217	< 0.01	747
Water-energy	Annual precipitation (+)	0.286	< 0.01	1452
Animal	Bird richness (+), Insect richness (+), Mammal richness (+)	0.106	< 0.01	1478
Habitat	Soil PH (—), Elevation range (+)	0.333	< 0.01	1448
Water-energy	Annual precipitation (+)	0.239	< 0.01	1143
Animal	Insect richness (+)	0.040	< 0.01	1150
Habitat	Soil PH (—), Elevation range (+)	0.228	< 0.01	1132

The variable selection was performed within each group separately. The direction of the relationships is shown in brackets for the significant terms. + represents positive correlation, — represents negative correlation.

226

Variance partitioning revealed that the largest amount of variation in richness was accounted for by the joint effects of water-energy and habitat variables, explaining 17.5 % of variation in total plant richness, 16.8 % in angiosperm richness and 15.3 % in fern richness (Fig.6). The independent effects of habitat was higher than that of water-energy and animal variables across different plant taxonomic groups. Water-energy, habitat and animal variables explain 48.8% of the variation in total species richness, 28.2% in gymnosperm richness, 44.2% in angiosperm richness, and 38.9% in fern richness.



234

Fig. 6. Results of variation partitioning for (a) total species richness, (b) gymnosperm richness, (c) angiosperm richness and (d) fern richness in terms of the fractions of variation explained where A: water-energy B: Animal C: habitat variables. The variation in species richness is explained by the three groups of explanatory variables (A, B, C), and unexplained is the undetermined variation. a, b and c are the unique effects of water-energy,animal and habitat. d, e, f and g are fractions indicating their joint effects.

241

#### 242 4. Discussion

Overall, plants richness is significantly lower with increasing latitude across China. 243 244 From high to low latitudes, the complexity of the environment increased, and the complexity of the fauna and flora also increases. This pattern is consistent with the 245 246 hypothesis that more complex environments foster higher species richness (MacArthur, 1969: Lomolino et al., 2010; Zellweger et al., 2017). Splitting plant assemblages into 247 248 taxonomic groups yields additional insights into biodiversity patterns, with individual groups responding slightly different to latitude (Brown, & Lomolino, 1998). Different plant 249 250 types have different environmental and habitat requirements, resulting in different latitudinal gradient distribution patterns. 251

Plant richness is positively related with current climate variables. Wiens and Graham
 (2005) argued that areas with warm, wet climates would harbor larger numbers of species

254 than cold or dry regions. The demand for water and energy is low in gymnosperms, so the 255 expected role of water and energy variables in explaining gymnosperm species diversity is lower than that for angiosperms and ferns. In our results, elevation range and soil PH 256 257 have significant effect on the richness in plants (p < 0.01). Habitat is considered to be a 258 more comprehensive factor influencing diversity patterns (Rowe, 2009). Larger elevation 259 range provide more complex habitats for the survival of plants with a variety of growth needs (Colwell, 2008). Animals have positive effects on plant (e.g. pollination and seed 260 261 dispersal) (Wunderle, 1997), and many plants can also provide the necessary conditions for survival and reproduction animals (Belsky, 1986). Thus, animals have beneficial 262 263 effects on plant reproduction and life history (Owen, 1980; Jordano et al., 2002; Strauss & Irwin, 2004). 264

265 Environmental factors are known to vary along latitudinal gradients and plant species 266 found at different latitudes are differentially adapted to these varying conditions. However, differentiating between the effects of environmental factors, habitat and animal factors is 267 268 important to better understand their relative contributions to present species distributional 269 patterns (Kraft et al., 2015). Our results showed that environmental variables related to 270 water-energy, habitat and animals are important factors for explaining the latitudinal 271 pattern of plants richness. Habitat and water-energy were most closely related to the latitudinal pattern of plants species richness, with animal variables accounting for a 272 273 smaller but considerable contribution (Fig.6). On macro scales, abiotic factors, not animal factors, appear to determining plant richness. The effects of animal diversity on plant 274 275 diversity are often indirect, while climate and habitat are the dominant factors that 276 determine the richness of plants and animals (Gaston, 2000; Hawkins et al., 2003). The mutual benefits between plants and animals facilitates the survival of each under complex 277 278 habitat and climatic conditions. For example, Miller-Struttmann (2015) found that climate change related changes in flower diversity and composition prevented bumble bees from 279 280 accessing honey and supporting plant pollination of their favorite deep flowers due to the shorter tongue length of the bumblebees, which was maladjusted to the flowers. These 281 results highlight the loss of some mutually beneficial ecological partnerships as a result of 282 283 global climate change and how climate change will remove the recognized coupling of 284 mutually beneficial symbiosis between bees and plants.

285 Habitat explains more of the variance in species richness in China (Fig.6). These findings are consistent with previous studies (Harrison et al., 2006; Wohlgemuth et al., 286 287 2008). Harrison (2006) found climate to be of lesser importance, and often used data from 288 specific sites within the larger study region. Using estimates of richness and ignores the influence 289 environmental parameters over large areas of the microenvironments in mountain ecosystems. 290

There are relatively few studies that provide empirical evidence of a link between climate and animal richness and plant richness along a latitudinal gradient within China. However, nearly 50% (Fig.6 a) of the variation of total plant species is still not explained by above three hypotheses and their associated variables. We acknowledge that geographic speciation events and spatially constrained evolutionary histories could be responsible for the remaining unexplained spatial variation (Chen et al., 2015).

297

#### 298 ACKNOWLEDEMENTS

299 This work was supported by the Beijing Common Construction Project Research and

300 demonstration on the regression technique of the minimum population of wild plants

301 (2016YFC0503106). Specifically, we would like to thank Dr. Joanne Maio for her

assistance with English language and grammatical editing of the manuscript.

303

#### 304 Author Contributions

J Gao and YH Liu designed the study, J Gao and X Du collected the data; J Gao and M

Bogonovich performed analyses and led the writing; J Gao and YH Liu contributedsubstantially to revisions.

308

#### 309 CONFLICT OF INTEREST

310 None declared.

311

#### 312 **REFERENCE**

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., . . . Dalling,
J. W. (2013). Soil resources and topography shape local tree community structure in
tropical forests. Philosophical Trans-actions of the Royal Society B: Biological Sciences,
280, 20122532.

Brown, J.H., Lomolino, M., 1998. Biogeography. Sinauer Associates, Sunderland, MA,USA.

Cardillo, M., Orme, C. D. L., Owens, I. P. F. (2005). "Testing for latitudinal bias in
 diversification rates: An example using New World birds". Ecology. 86, 2278-2287.

Colwell, R. K. (2008). RangeModel: Tools for exploring and assessing geometric
 constraints on species richness (the mid-domain effect) along transects. Ecography, 31,
 4-7.

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches
from stochastic processes across scales. Philosophical Transactions of the Royal
Society B: Biological Sciences, 366, 2351–2363.

327 Ellenberg, H. (1988). Vegetation ecology of Central Europe (4th ed.). Cam-bridge, U.K.:
328 Cambridge University Press.

- Evans, K. L., Newson, S. E., Storch, D., Greenwood, J. J. D, Gaston, K. J. (2008) Spatial
  scale, abundance and the species–energy relationship in British birds. Journal of
  Animal Ecology, 77, 395–405.
- Dalby, L., McGill, B. J., Fox, A. D., Svenning, J. C. (2014) Seasonality drives global-scale
  diversity patterns in waterfowl (Anseriformes) via temporal niche exploitation. Global
  Ecology and Biogeography, 23, 550-562.
- Fick, S.E. and R.J. Hijmans, 2017. Worldclim 2: New 1-km spatial resolution climate
  surfaces for global land areas. International Journal of Climatology.
- Fjeldså, J., Bowie, R. C. K. & Rahbek, C. (2012). The role of mountain ranges in the
  diversification of birds. Annu. Rev. Ecol. Evol. Syst, 43, 249 265.
- Gao, J., Zhang, X., Luo, Z. F., Lan, J. J., Liu, Y. H. (2017). Elevational diversity gradients
   across seed plant taxonomic levels in the Lancang River Nature Reserve: Role of
- temperature, water and the mid-domain effect. Journal of forestry research, 31, 1-7.
- Gaston, K. J. (2000). Global patterns in biodiversity. Nature, 405, 220-227.
- Hawkins, B. A., Field, R., Cornell, H. V. (2003). Energy, water, and broad-scale
  geographic patterns of species richness. Ecology, 84: 3105 3117.
- Harrison, S., Safford, H. D., Grace, J. B., Viers, J. H. & Davies, K. F. (2006) Regional and
  local species richness in an insular environment: Serpentine plants in California.
  Ecological Monographs, 76, 41-56.
- Heikkinen, R. K., Luoto, M., Kuussaari, M., Pöyry J. (2005). New insights into butterfly—
  environment relationships using partitioning methods. Proc. R. Soc. B, 272, 2203–2210.
- Hughes, C. & Eastwood, R. (2006). Island radiation on a continental scale: exceptional
  rates of plant diversification after uplift of the Andes. Proc. Natl. Acad. Sci. USA, 103,
  10334 10339.
- Kallimanis, A. S., Bergmeier, E., Panitsa, M., Georghiou, K., Delipetrou, P. & Dimopoulos,
  P. (2010). Biogeographical determinants for total and endemic species richness in a
  continental archipelago. Biodiversity and Conservation., 19, 1225 1235.
- Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant
   diversity. Proceedings of the National Academy of Sciences, 104(14), 5925-5930.
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., Levine, J. M., & Fox, J.
  (2015). Community assembly, coexistence and the envi-ronmental filtering metaphor.
  Functional Ecology, 29, 592–599.

Lee, P.-Y., & Rotenberry, J. T. (2005). Relationships between bird species and tree
species assemblages in forested habitats of eastern North America. Journal of
Biogeography, 32, 1139–1150.

- Lomolino, M. V., Riddle, B. R., Whittaker, R. J., Brown, J. H. (2010) Biogeography.
  Sinauer Associates, Inc. Sunderland, Massachusetts, USA.
- Millerstruttmann, N. E., Geib, J. C., Franklin, J. D., Kevan, P. G., Holdo., R. M. (2015).
  Science, 349 (6255) :1541.
- Palmer, M. (1994) Variation in species richness: towards a unification of hypotheses. Folia
  Geobotanica, 29, 511 530.
- Ponisio, L. C., M'Gonigle, L. K., & Kremen, C. (2016). On-farm habitat restoration counters
  biotic homogenization in intensively managed agriculture. Global Change Biology, 22,
  704–715.
- 373 Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity.
  374 Ecology Letters, 7, 1–15.
- Rowe, R. J. (2009). Environmental and geometric drivers of small mammal diversity along
  elevational gradients in Utah. Ecography, 32, 411-422.
- Stein, A., Gerstner, K., Kreft, H. (2014). Environmental heterogeneity as a universal driver
  of species richness across taxa, biomes and spatial scales. Ecology Letters, 17,
  866-880.
- Tews, J., Brose, U., Grimm, V., Tielb € orger, K., Wichmann, M.C., Schwager, M. et al.
  (2004). Animal species diversity driven by habitat heterogeneity/diversity: the
  importance of keystone structures. Journal of Biogeography, 31, 79 92.
- Wiens, J. J. & Donoghue, M. J.. (2004). Historical biogeography, ecology, and species
  richness. Trends in Ecology & Evolution, 19, 639-644.
- Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: integrating evolution, ecology,
  and conservation biology. Annual Review of Ecology, Evolution, and Systematics, 36,
  519-539.
- Wohlgemuth, T., Nobis, M. P., Kienast, F. & Plattner, M. (2008) Modelling vascular plant
  diversity at the landscape scale using systematic samples. Journal of biogeography, 35,
  1226-1240.
- Zellweger, F., Roth, T., Bugmann, H., Bollmann, K. (2017). Beta diversity of plants, birds
  and butterflies is closely associated with climate and habitat structure. Global ecology
  and biodiversity, 26, 898-906.

395 Appendix



396

Fig.S1 Strip plot and boxplot displays of species (total species, gymnosperms, angiosperms and ferns) richness.

399



400

Fig. S2 Pearson's correlation coefficients between biotic variables using R package. The
amount of blue or red in the circles indicates the magnitude of the correlation of the factors.
Blue signifies a positive correlation, red signifies a negative correlation.

404



406

407 Fig.S3 Correlograms for total species, gymnosperm, angiosperm and fern richness.

408

#### 409 Table. S1 The studied areas.

National Nature Reserves	Survey Time	Lng	Lat
Baagongshan	1984	29.5	109.9
Baishilizi	1998	40.5	124.5
Caohai	2005	26.8	104.2
Dawei Mountain	1999	23	104
Dawuling forest area	2012	22.3	111.2
Dong Zhai	1996	32	114
Longxi	2002	31.2	103.5
Fanjing	1982	27.9	108.8
Foping	2006	33.7	107.8
Extra Arid Desert	2014	40	94.8
Westlake	2010	40	93
Tao River	2006	34.4	103

Gaoligongshan	1998	26.2	98.7
Guniujiang	2006	30.1	117.8
Gudou Mountain	2017	22.2	113
Nanling	1993	24.7	113
Neilingding Island	2000	22.4	113.8
Xiangtau Mountain	2003	23.3	114.4
Daming Mountain	2010	23.4	108.6
Huaping forest area	2008	25.6	109.9
Nong Gang	2003	22.4	106.9
Ichang Orchidaceae	2012	24.8	106.3
Kanas	1989	48.9	87.4
Jianfengling	2001	18.6	108.9
Yinggeling	2012	19	109.4
Sea tutuo	2014	40.6	115.8
Red pine depression	2005	42.3	117.4
Dabie Mountain	2012	31.8	115.5
Heilongjiang South urn	1999	51.4	125.5
Zhalong	2005	47.2	124.2
Hubei Back River	2005	30.1	110.6
Hubei nine Gong Mountain	2002	29.4	114.6
Hubei Nanhe	2010	32	111.4
Seven sisters	2006	29.9	109.7
Zhangzhou and Heyuan	2008	29	111
Taoyuan Hunan linghsien hole	1993	26.8	113.6
Six step brook	2005	28.4	110.9
Hunan Xiaoxi	2000	28.8	110.3

Yanling Taoyuan Hunan cave	2001	26.5	114.1
The great Jia River	2002	46.9	133.6
Hunchun	2002	43.1	130.8
Jiangsu Dafeng elk	1998	32.9	120.9
Jiangxi ganjianyuan	2013	26.3	116.4
Jiangxi nine Mountain	2009	28.9	115.5
Tao Hong Ling, Jiangxi	2004	29.8	116.6
Jinggangshan	1998	26.5	114.1
Shi Na Si	1996	48.9	87.3
Wide water forest area	2004	28.2	107.1
Lancang River	2012	24.1	99.8
Old snake flush	2003	26.5	107.4
Leigong Mountain	1989	26.4	108.2
Liaoning Xian Man Cave	2002	40	123
Six Panshan reserve	2013	35.5	106.3
Mayang River	2015	28.8	108.2
Peony peak	1992	44.4	129.8
Mulan Wei Chang	2005	41.9	116.9
Southern Dongting Lake	1994	28.8	112.6
South China Zhongshan	1989	24.5	100.9
Nanji Islands	2000	27.5	120
Dali Noel	2017	43.3	116.7
Inner Mongolia Honghuaerji sylvestris Forest	2001	47.9	122.4
Ningxia Baijitan	1992	38.1	106 5
			100.5
Helan mountain protection area in Ningxia	2011	38.8	106.2

Qinghai Chaidamu Haloxylon ammodendron Forest	2004	36.7	96.4
Qilian Mountains	2007	38.1	100.6
Qinglong River	2013	40.8	119
Pang Quan gully, Shanxi	2014	37.8	111.5
Shedao LaoTieShan reserve	2016	39	121
Shennongjia	2015	31.5	110.3
Baoding Mountain	2008	32.5	104.1
Xiaolongshan	2012	34.3	106
Arhorchin	2015	44.1	120.3
Xilin Gol Grassland	2008	44	116.4
Baxian Mountain	2006	40.2	117.6
Wenshan	2002	35	111.4
West Ordos	1997	40	108.5
Cayman	1996	33.7	103.2
Small 5 Taishan	2002	40	115.1
Ungulate wild animal nature reserve in Mt. Cara, Cara	2012	45.3	89.3
Xuefeng Mountain	1999	27.3	110.4
The mountains of Yunnan	2016	27.4	103.3
Jinping watershed	2002	22.7	103
Yunnan Nan Gang	2015	23.3	99
Yunnan Wumengshan	2008	28	104.3
Changqing	2000	33.5	107.6
DaPan Mountain	2011	29	120.5
Gutian Mountain	1999	29.3	118.2
Jinyun Mountain	1982	29.8	106.3

Chongqing five miles	2008	31.4	110
Zhejiang Feng Yangshan - Baishan ancestor	2006	27.7	119.2
Hunan golden hills	2011	26.3	110.3
Beijing Baihua Mountain	2012	40	116
Songshan, Beijing	2012	40.3	115.4
Wuling Mountain in Hebei	2014	40.35	117.2
Mau Jing dam	2006	41.3	117.45
The Luanheshangyou	2003	42	116.83
Saihan dam	2015	42.4	118.35
Tuoliang	2007	38.4	113.49
Green Cliff Village	2008	36.5	113.78
Heicha mountain	2009	37.78	111.3
Ling Mountain	2015	36.38	112.08
Mount Daqing in Inner Mongolia	2008	40.87	111
Gourgues Tai Hamura	2013	44.76	119.2
Saihan URA	2007	43.96	118.31
Baiyinaobao	1998	43.31	117.12
Hei Li River	2000	41.3	118.2
Big Black Mountain	2011	41.73	120.3
Daqinggou	1998	42.46	122.14
Eergu'Na	2001	51.78	120.3
Greater Khingan Range Hanma	2011	51.31	122.35
The Yarlung Zangbo River Grand Canyon	2000	29.6	95.5
Zayu Cibagou	2000	28.7	96.8
Yunnan sedan Hill	2009	26.1	102.5
Ailao Mountain	1988	23.9	100.9

Yaoshan	2003	27.1	102.9
Boundless mountain	1994	24.4	100.3
The Great Snow Mountain in Yongde	2003	24.1	99.4
Coptidi Montana	2001	22.5	102.2
Maolan	1998	25.1	107.9
Hongkou Longxi, Sichuan	2004	31.1	103.4
Guizhou Xishui	2011	28.2	105.9
Shui Qin	2008	28.7	112.4
Xishuangbanna	2013	21.7	100.8
Xishuangbanna nnban river basin	1989	22.1	100.9
Baima Snow Mountain	2004	27.8	98.4
Yunlong Tianchi Mountain	2009	25.8	99.2
White River	2008	31.3	103.6
M Cangshan	2001	32.4	107.2
Changning Zhuhai	2001	31.2	103.4
Calyx mountain	2012	31.33	108.1
Huzhong	2007	51.5	122
Heilongjiang Shuanghe	2009	53	125
Maolan gully	2011	49	129.5
Taiping gully	2008	47.8	130.8
Grand Canyon	2006	48	131
The cool peak of Ling'an, Zhejiang	1997	30	119
Uyanling	1984	27.5	119.5
Yaoluoping	2016	31	116
Jinzhai Tianma	2007	31	115.5
Anhui cool peak	2004	30	119

Fujian Jun Zi peak	2005	26.5	117
Longqishan	1997	26.5	117.3
Minjiang source	2004	26.7	116.8
Fabri	2010	25.7	118.2
Tiger bebot	2010	24.7	117.3
Wuyishan, Fujian	1993	27.7	117.7
Plum Blossom Hill	1996	25.4	116.9
Mount liangye	2001	25.2	116.2
Huang Chulin of the Xijiang River	2010	26.3	118.46
Tingjiangyuan	2014	25.5	116.16
Helan Mountain	2011	38.5	105.6
Han Shan	2011	45.2	119.7
Ulan dam	2013	44.2	118.9
Hengren Laotudingzi	1997	41.2	124.7
Yiwulv mountain	2015	41.5	121.5
Zhanggutai	2008	42.6	122.4
Haitang mountain	2003	41.8	121.8
Nu Ruhr Tiger Mountain	2012	41.9	120.2
White Wolf Mountain	2013	40.8	119.6
Huludao Hongluo Mountain	1998	41.1	120.6
Liaoning grand Montenegro	2010	42.1	120.3
Songhua River	2006	42.5	127.3
Yellow mud river	2005	44	128.1
Changbai Mountain, Jilin	1998	42.3	127.9
jl An	2008	41.3	126.1
Wangqing	2006	43.5	129.7

Fenglin	2001	48.1	128.8
Cold water	2017	47.1	1228.5
Xiao Bei Lake	2009	44.1	128.3
Sheng Shan	2015	49.2	126.7
Mangdangshan	2003	26.4	118.1
Nine hill	2002	24.3	114.2
Guan Shan	2005	28.3	114.3
Matau Mountain	2006	27.5	117.1
Wuyi Mountain	2001	27.4	117.8
Qiyun Mountain	2010	25.5	113.8
Tongbo Mountain	1998	28.1	118.2
Lu Mountain	2010	29.3	115.8
Kunyu Mountain	2002	37.1	121.4
Small Qinling Mountains	2004	34.3	110.3
Funiu Mountain	1994	33.5	112.5
Berman mountain	1994	33.3	111.9
Lian Kang Mountain	2009	31.3	114.5
Hubei wood forest	2009	30	109.9
Dabie Mountain	2010	31	115.8
Yangtze River Source	2002	34.5	96.3
Balurk Mountain	2013	46.3	82.7
West Tianshan	2009	43.1	82.8
Tomur	2015	41.8	80.5
Ningxia Yun Shan	2013	36.1	106.2
Southern Huashan	2005	27.9	109.6
Luoshan	1997	37.3	106.23

Qinghai Datong Beichuan	2009	37.1	101.4
Meng Da, Xunhua	2005	35.8	102.7
Gansu Liancheng	2002	36.7	102.7
Xinglong mountain	2015	35.8	103.7
The Tai Tong Kongtong Mountain	2015	35	106
Qilian Mountains	2007	38	96.8
Lotus Hill	2002	35	103.8
Gahai zecha	2004	34.3	102.5
Prince Edward Hill	2007	35.3	103.2
Taibai Mountains in Shaanxi	2004	34	107.7
Ziwuling Mountain	2004	35.9	108.6
M Cangshan	2001	32.6	106.5
Hua Longshan	1999	32	109.4
Old county town	2006	33.8	107.7
Guanyin Mountain	2006	33.7	108.4
Huangbaiyuan	2009	33.8	107.6
Pinghe beam	2008	33.5	108.5
Qomolangma	2004	28.6	86.5
Dinghu mountain	1986	23.1	112.5
Shimen station	2017	24.4	113
Yun Kai mountain	2009	22.3	111.3
Crocodile Lizard	2006	24.6	113.3
Heng Mountain in Hunan	2013	27.5	112.8
Hnangsang	2006	26.5	109.9
Shunhuangshan	2011	26.5	110
Dark cloud boundary	2006	28.5	111.3

Kettle mountain	2004	30	110.5
Dongan Shunhuangshan	2002	26.28	110.84
Jiuyi Mountains	2011	26.66	111.72
High horizon	2006	28.41	114.81
Olecranon boundary	2003	26.53	109.54
Borrow from the mother stream	2010	28.52	110.25
Yongzhou Douling Pang	2004	25.26	111.16
Yangmingshan	2015	26.05	111.54
Eight face mountain	1985	25.8	113.48
Mangshan	1993	24.91	112.72
Gongga mountain	2006	29.5	101.5
Aden	2004	28.2	99.5
Heizhugou	2008	28.5	102.5
Daba Mountain, Chongqing	2015	31.5	108.5
Xuebaoshan	2004	31.3	108.5
Yin stripe ridge	2009	31.3	109.5
Hainan hanging Luoshan	2006	18.5	109.5
Five Fingers Group	1996	18.5	109.3
Guangxi thousand holes	1988	25.3	111.1
Parrot ridge	2007	18.8	109.2
Cat Hill	2016	25	110.2
One hundred thousand Mountains	2002	21.5	107.5
CEN Wang Lao Shan	2005	24.3	106.2
Nine Mountains	2010	25.1	108.4
Mulun	1998	25.1	107.6
Dayao	2014	23.5	109.5

Eunsung	2011	22.4	106.8
Yuanbao Mountain	2011	25.2	109.1
Seven red	2012	24	110.5
Guangdong car eight ridge	2008	24.3	114.1