# The mid-domain effect of species diversity of mountainous plants is determined by community life form and family flora in a temperate semi-arid region of China

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The mid-domain effect (MDE) is a vital hypothesis to explain altitudinal patterns of species diversity of mountainous plants with different gradients, but it is bounded in terms of its application at the plant level. To verify the MDE hypothesis, we chose a typical mountain with obvious elevation gradients and considerable plant coverage as a study area in the east of the Loess Plateau and partitioned various elevation belts across this mountain. Through measuring the species diversity of arbor, shrub and herb communities in forest ecosystems, we explored altitudinal patterns of species diversity of mountainous plants with different gradients. We determined that the family numbers of the herb and shrub communities, as well as the species diversity of the arbor community, reached their maximums at intermediate elevations. The family numbers of the herb and shrub communities presented unimodal patterns across altitudinal gradients, and the highest values occurred at intermediate elevations. The family number of the arbor community showed a monotonic decreasing pattern, and the importance values of dominant families in the shrub and arbor communities presented unimodal patterns, but the lowest values occurred at intermediate elevations. The species diversity of the herb, shrub and arbor communities conformed to unimodal change patterns following altitudinal gradients, but the greatest diversity occurred at high, low and intermediate elevations, respectively. At higher elevations, weeds and grasses grew well, whereas sedges grew well at lower elevations. With respect to the importance values of different arbor life forms, their responses to altitudinal gradients indicated a certain variation pattern, which was greater for evergreen coniferous arbor species than for deciduous coniferous arbor species and deciduous broad-leaved arbor species. It is concluded that the MDE hypothesis of species diversity for mountainous plants is influenced greatly by the community life form and family flora at the plant level in a temperate semi-arid region of the Loess Plateau, China. This conclusion tests and modifies the MDE hypothesis and can be valuable for fueling prediction of biodiversity models and for the comparison with similar studies in different

regions.

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15 **Author contributions:**

16 MHX conceived and designed the experiments. MHX and JW performed the experiments,

17 analysed the data, and revised the manuscript. MHX wrote the paper. JW contributed reagents,

18 materials, and analysis tools.

19 **Conflict of interest:**

20 No.

21 **Data Accessibility Statement**

22 We agree to archive our data in a publicly accessible repository (except for Dryad) for free when

23 this manuscript is accepted for publication.

24 **Abstract**

25 The mid-domain effect (MDE) is a vital hypothesis to explain altitudinal patterns of species diversity of

26 mountainous plants with different gradients, but it is bounded in terms of its application at the plant level. To

27 verify the MDE hypothesis, we chose a typical mountain with obvious elevation gradients and considerable

28 plant coverage as a study area in the east of the Loess Plateau and partitioned various elevation belts across this

29 mountain. Through measuring the species diversity of arbor, shrub and herb communities in forest ecosystems,

30 we explored altitudinal patterns of species diversity of mountainous plants with different gradients. We

31 determined that the family numbers of the herb and shrub communities, as well as the species diversity of the

32 arbor community, reached their maximums at intermediate elevations. The family numbers of the herb and

33 shrub communities presented unimodal patterns across altitudinal gradients, and the highest values occurred at

34 intermediate elevations. The family number of the arbor community showed a monotonic decreasing pattern,

35 and the importance values of dominant families in the shrub and arbor communities presented unimodal

36 patterns, but the lowest values occurred at intermediate elevations. The species diversity of the herb, shrub and

37 arbor communities conformed to unimodal change patterns following altitudinal gradients, but the greatest

38 diversity occurred at high, low and intermediate elevations, respectively. At higher elevations, weeds and

39 grasses grew well, whereas sedges grew well at lower elevations. With respect to the importance values of

40 different arbor life forms, their responses to altitudinal gradients indicated a certain variation pattern, which

41 was greater for evergreen coniferous arbor species than for deciduous coniferous arbor species and deciduous

42 broad-leaved arbor species. It is concluded that the MDE hypothesis of species diversity for mountainous

43 plants is influenced greatly by the community life form and family flora at the plant level in a temperate semi-

44 arid region of the Loess Plateau, China. This conclusion tests and modifies the MDE hypothesis and can be

45 valuable for fueling prediction of biodiversity models and for the comparison with similar studies in different

46 regions.

47 **KEYWORDS**

48 Mountain, altitudinal gradient, importance value, species diversity, mid-domain effect

## 1  INTRODUCTION

The variation in biodiversity along environmental gradients is a significant topic in biodiversity research. Species diversity is the simplest and most effective method to determine community and regional diversity, which is considered to be an essential component of biodiversity (Jin et al, 2017; Ge, 2017; Venterink et al, 2003; Yao et al, 2017) . Species distribution patterns are outcomes of multiple ecological processes, and these processes are primarily controlled by species evolution, geographic variation and environmental factors (Aerts and Beltman, 2003; Andersen and Hessen, 2004; Elser et al, 2000; Lin et al, 2017). Studies on gradient patterns of species diversity are the foundation of conservation biology, together with the ecological factors that control these patterns.

The distribution patterns of species diversity are mainly correlated with climate, community productivity and other factors and are also affected by plant evolutionary history to varying degrees (Braakhekke and Hooftman, 1999; Gusewell et al, 2005; Xie et al, 2016). At a regional scale, ecological factors that impact the distribution patterns of species diversity interact with each other and act on species together; thus, they are difficult to distinguish in studies on gradient features of species diversity (Newman, 1973; Zhao et al, 2017). Similar to latitudinal gradients, altitudinal gradients have become a vital aspect to research the gradient patterns of species diversity due to their strong relationships with temperature, humidity, radiation and other environmental factors. Variations in these environmental factors occur 1000 times faster along altitudinal than latitudinal gradients and are thus an important research object for ecologists (Gaston, 2000; Tan et al, 2017).

Mountains are geomorphic units with considerable fluctuation at the surface; consequently, their changes in elevation, slope and aspect can directly induce variations in temperature, humidity, heat and radiation, thus forming different habitats that produce multiple vegetation forms and complex ecosystems (Burt and Butcher, 1985; Dorji et al, 2014; Li et al, 2017). Altitudinal gradients have significant influences on the redistribution of hydrothermal resources in mountains, which indirectly affect the species composition and hierarchical structure of the plant community. Therefore, variations in the species diversity of a plant community are always an interesting issue for ecologists, especially in response to altitudinal gradients across mountains (Bai et al, 2007; Kessler et al, 2014; Niu et al, 2017). However, most studies have focused on tropical mountains and have omitted patterns of species diversity in temperate mountains; furthermore, the research results are not

76    in agreement.

77         The changing patterns of species diversity of plant communities can be divided into five groups along

78    altitudinal gradients: negative correlation (Vazquez and Givnish, 1998), positive correlation (Baruch, 1984) or

79    no correlation (Dolezal and Srutek, 2002) with elevation, and the highest (Lieberman et al, 1996) or lowest

80    (Peet, 1981) values can occur at medium elevations. Considerable research conducted in recent years verifies

81    the conclusion that the species diversity of a plant community reaches a maximum at intermediate elevation

82    gradients of mountains, which further supports the mid-domain effect (MDE) hypothesis (Colwell and Lees,

83    2000). The MDE hypothesis was proposed based on geometric constraints along geographical gradients and

84    species overlap in distribution ranges and is another vital mechanism that impacts species diversity patterns in

85    addition to the environmental gradient, area, heterogeneity and disturbance (Bachman et al, 2004; Colwell and

86    Gotelli, 2004; Kattan and Franco, 2004). According to the MDE hypothesis, a species is continuously

87    distributed across its distribution range, and the ranges of different species overlap. Within a domain, owing to

88    the restriction of borders on species distribution, the ranges of different species have smaller overlapping

89    degrees at the border region and greater overlap in the central region, which results in more species in the

90    central region and larger species diversity, i.e., the restriction of the border on species distribution leads to

91    unimodal distribution patterns of species diversity.

92         Nevertheless, at different study scales, species diversity has disparate distribution patterns along

93    altitudinal gradients, and their formative factors differ greatly. In studies on species diversity patterns and their

94    formation, various scales should be considered (Mittelbach et al, 2001); these scales include those along

95    environmental gradients and those in different taxonomic hierarchies (Loreau et al, 2001). Therefore, further

96    studies should be carried out on the vertical distribution patterns of mountainous vegetation and their

97    formation mechanisms. The MDE hypothesis also needs to be further tested, and selective analysis should be

98    performed on the influential factors of the hypothesis.

99         Special environmental conditions result in fragile ecosystems in arid and semiarid regions where plant

100   diversity is threatened most severely (Zhu et al, 2017). The Loess Plateau is a region with the most serious soil

101   erosion and the most frail ecological environment in China, and possibly the world, due to its drought climate,

102   low precipitation and sparse vegetation (Liu et al, 2018; Zhang and Zhang, 2018). A warm-temperate and mid-

103  temperate zone occur from south to north across the plateau, and a semi-humid and semi-arid region occur

104  from east to west; thus, the vegetation on the plateau exhibits typical characteristics along environmental

105  gradients (Yu et al, 2018; Zhao et al, 2018).

106      Mountains, with their significant topography across the plateau, have considerable elevations and distinct

107  elevation gradients, and subalpine belts occur in many mountain systems. To verify the MDE hypothesis at the

108  plant level, the Lvliang Mountain system, with obvious elevation gradients and high vegetation coverage, in

109  the eastern part of the plateau, was selected as a model mountain and divided into various belts with different

110  elevation gradients. In each belt, forest ecosystems were separated into three hierarchical structures: the arbor

111  community, shrub community and herb community. Species diversity surveys were first conducted in each

112  community, and then altitudinal patterns of species diversity of mountainous vegetation were analyzed across

113  different elevations, and the influential factors were determined at the plant level with respect to the MDE

114  hypothesis.

115  ## 2    MATERIALS AND METHODS

116  ### 2.1   Description of the study area

117  The Lvliang Mountain system belongs to an eastern mountain of the Loess Plateau with a length of about 400

118  km from south to north and a width of about 50 km from east to west, including primarily Guancen Mountain

119  in the northern section, Guandi Mountain in the middle section, and Wulu Mountain in the southern section.

120  These mountains are located in Xinzhou City, Lvliang City, and Linfen City, respectively, of Shanxi Province

121  in China (Fig. 1).

122      Guancen Mountain is located in Dongzhai Town of Ningwu County in Xinzhou City with geographical

123  coordinates of 38°57′—39°03′ (northern latitude) and 112°36′—112°37′ (eastern longitude). The sample plots

124  across this mountain have elevations from 1740 m to 2745 m, an annual mean air temperature of 6°C to 7°C,

125  average annual precipitation of 450 mm to 500 mm, and a frost-free season of 90 d to120 d. The soil type is

126  cinnamon soil, brown soil and subalpine meadow soil from low to high elevations, and the vegetation includes

127  bush, mixed coniferous broad-leaved forest, coniferous forest and subalpine meadow.

128      Guandi Mountain is located in Pangquangou Town of Jiaocheng County in Lvliang City with

129  geographical coordinates of 37°20′—38°20′ (northern latitude) and 110°18′—111°18′ (eastern longitude). The

130    sample plots across this mountain have elevations from 1800 m to 2690 m, an annual mean air temperature of

131    3°C to 4°C, average annual precipitation of 600 mm to 800 mm, and a frost-free season of 100 d to130 d. The

132    soil type is also cinnamon soil, brown soil and subalpine meadow soil from low to high elevations, and the

133    vegetation includes broad-leaved forest, mixed coniferous broad-leaved forest, coniferous forest and subalpine

134    meadow.

135        Wulu Mountain is located in a junction between Pu and Xi counties in Linfen City, with geographical

136    coordinates of 36°23′—36°38′ (northern latitude) and 111°2′—111°18′ in (eastern longitude). The sample plots

137    across this mountain have elevations from 1324 m to 1586 m, an annual mean air temperature of 8°C to 9°C,

138    average annual precipitation of 500 mm to 560 mm, and a frost-free season of 150 d to180 d. The soil type is

139    cinnamon soil and brown soil, and the vegetation includes bush and broad-leaved forest.

140    **2.2   Arrangement of experimental plots**

141    Lvliang Mountain has evident elevation gradients, high vegetation coverage and diverse vegetation types;

142    consequently, this can be considered as an ideal region to determine the altitudinal patterns of species diversity

143    of various plant communities. In previous research conducted in July of 2015 (Xu et al, 2017), we determine

144    the plant community characteristics across 12 elevation gradients. On this basis, from July to August in 2017,

145    we carried out new selections and surveys in experimental plots on this mountain for a period of one month. In

146    the horizontal direction, we chose the following study areas: northern Guancen Mountain, central Guandi

147    Mountain, and southern Wulu Mountain in the Lvliang mountain system with mean latitudes of 38.5° N, 37.5°

148    N and 36° N, respectively.

149        For each mountain in the vertical direction, experimental plots were established according to different

150    elevation gradients to conduct surveys on species diversity of plant communities. The plant communities were

151    divided into three biotypes: arbor, shrub and herb communities. In total, 21 elevation gradients were selected

152    from the three mountains: 1324, 1370, 1459, 1586, 1740, 1800, 1892, 1900, 1950, 2001, 2179, 2222, 2270,

153    2395, 2460, 2571, 2610, 2666, 2675, 2690 and 2745 m. The difference was 1421 m between the highest and

154    the lowest elevations. Among these gradients, the arbor community covered 13 gradients which were 1459,

155    1586, 1740, 1892, 1900, 1950, 2001, 2179, 2222, 2270, 2395, 2571 and 2610 m; the shrub community covered

156    6 gradients which were 1324, 1370, 1586, 1800, 1950 and 2675m; and the herb community covered 14

157     gradients which were 1324, 1459, 1586, 1900, 2001, 2179, 2222, 2395, 2460, 2571, 2666, 2675, 2690 and

158     2745 m.

159        Along each gradient, quadrats with different areas were designed for investigation based on the type of

160     plant community. The area of the quadrat in the arbor community was 1000 $m^2$ (50 m×20 m), and 2 quadrats

161     were used. The quadrat area in the shrub community was 400 $m^2$ (20 m×20 m), and 4 quadrats were used, and

162     the quadrat area in the herb community was 1 $m^2$ (1 m×1 m), and 20 quadrats were used. Hence, the total

163     number of quadrats was 26, 24 and 280 in the arbor, shrub and herb communities, respectively. The species

164     surveyed in all plots were merged along each gradient, and growth indices of identical species were averaged

165     for statistical purposes.

166     **2.3    Measurement of plant diversity**

167 The methods adopted in the characteristic measurements of the plant communities here are accordant with

168     those in previous research. The measurement indices for the arbor species included species name, quantity,

169     diameter at breast height, basal diameter, height and crown breadth; those for the shrub species included

170     species name, quantity, height and crown breadth; and those for the herb species included species name,

171     quantity, height, frequency and coverage (data in Supplementary Table). The main measurement tool was a

172     homemade aluminum quadrat frame with a size of 1 m×1 m (Fig. 2), and its interior was separated into 100

173     grids 10 cm×10 cm in size.

174        In addition, during the measurements, arbor species with a height of less than 5 m were classified into the

175     shrub layer, and seedlings of woody plants were considered herbaceous plants. Finally, definite life forms of

176     various species were confirmed using a book called the Flora of China (the website is http://foc.eflora.cn/). The

177     specific measurement methods have been described in detail (Xu et al, 2017).

178     **2.4    Data analysis**

179 α-Diversity principally focuses on species number in a homogeneous habitat at local scales and is thus called

180     within-habitat diversity. At this scale, the major ecological factors that sustain diversity are niche diversity and

181     interaction among species, while niche diversity is closely related to environmental energy, and thus α-

182     diversity has an intimate relationship with environmental energy. As a result, α-diversity is preferably used to

183     explain the MDE hypothesis.

184     In this study, with the purpose of further verifying the MDE hypothesis, α-diversity indices were

185     employed to analyze variation patterns of species diversity along altitudinal gradients in the arbor, shrub and

186     herb communities of Lvliang Mountain, such as the Richness index, Simpson index, Shannon index and Pielou

187     index (Gotelli and Colwell, 2001; Smith and Wilson, 1996; Xu et al, 2017). Their computational formulas are

188     as follows:

189
$$IV_{\text{Arbor and shrub}} = \frac{ra + rh + rc}{3}, \qquad (\text{Eq. 1})$$

190
$$IV_{\text{Herb}} = \frac{ra + rh + rf + rc}{4}, \qquad (\text{Eq. 2})$$

191
$$H' = 1 - \sum_{i=1}^{S} p_i^2, \qquad (\text{Eq. 3})$$

192
$$H = -\sum_{i=1}^{S} p_i \ln(p_i), \qquad (\text{Eq. 4})$$

193
$$E = \frac{H}{\ln(S)}, \text{ and} \qquad (\text{Eq. 5})$$

194
$$p_i = \frac{IV_i}{IV_{total}}. \qquad (\text{Eq. 6})$$

195     In these equations, $IV$ is the importance value (a comprehensive quantity index to reflect function and

196     position of a certain species in forest communities), $ra$ is the relative abundance, $rh$ is the relative height, $rf$ is

197     the relative frequency, and $rc$ is the relative coverage; $H'$ is the Simpson index, $H$ is the Shannon index, and $E$

198     is the Pielou index; $i$ and $S$ (i.e. the Richness index) represent plant species $i$ and the sum of all plant species in

199     the quadrat frames of the experimental plots, respectively.

200     **3    RESULTS**

201     **3.1    Altitudinal patterns of species diversity in the herb community**

202     3.1.1    *Variations in herbaceous families with elevation*

203     The importance value and number of different families differ greatly in the herb community at different

204     elevation gradients, but they are roughly the same among elevations for dominant families (Fig. 3). In terms of

205     the 14 altitudinal gradients used to describe the herb community distribution, the importance value of

206     Cyperaceae, with an average of 42.37%, is maximal at elevations of 1324, 1459, 1586, 1900, 2179, 2222, 2395,

207    2571, 2675 and 2745 m. The maximum importance values are 13.24% for Rosaceae at 2001 m, 19.93% for

208    Saxifragaceae at 2460 m, and a mean of 19.96% for Polygonaceae at 2666 m and 2690 m. Hence, Cyperaceae

209    is the dominant family in the herb community.

210         A family number of 12 is used as a dividing line, and based on that number, the herb community is

211    divided into two altitudinal ranges (Fig. 3 and Fig. 4). The first range is between 1324 m and 2395 m and

212    contains 7 elevations. In this range, each elevation has a family number that exceeds 12 except for 1586 m

213    (only 9 families). The second range is between 2460 m and 2745 m and contains 6 elevations with a family

214    number less than 12. Therefore, from lower elevations in the first range to higher elevations in the second

215    range, the family number presents a decreasing trend. Specifically, the family number increases initially and

216    then decreases with increasing elevation ($P<0.01$), showing a unimodal change pattern with high values at

217    central elevations (Fig. 4). It can be concluded that the family number of the herb community reaches its

218    maximum at an intermediate elevation.

219    3.1.2    *Variations in herbaceous life forms with elevation*

220    Grasses, sedges and weeds were separated from the herb community (Fig. 5). The importance value of sedges

221    is greater than that of grasses and weeds at different elevation gradients except for 2690 m. In the first

222    elevation range from 1324 m to 2395 m, the importance value of the sedges is obviously greater than that of

223    grasses and weeds, with mean differences of 43.08% and 43.97%, respectively; while in the second elevation

224    range from 2460 m to 2745 m, the dominance of the sedges tends to decrease and its mean differences are

225    12.79% and 11.86% with respect to the grasses and weeds. Therefore, the importance value of the sedges

226    conforms to a decreasing pattern with increased elevation ($P<0.05$).

227         Relative to decrease in the importance value of the sedges, the importance values of the grasses and

228    weeds increase with increasing elevation ($P<0.05$), and the most significant correlation ($P<0.01$) occurs

229    between weeds and the elevation gradient. The importance values of sedges, grasses and weeds exhibit

230    significant exponential relationships with altitudinal gradients ($P<0.05$); the coefficients of determination are

231    ranked from lowest to highest as sedges, grasses and weeds, respectively. It can be concluded that altitudinal

232    gradients have greater effects on weeds, and more weeds and grasses are distributed at higher elevations

233    whereas sedges tend to grow at lower elevations.

234 3.1.3 *Variations in herbaceous species diversity indices with elevation*

235 Normal function fitting was conducted on the relationships between species diversity and altitudinal gradients

236 in the herb community (Table 1). Not all of the functional relationships of the Richness index are significant

237 ($P$>0.05). In these relationships, the highest $R^2$ value is associated with a quadratic polynomial function,

238 according to which 34.11% of the variation in the Richness index is caused by altitudinal gradients.

239 All of the functional relationships of the Simpson index are significant with respect to the altitudinal

240 gradients ($P$<0.05), and the highest $R^2$ value is also associated with a quadratic polynomial function, which

241 indicates that 35.49% of the variation in the Simpson index is caused by altitudinal gradients. Not all of the

242 functional relationships of the Shannon index are significant ($P$>0.05), and the highest $R^2$ value is associated

243 with an exponential function, which indicates that 21.59% of the variation in the Shannon index is caused by

244 altitudinal gradients. All of the functional relationships of the Pielou index reach the most significant level

245 ($P$<0.01), and a quadratic polynomial function results in the highest $R^2$ value in these relationships; according

246 to this function, 54.65% of the variation in the Pielou index is caused by altitudinal gradients.

247 Hence, relationships of herbaceous species diversity can be fit to altitudinal gradients using a quadratic

248 polynomial function that explains an average of 41.42% of the variation in species diversity. An increase in

249 elevations results in an increase in the Simpson index, Shannon index and Pielou index, whereas the Richness

250 index demonstrates a unimodal change trend with its peak value occurring intermediate elevations, illustrating

251 a distribution pattern of greater species diversity at higher elevation gradients, where fewer herbaceous species

252 occur but are evenly and steadily distributed (Fig. 6).

253 **3.2 Altitudinal patterns of species diversity in the shrub community**

254 3.2.1 *Variations in shrub families with elevation*

255 Relative to the herb community, fewer families in the shrub community are distributed at different elevation

256 gradients, and the variation range is between 2 and 5 families (Fig. 7). More families are distributed in central

257 elevations of 1586 m and 1950 m, with family numbers of 4 and 5, respectively, whereas fewer families are

258 distributed at lower elevations of 1324 m and 1370 m as well as a higher elevation of 2675 m, with

259 corresponding family numbers of 2.5 and 2. The family number exhibits the most significant changes with

260 altitudinal gradients in the shrub community ($P$<0.01), demonstrating a unimodal pattern with a peak value at

261   intermediate elevations, i.e. the family number of the shrub community has the greatest distribution at an

262   intermediate elevation.

263       Across the 6 altitudinal gradients of the shrub community, the families with the highest importance value

264   are not the same and are successively Asteraceae (55.92%), Rosaceae (20.72%), Ulmaceae (17.65%),

265   Elaeagnaceae (33.44%), Saxifragaceae (67.36%) and Leguminosae (79.83%) (Fig. 7). At a lower elevation of

266   1324 m, Asteraceae dominates, whereas the dominance of Leguminosae increases at a higher elevation of 2675

267   m. Rosaceae exists at various elevation gradients, with a mean importance value of 13.17% and is thus

268   considered as a dominant family in the shrub community. The importance value of Rosaceae decreases initially

269   and then increases with increasing elevations ($P<0.05$), exhibiting a unimodal change pattern with a small

270   value at intermediate elevations, i.e. the importance value of the dominant family in the shrub community is

271   the lowest at an intermediate elevation.

272   3.2.2   *Variations in shrub species diversity indices with elevation*

273   The fitting of functional relationships between species diversity indices and altitudinal gradients in the shrub

274   community indicates that a quadratic polynomial is the best function, but it is not significant (Table 1). Based

275   on this function, the amount of variation in species diversity explained by altitudinal gradients is higher than

276   that explained by other conventional functions: 56.78% for the Richness index, 73.48% for the Simpson index,

277   69.2% for the Shannon index, and 51.89% for the Pielou index.

278       Therefore, the relationships between shrub species diversity and altitudinal gradients accord with the

279   quadratic polynomial functions, and the amount of variation explained by altitudinal gradients reaches 62.84%

280   for the different species diversity indices. Species diversity indices tend to decrease with increased elevation

281   ($P>0.05$), indicating that most shrub species are primarily distributed at lower elevations, where species are

282   more balanced and stabilized and thus produce a distribution pattern of greater species diversity (Fig. 8).

283   **3.3   Altitudinal patterns of species diversity in the arbor community**

284   3.3.1   *Variations in arboreal families with elevation*

285   Similar to the shrub community, the arbor community also has a smaller distribution at different elevation

286   gradients, and its variation range is between 1 and 5 families (Fig. 9). A family number of 3 is used as a

287   dividing line to separate the arbor community. Arbor communities with a family number higher than 3 develop

288    at intermediate elevations of 1900, 2001 and 2179 m, and their family numbers are 5, 4 and 4, respectively.

289    Arbor communities with a family number smaller than 3 develop at lower elevations (family number of 2) of

290    1740 m and 1892 m, as well as higher elevations (family number of 1) of 2222, 2270, 2395, 2571 and 2610 m,

291    and arbor communities with a family number of 3 develop at lower elevations of 1459 m and 1586 m, as well

292    as an intermediate elevation of 1950 m. Changes in the exponential function of the family number reach a

293    significant level with altitudinal gradients in the arbor community ($P<0.05$), assuming a decreasing pattern.

294    That is to say, the family number of the arbor community has a maximum distribution at lower elevations.

295        Across 13 altitudinal gradients of the arbor community, the highest importance value is obtained for

296    Pinaceae, Salicaceae and Betulaceae (Fig. 9). For Pinaceae, maximum importance values with an average of

297    49.14% occur at 9 elevations of 1459, 1586, 1892, 1900, 2222, 2270, 2395, 2571 and 2610 m; for Salicaceae,

298    maximum importance values with an average of 57.17% occur at 2 elevations of 1740 m and 2001 m; and for

299    Betulaceae, 2 elevations of 1950 m and 2179 m have maximum importance values; their mean is 28.65%. At

300    intermediate elevations from 1950 m to 2179 m, Salicaceae and Betulaceae species dominate, whereas

301    Pinaceae species only appear at higher elevations exceeding 2222 m, indicating a transformation of the arbor

302    community from a mixed coniferous and broad-leaved forest to a pure coniferous forest. Therefore, Pinaceae is

303    a dominant family in the arbor community and is distributed across all elevations except 1740 m (the pure

304    broad-leaved forest). With increasing elevation, the importance value of Pinaceae initially decreases and then

305    increases ($P<0.05$), indicating a unimodal change pattern with a small value at intermediate elevations, i.e., the

306    importance value of the dominant arbor family is minimal at an intermediate elevation.

307        According to life forms, arboreal species are divided into deciduous broad-leaved trees, deciduous

308    coniferous trees and evergreen coniferous trees (Table 2). Deciduous broad-leaved trees are mainly distributed

309    at medium and low elevation gradients of less than 2179 m, and their importance values show a non-significant

310    tendency with increasing elevation ($R^2<0.1$, $P>0.05$); deciduous coniferous trees are mainly distributed at

311    intermediate and high elevation gradients that exceed 1892 m, and their importance values tend to increase

312    with increasing elevations ($R^2=0.3$, $P>0.05$). Evergreen coniferous trees are distributed across all elevations

313    except 1740 m, and their importance values tend to decrease initially and then to increase following an

314    increase in elevation ($R^2=0.4$, $P>0.05$). Hence, the responses of the importance values of various arbor species

315    to altitudinal gradients are successively greater for evergreen coniferous trees than for deciduous coniferous

316    trees, followed by deciduous broad-leaved trees. It can be concluded that the effects of altitudinal gradients on

317    the importance values of coniferous trees are greater than those of broad-leaved trees, and the effects of

318    altitudinal gradients on the importance values of evergreen trees are greater than those of deciduous trees.

319    3.3.2    *Variations in arboreal species diversity indices with elevation*

320    The fitting of regular functions indicated that quadratic polynomial functions also exist in correlations between

321    species diversity indices and altitudinal gradients in the arbor community. In these correlations, the Pielou

322    index reached the most significant level with respect to altitudinal gradients ($P<0.01$) (Table 1). The amount of

323    variation in species diversity indices explained by altitudinal gradients is higher for the quadratic polynomial

324    functions than for the other regular functions, i.e., 37.17% for the Richness index, 42.09% for the Simpson

325    index, 39.66% for the Shannon index, and 79.75% for the Pielou index.

326        Therefore, relationships between arbor species diversity and altitudinal gradients conform to quadratic

327    polynomial functions; the average amount of variation explained is 49.67%. With increasing elevation,

328    unimodal change trends are observed, with an initial increase and then a decrease for the Richness, Simpson

329    and Shannon indices ($P>0.05$), whereas a significant increase is observed in the Pielou index ($P<0.01$),

330    illustrating that arbor species are mostly distributed at an intermediate elevation, where species are in balance

331    and stable and they thus develop a distribution pattern of higher species diversity (Fig. 10).

332    **4    DISCUSSION**

333    **4.1    MDE hypothesis**

334    Gradient features of species diversity of plant communities refer to regular changes in species diversity along a

335    gradient of environmental factors at the community level (Zhao et al, 2017a; Zhao et al, 2017b), while the

336    altitudinal gradient includes gradient effects of multiple environmental factors; thus, it is important to study

337    altitudinal patterns of species diversity to reveal changes in biodiversity along environmental gradients. In this

338    study, forest ecosystems were separated into three hierarchical structures: arbor, shrub and herb communities,

339    and then the altitudinal patterns and factors that influence species diversity of mountainous vegetation at the

340    plant level were determined. We discovered that correlations of species diversity with altitudinal gradients

341    conformed to unimodal change patterns for herb, shrub and arbor communities, which presented greater

342    species diversity at higher, lower and intermediate elevations, respectively. Moreover, more weeds and grasses

343    developed at higher elevations, whereas more sedges occurred at lower elevations, and responses of the

344    importance values of arbor species to altitudinal gradients demonstrated the following variation patterns:

345    evergreen coniferous trees had higher importance values than deciduous coniferous trees, followed by

346    deciduous broad-leaved trees.

347        The width and range of species distribution along geographical gradients reflect species ecological

348    adaptability, diffusivity and evolutionary history (Kreft and Barthlott, 2006). To some extent, geographical

349    distribution patterns of species diversity can be interpreted as outcomes of synthetic actions across altitudinal

350    gradients resulting from eurychoric species with a greater distribution width and stenochoric species with a

351    smaller distribution range along geographical gradients (Kreft and Barthlott, 2006). Hence, the MDE,

352    environmental gradient, distribution area, human disturbance and habitat heterogeneity all have effects on the

353    vertical distribution patterns of species diversity (Greenslade, 1977; White and Miller, 1988). According to the

354    MDE hypothesis, there is overlap in the distribution range of species along altitudinal gradients; the highest

355    overlap intensity occurs at intermediate elevations. There is relatively low overlap intensity at low and high

356    elevation areas, and the peak values of species diversity occur at intermediate elevations. This shows that MDE

357    is another important factor that affects the distribution patterns of species diversity along regional altitudinal

358    gradients, in addition to temperature, precipitation and the terrain.

359    A large number of studies have already verified that MDE is a significant mechanism that influences the

360    gradient patterns of species diversity, which not only functions along altitudinal gradients but also acts along

361    latitudinal and temporal gradients (Bachman et al, 2004; Colwell and Gotelli, 2004; Kattan and Franco, 2004;

362    Morales and Inouye, 2005). However, the effects of MDE on species diversity patterns are a highly

363    controversial issue. Some studies considered MDE as the main factor that results in unimodal patterns of

364    species diversity (McCain, 2004; Morales and Inouye, 2005), whereas other studies affirmed that the effects of

365    MDE are smaller in contrast to the functions of the distribution area, environmental gradient and other factors

366    (Bachman et al, 2004; Kattan and Franco, 2004). Besides MDE, other factors may also lead to unimodal

367    vertical gradient patterns of species diversity, such as plant productivity, human disturbance and the regional

368    climate (McCoy, 1990; Greenslade, 1977). Our research indicated that the relationships of species diversity

369 conformed to unimodal change patterns along altitudinal gradients for mountainous herb, shrub and arbor

370 communities in a semi-arid region of the temperate zone. It can be concluded that vertical patterns of species

371 diversity with a unimodal type may be a more universal phenomenon, relative to monotone decreasing or

372 increasing patterns of species diversity with increasing elevation.

373 **4.2    Factors influencing MDE at the plant level**

374 Species diversity of different life forms responds differently to the environment, and plant species with

375 different life forms present different diversity patterns along altitudinal gradients (Ojeda and Arroyo, 2000). In

376 New Zealand, the species number of arborous plants decreased with increasing elevation, and the total species

377 number of all plants also decreased significantly, while species diversity had no significant distribution trend in

378 response to altitudinal gradients when plants under layers were considered (Ohlemueller and Wilson, 2000).

379 Regarding arborous plants, negative correlations of species diversity generally exist in various ecosystems,

380 with a decreasing trend in response to increasing elevation. In studies in tropical forests, although species

381 diversity changed slightly in arborous layers along altitudinal gradients, the species diversity of arborous plants

382 demonstrated a monotonous decreasing trend with elevation due to a reduction in species diversity of shrubs in

383 response to increased elevation (Vazquez and Givnish, 1998). Research conducted in the temperate forests of

384 Slovakia also showed that species diversity of arborous plants decreased with increasing elevation (Dolezal

385 and Srutek, 2002).

386     MDE is a common pattern of species diversity of arborous plants along altitudinal gradients. Research

387 from Kinabalu Mountain in Sabah, Malaysia, indicated an obvious MDE pattern of species number with

388 elevation (Nor, 2001); and in Haleakala Mountain, Hawaii, USA, the highest species diversity occurred at

389 intermediate elevations, which also accords with the MDE hypothesis (Kitayama, 1996). The MDE hypothesis

390 was also proved by studies conducted in Yu Mountain of Taiwan and Emei Mountain of Szechwan in China

391 (Tang and Ohsawa, 1997). Our study area, located on the Loess Plateau of China, belongs to a semi-arid

392 mountainous area in the temperate zone where the maximum species diversity of the arbor community

393 occurred at intermediate elevations; this result agrees with the MDE hypothesis. The MDE pattern of species

394 diversity is caused by precipitation, which is the highest at intermediate elevations (Nor, 2001). Of course, the

395 species diversity of arborous plants responds to other altitudinal patterns. For example, species diversity

396    increased with increasing elevations in evergreen broad-leaved forests of Japan, but this pattern appeared

397    mainly at lower altitudinal gradients (Itow, 1991).

398        There are many factors that affect the distribution of herbaceous plants, so the variations in species

399    diversity with elevation are complex. In Siskiyou Mountain in Oregon, USA, species diversity of herbaceous

400    plants had a significantly positive correlation with elevation. This correlation occurred mainly due to an

401    increase in the number of grass species, which was the primary reason that radiation was enhanced by a drastic

402    reduction in community coverage as a result of increased elevation, and consequently, there was an increase in

403    the species diversity of herbaceous plants (Dolezal and Srutek, 2002). In this study, we also found that the herb

404    community exhibited higher species diversity at higher elevations; more weeds and grasses were distributed at

405    higher elevations, whereas more sedges were distributed at lower elevations. In addition, a decrease in species

406    diversity with increased elevation is a more familiar pattern for herbaceous plants, which exist in temperate

407    (Glenn-Lewin, 1977) and tropical (Vazquez and Givnish, 1998) forests.

408        In arid grasslands of the temperate zone, species diversity indicated a distribution pattern of MDE (Wang

409    et al, 2002). For example, the species diversity of herbaceous plants presented an MDE pattern in drought

410    areas of Siskiyou Mountain (Whittaker, 1960). In semi-humid mountains of the temperate zone, the species

411    diversity of herbaceous plants was principally in control of the community structure, but community coverage

412    did not respond uniformly to elevation; therefore, relationships between the species diversity of herbaceous

413    plants and altitudinal gradients were not clear. Studies in New Zealand also showed that there were no evident

414    distribution trends for species diversity of herbaceous plants along altitudinal gradients (Ohlemueller and

415    Wilson, 2000). The evolutionary process also affects the altitudinal distribution of species diversity. In low

416    bush communities of Chile, the species diversity of herbaceous plants declined with increasing elevation after

417    longstanding succession but increased during the early stage of succession (Sax, 2002).

418        The major factors that control the distribution areas of species differ among different families and genera,

419    and thus the vertical distribution patterns of species diversity differ. For example, the distribution of fern and

420    Melastomataceae species is principally related to humidity, that of Acanthaceae and Bromeliaceae species is

421    correlated with temperature, and that of Araceae species is related to transpiration (Kessler, 2000). Due to

422    various distribution patterns of these environmental parameters along altitudinal gradients, the distribution

423    patterns of species diversity show large changes with elevation (Kessler, 2000). Research conducted in Gongga

424    Mountain, China, showed that the diversity of species with different floral components exhibited different

425    distribution patterns along altitudinal gradients due to differences in species origin (Shen et al, 2001). We also

426    discovered that family numbers in the herb and shrub communities on the Loess Plateau presented variation

427    patterns of MDE along the altitudinal gradient. However, the family number in the arbor community showed a

428    monotone decreasing pattern, and the importance values of dominant families in the shrub (Rosaceae) and

429    arbor (Pinaceae) communities exhibited changing patterns in contrast to MDE. In our study, only the family

430    numbers in the herb and shrub communities, as well as species diversity in the arbor community, conformed to

431    the MDE hypothesis. Therefore, we conclude that the MDE hypothesis of species diversity of mountainous

432    vegetation is influenced by life form and the family flora of the communities in this temperate semi-arid region

433    of China.

434    **5    CONCLUSION**

435    Eastern mountains in the Loess Plateau have obvious elevation gradients. The forest ecosystems in these areas

436    have intact structural layers of arbor, shrub and herb communities. The family number of the herb community

437    with Cyperaceae as the dominant family follows the MDE pattern across altitudinal gradients, but there is

438    greater species diversity at higher elevations, and 41.42% of the variation can be explained, which does not

439    conform to the MDE hypothesis. Moreover, weeds and grasses occur mostly at higher elevations, whereas

440    sedges occur mostly at lower elevations, and the importance value of sedges is greater than that of weeds and

441    grasses.

442        The family number of the shrub community with Rosaceae as the dominant family also exhibits the MDE

443    pattern across altitudinal gradients, but the importance value of the dominant family shows the opposite pattern

444    for MDE with elevation, i.e., higher species diversity at lower elevations, and 62.84% of the variation can be

445    explained, which does not conform to the MDE hypothesis.

446        The family number and importance value of the arbor community with Pinaceae as the dominant family

447    do not present MDE patterns along variations in altitudinal gradients. However, higher species diversity is

448    observed at intermediate elevations; 49.67% of the variations can be explained, which conforms to the MDE

449    hypothesis. In addition, the responses of the importance values of different species demonstrate variation

450  patterns that are greater for evergreen coniferous trees than for deciduous coniferous and deciduous broad-

451  leaved trees.

452      As a whole, the family number of the herb and shrub communities as well as the species diversity of the

453  arbor community accord with the MDE hypothesis, indicating that the MDE hypothesis of species diversity is

454  influenced by community life form and family flora of mountainous vegetation in this temperate semi-arid

455  region of China.

456  **ACKNOWLEDGMENTS**

461  **LEGENDS**

462  **Figure legends**

463  **FIGURE 1** Distribution of experimental plots. Among 21 altitudinal gradients, communities across 9, 8 and 4

464  elevations were observed at Guancen Mountain, Guandi Mountain and Wulu Mountain, respectively. At

465  Guancen Mountain, 6 quadrats were used for herbs, 1 for shrubs and 6 for arbor communities; at Guandi

466  Mountain, 5, 2 and 5 quadrats were used for herb, shrub and arbor communities, respectively; at Wulu

467  Mountain, the corresponding number of quadrats were 3, 3 and 2 in the herb, shrub and arbor communities.

468  **FIGURE 2** Quadrat frame used in the experiment. The frame is made of aluminum, which is very light to

469  carry. In the interior of the frame, 100 grids were separated to accurately measure plant frequency and

470  coverage. Frequency was calculated by the number of grids in which a plant appeared divided by 100.

471  Coverage was calculated by the number of hits of litter or plants divided by 100.

472  **FIGURE 3** Distribution of the importance values of the herb family at different elevations. There were 14

473  elevations for the herb community. At each elevation, the importance values of the herb family were arranged

474  in ascending order or descending order for the sake of selecting the largest one. Data for each herb family were

475  averaged from 20 quadrats at each elevation.

476  **FIGURE 4** Variation in herb family number with altitudinal gradients. The family number of the herb

477    community was counted at each elevation, and curve fittings were conducted on the variation in family number

478    with altitudinal gradients. Data for the family number were obtained from 20 quadrats at each elevation.

479    **FIGURE 5** Distribution and variation of the importance values of grasses, sedges and weeds at different

480    elevations. The grass, sedge and weed species belonged to Gramineae, Cyperaceae and other families,

481    respectively. At each elevation, species of the herb community were divided into these three life forms. Their

482    importance values were used in regression analyses with altitudinal gradients. Data for the importance values

483    of grasses, sedges and weeds were averaged from 20 quadrats at each elevation.

484    **FIGURE 6** Variation in herb species diversity with altitudinal gradients. α-Diversity indices for each elevation

485    were calculated, such as the Richness index, Simpson index, Shannon index and Pielou index. Their trends

486    were curve-fitted with altitudinal gradients. Species from 20 quadrats were first merged at each elevation and

487    then these indices were calculated according to relative abundance, relative height, relative frequency and

488    relative coverage. One data point from each elevation represented the index of species diversity.

489    **FIGURE 7** Distribution and variation of importance values and numbers of shrub families at different

490    elevations. There were 6 elevations for the shrub community. At each elevation, the importance values of the

491    shrub families were arranged in ascending order to obtain the largest one. Data for each shrub family were

492    averaged from 4 quadrats at each elevation. Finally, regression analyses were carried out on relationships

493    between the family number of the shrub community and the importance value of the dominant family

494    (Rosaceae) along altitudinal gradients.

495    **FIGURE 8** Variation in shrub species diversity with altitudinal gradients. Similar to the herb community, the

496    Richness index, Simpson index, Shannon index and Pielou index were also chosen as species diversity indices

497    in the shrub community. However, their calculations were merely basing on relative abundance, relative height

498    and relative coverage. Species from 4 quadrats were initially merged at each elevation, and then these indices

499    were calculated. One data point from each elevation represented the index of species diversity. Therefore, six

500    data points were used in the curve-fitting analyses along altitudinal gradients.

501    **FIGURE 9** Distribution and variation of the importance values and numbers of arbor families at different

502    elevations. Thirteen elevations were observed for the arbor community. At each elevation, the importance

503    values of the arbor families were arranged in ascending order to obtain the largest one. Data for each arbor

504  family were averaged from 2 quadrats at each elevation. Regression analyses were performed on the

505  relationships between the family number of the arbor community and the importance value of the dominant

506  family (Pinaceae) along altitudinal gradients.

507  **FIGURE 10** Variation in arbor species diversity along altitudinal gradients. Similar to the shrub community,

508  the Richness index, Simpson index, Shannon index and Pielou index were also chosen as species diversity

509  indices; their calculations were based on relative abundance, relative height and relative coverage. Species

510  from 2 quadrats were initially merged at each elevation, and then these indices were calculated. One data point

511  from each elevation represented the index of species diversity. Therefore, 13 data points were used in the

512  curve-fitting analyses across the altitudinal gradients.

513  **Table Legends**

514  **TABLE 1** Various functional relationships between species diversity and altitudinal gradients. The α-Diversity

515  indices used in this study are the Richness index, Simpson index, Shannon index and Pielou index.

516  Conventional functions selected in this study are the exponential function, linear function, logarithmic function,

517  quadratic polynomial function and power function. Data not presented in parentheses are the coefficients of

518  determination of the equations, and data in parentheses are the P values of the significance testing of the

519  equations. The number of data points are 14, 6 and 13 for the herb, shrub and arbor communities, respectively.

520  **TABLE 2** Distributions of importance values of various arbor species at different elevations. Thirteen

521  elevations represent the arbor community. Arbor species are divided into deciduous broad-leaved trees,

522  deciduous coniferous trees and evergreen coniferous trees. "—" indicates no value at that elevation. At 1740 m,

523  there was only one arbor species, a deciduous broad-leaved tree. Data for different arbor species were obtained

524  from 2 quadrats at each elevation.

525  **SUPPLEMENTARY TABLE** Statistics pertaining to the growth indices of all plant species in the plots.

526  Growth indices of height, coverage, density and frequency were averaged for each plant species in all plots

527  according to life forms. Here, herbaceous species present these 4 indices, and shrub and arbor species present 3

528  indices, i.e., height, coverage and density.

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633    stoichiometry on biomass and species diversity of the Artemisia ordosica community in Habahu National Nature Reserve. *Acta*

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638    plant species diversity and biomass of common species in the Hulunbuir Leymus chinensis meadow steppe. *Acta Prataculturae*
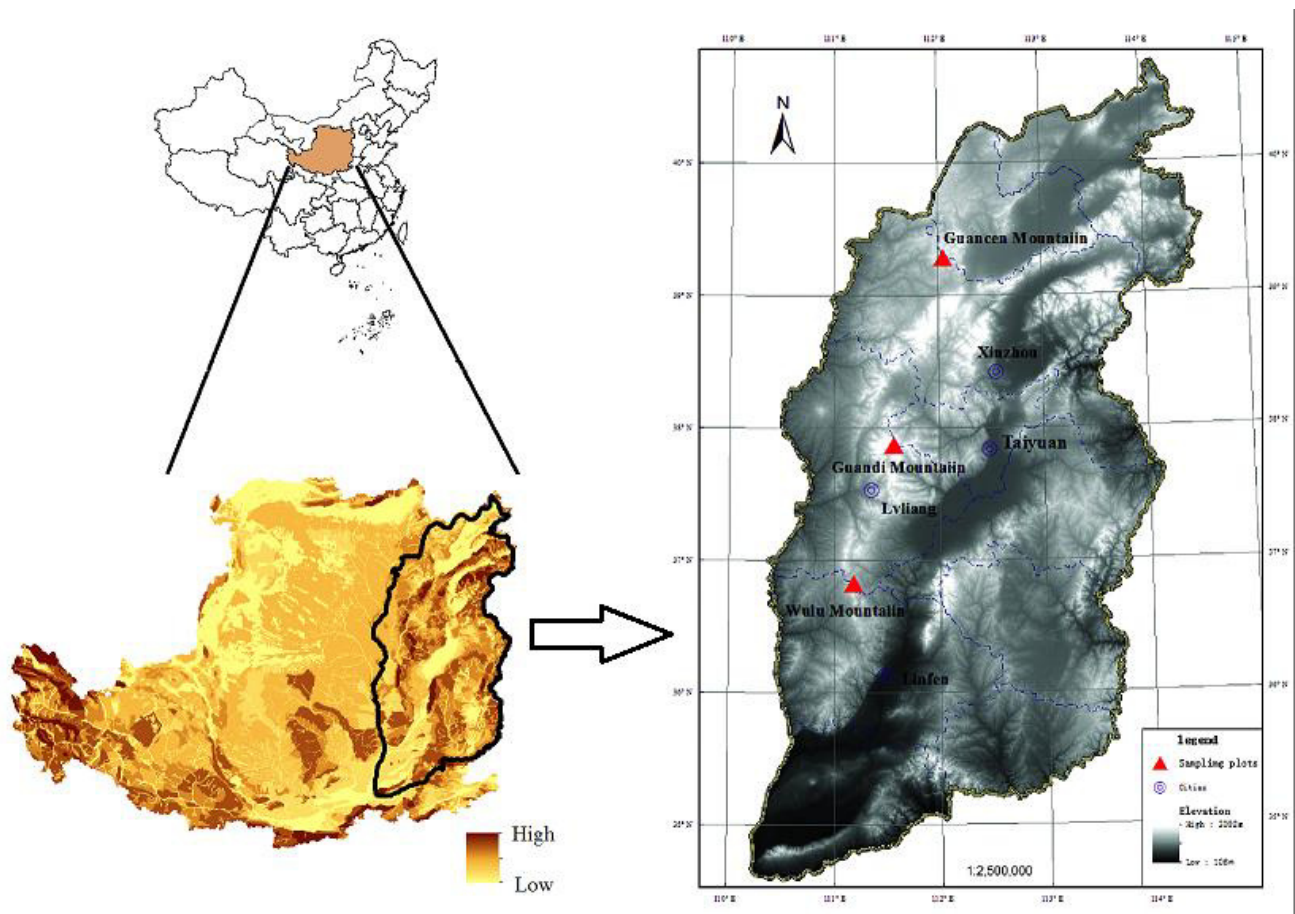
639    *Sinica* **26:** 108-117. DOI: 10.11686/cyxb2017171

640    Yu BW, Liu GH, Liu QS, Wang XP, Feng JL, Huang C (2018) Soil moisture variations at different topographic domains and

641    land use types in the semi-arid Loess Plateau, China. *Catena* **165:** 125-132. DOI: 10.1016/j.catena.2018.01.020

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645    *the Total Environment* **626:** 842-850. DOI: 10.1016/j.scitotenv.2018.01.156

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647    Loess Plateau, China. *Catena* **163:** 165-171. DOI: 10.1016/j.catena.2017.12.016

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651    diversity of sandy communities during the process of restoring succession in the Horqin Sandy Land, China. *Acta Ecologica*

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653    Zhu L, Xu GQ, Li Y, Tang LS, Niu ZR (2017) Relationships among plant species diversity, biomass, and the groundwater table

654    in the Hailiutu River basin. *Acta Ecologica Sinica* **37**: 1912-1921. DOI: 10.5846/stxb201510302194

**Figure 1**(on next page)

Figures in manuscript

All figures in manuscript.

**FIGURE 1**

**FIGURE 2**

**FIGURE 3**

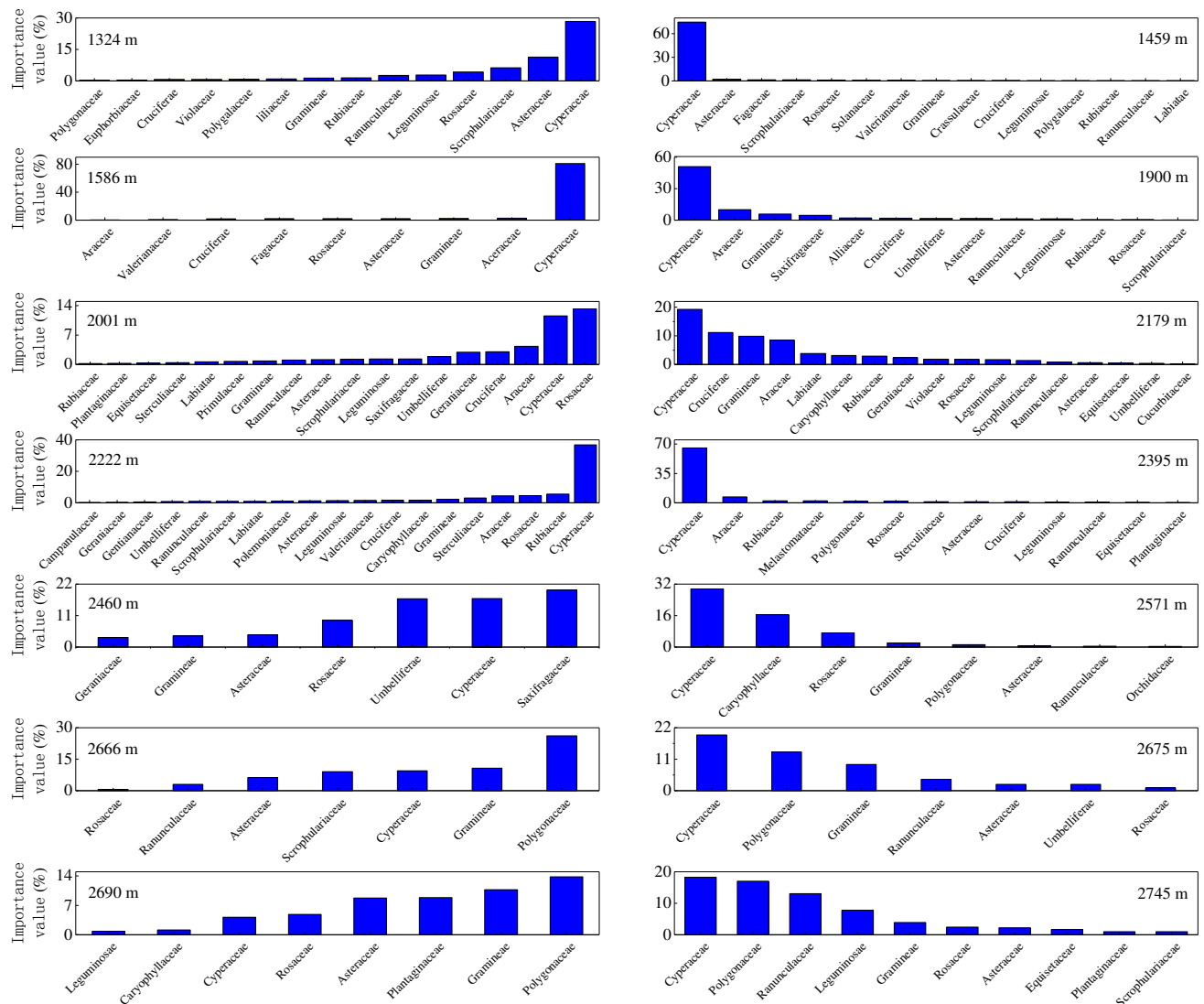**FIGURE 4**



$y = -1\text{E-}05x^2 + 0.0446x - 26.246$

$R^2 = 0.514, P=0.009$

**FIGURE 5**

**FIGURE 6**



$y = -2E-05x^2 + 0.0828x - 52.979$

$y = 8E-08x^2 - 0.0001x + 0.6$

$y = 1.007e^{0.0003x}$

$y = 2E-07x^2 - 0.0005x + 0.8559$

**FIGURE 7**

**FIGURE 8**



Richness index: $y = -8\text{E-}06x^2 + 0.0309x - 20.464$

Simpson index: $y = -3\text{E-}07x^2 + 0.0009x + 0.1023$

Shannon index: $y = -1\text{E-}06x^2 + 0.0038x - 1.5486$

Pielou index: $y = 1\text{E-}07x^2 - 0.0007x + 1.5266$

Altitude (m)

**FIGURE 9**

**FIGURE 10**



$y = -7\text{E-}07x^2 + 0.003x - 2.4332$

$y = -7\text{E-}06x^2 + 0.0283x - 23.249$

$y = -2\text{E-}06x^2 + 0.0076x - 6.3849$

$y = -3\text{E-}07x^2 + 0.0012x - 0.5804$
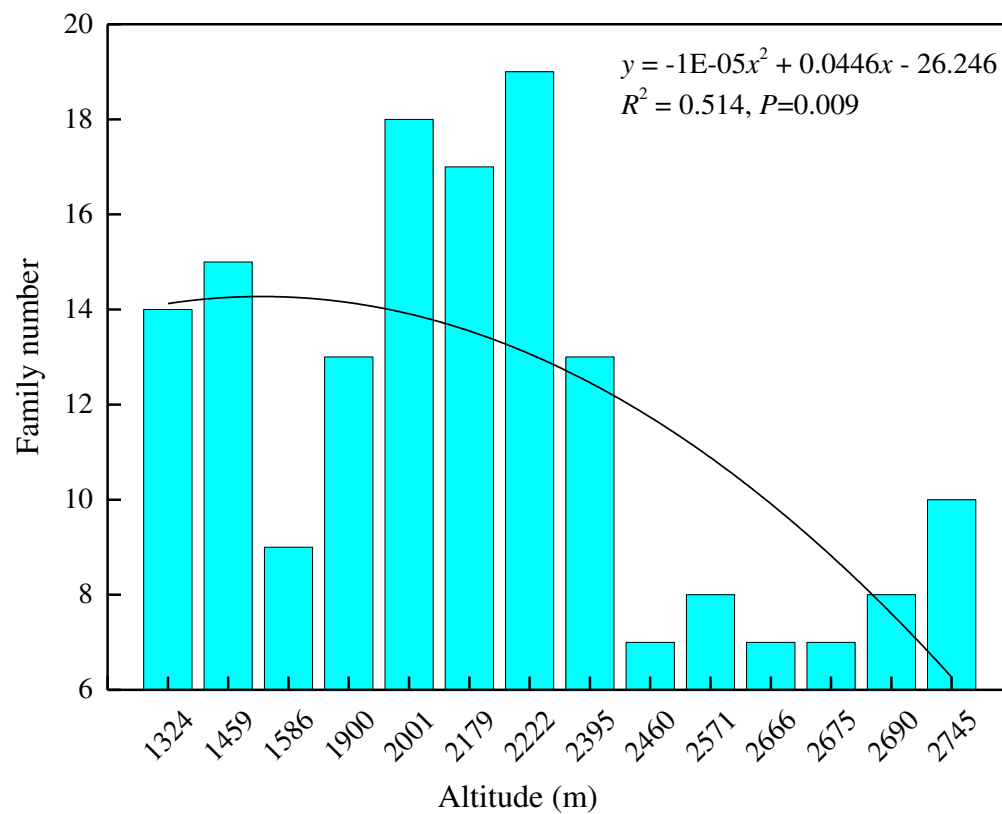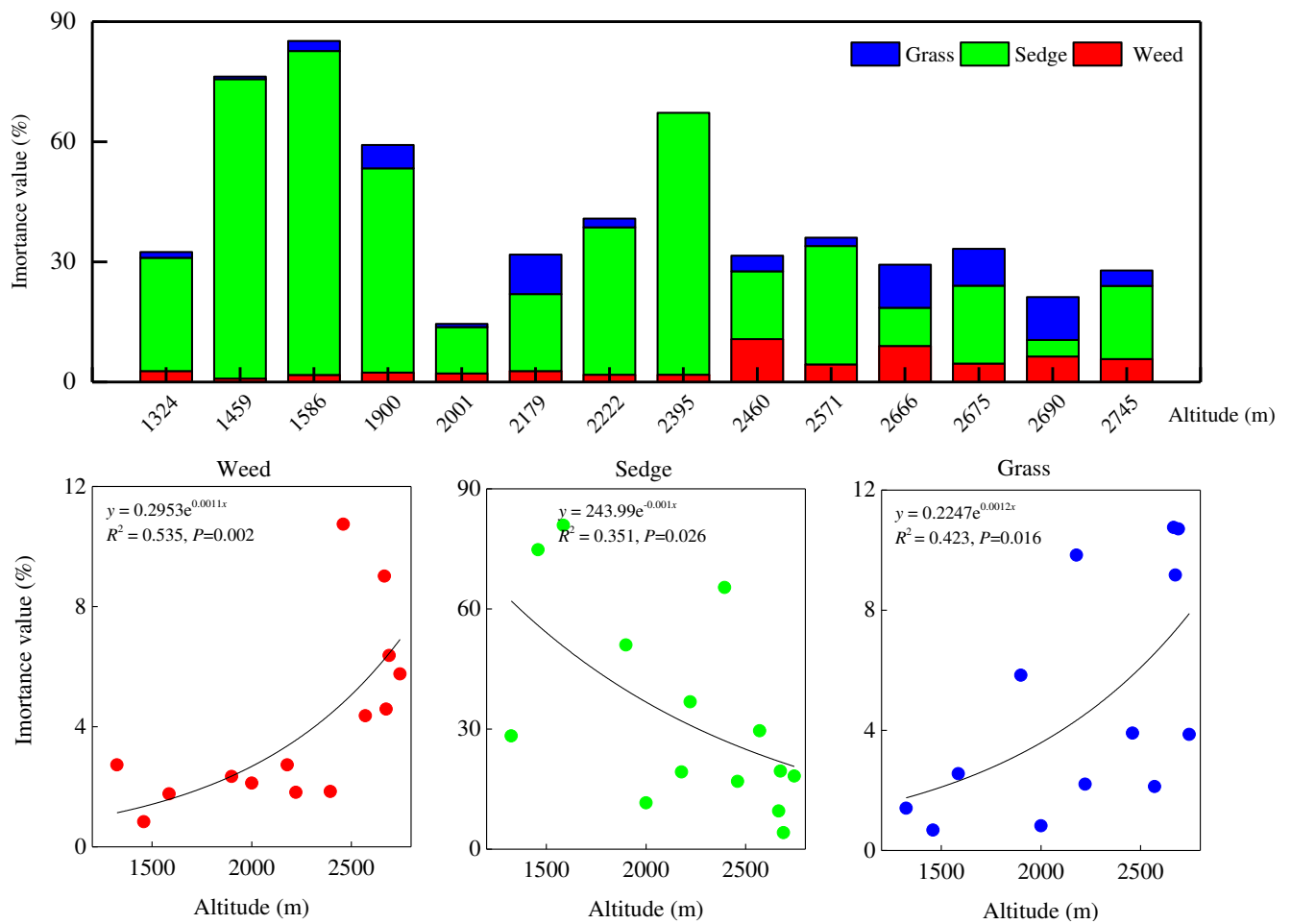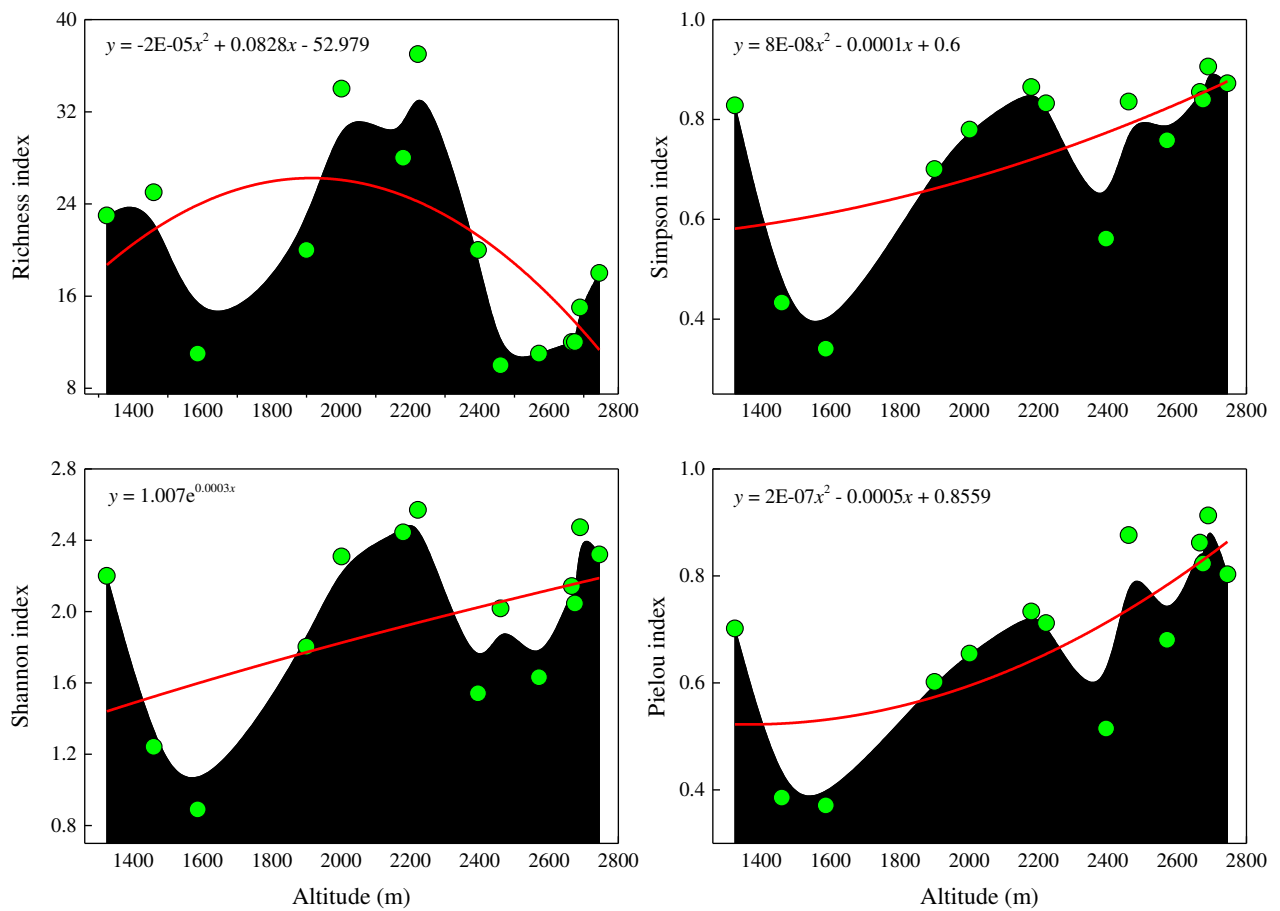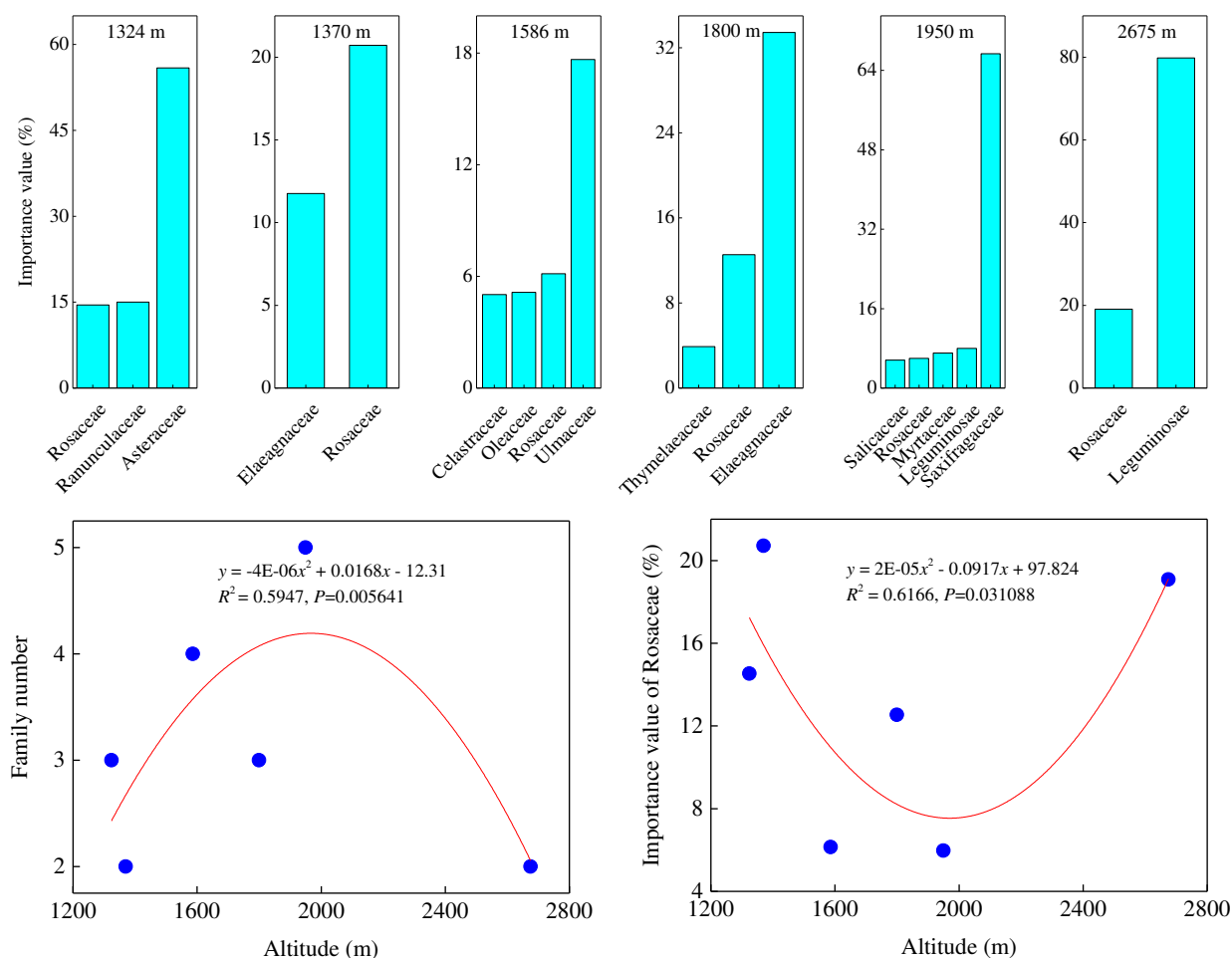
**Table 1**(on next page)

Tables in manuscript.

All tables in manuscript.

**TABLE 1**

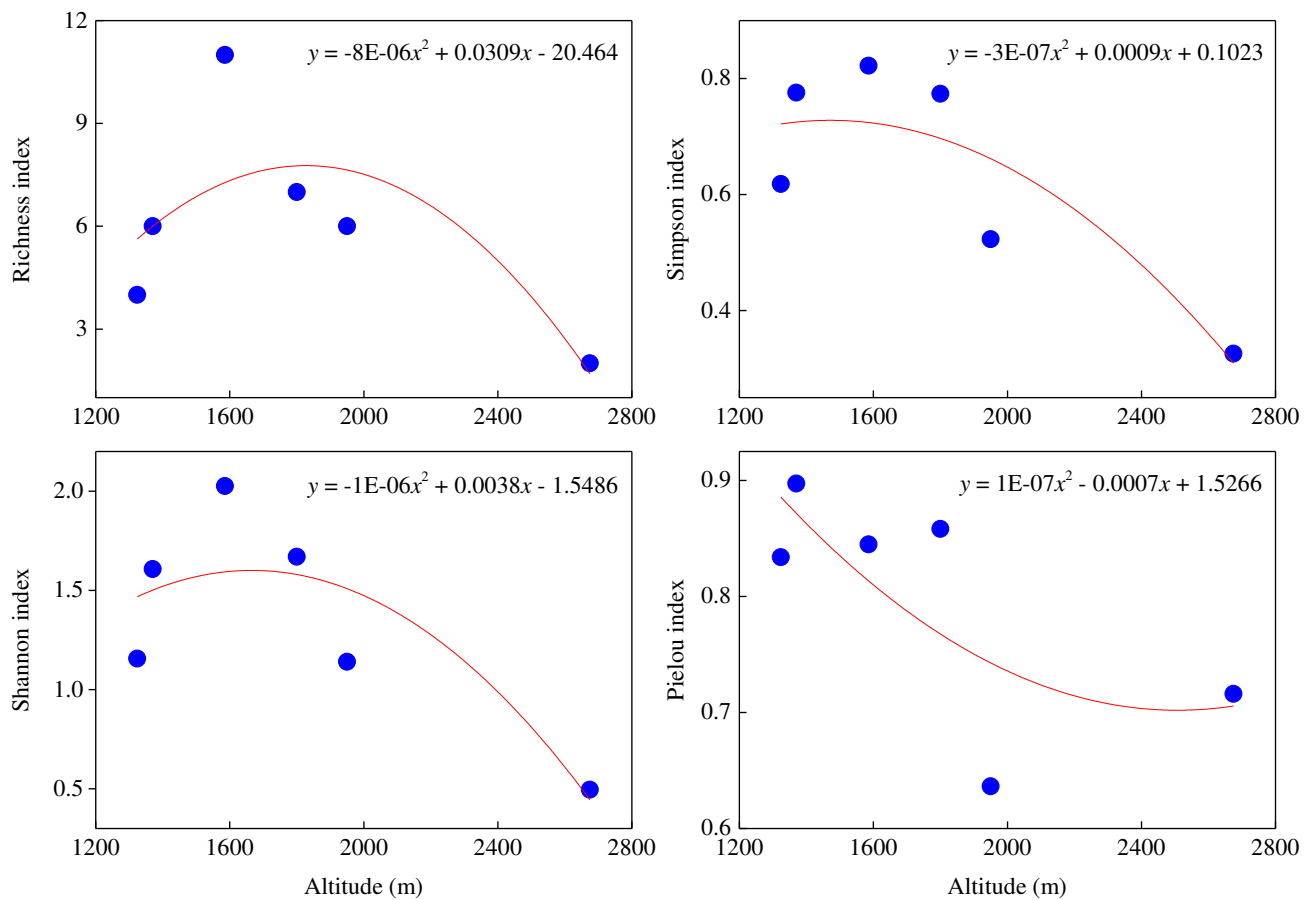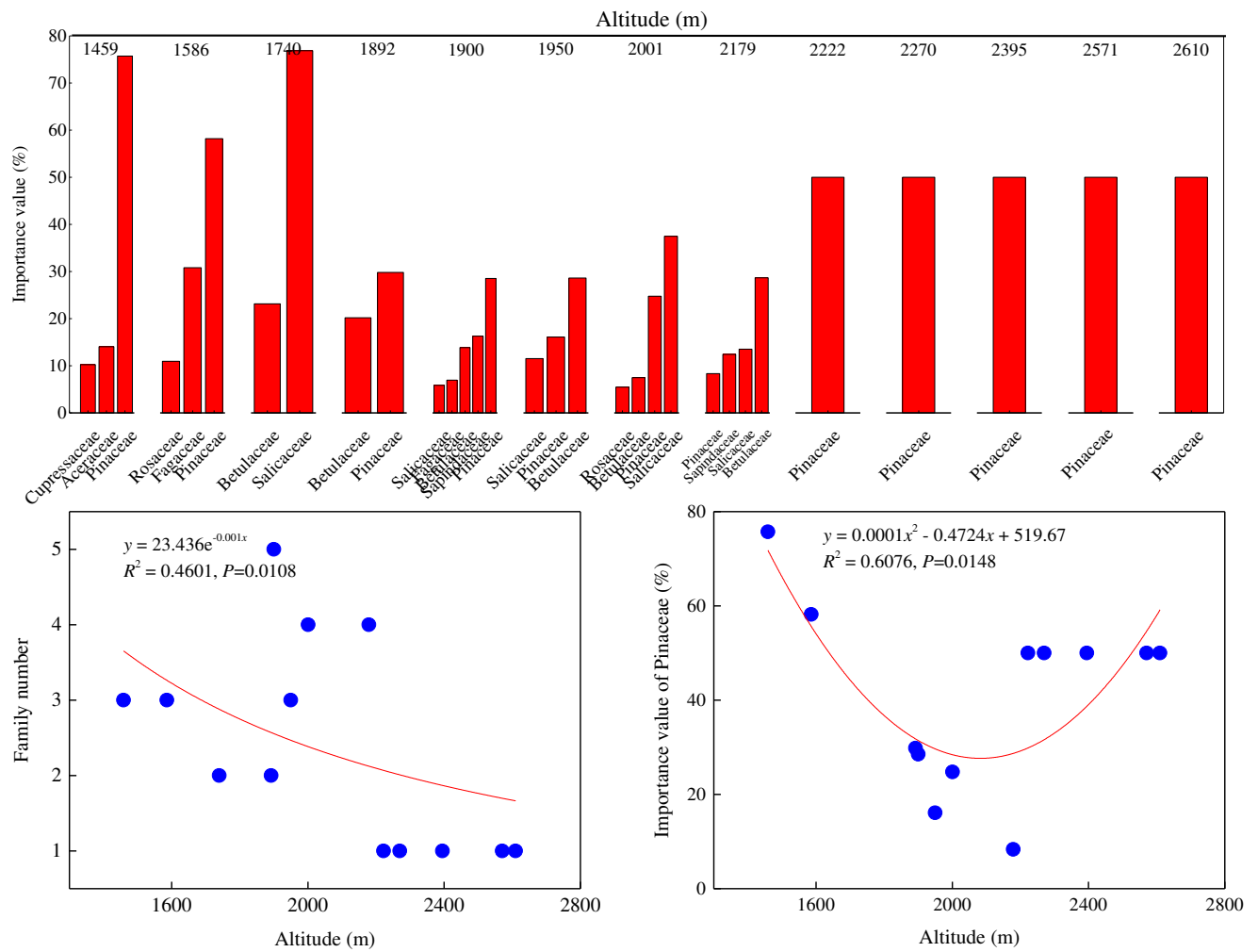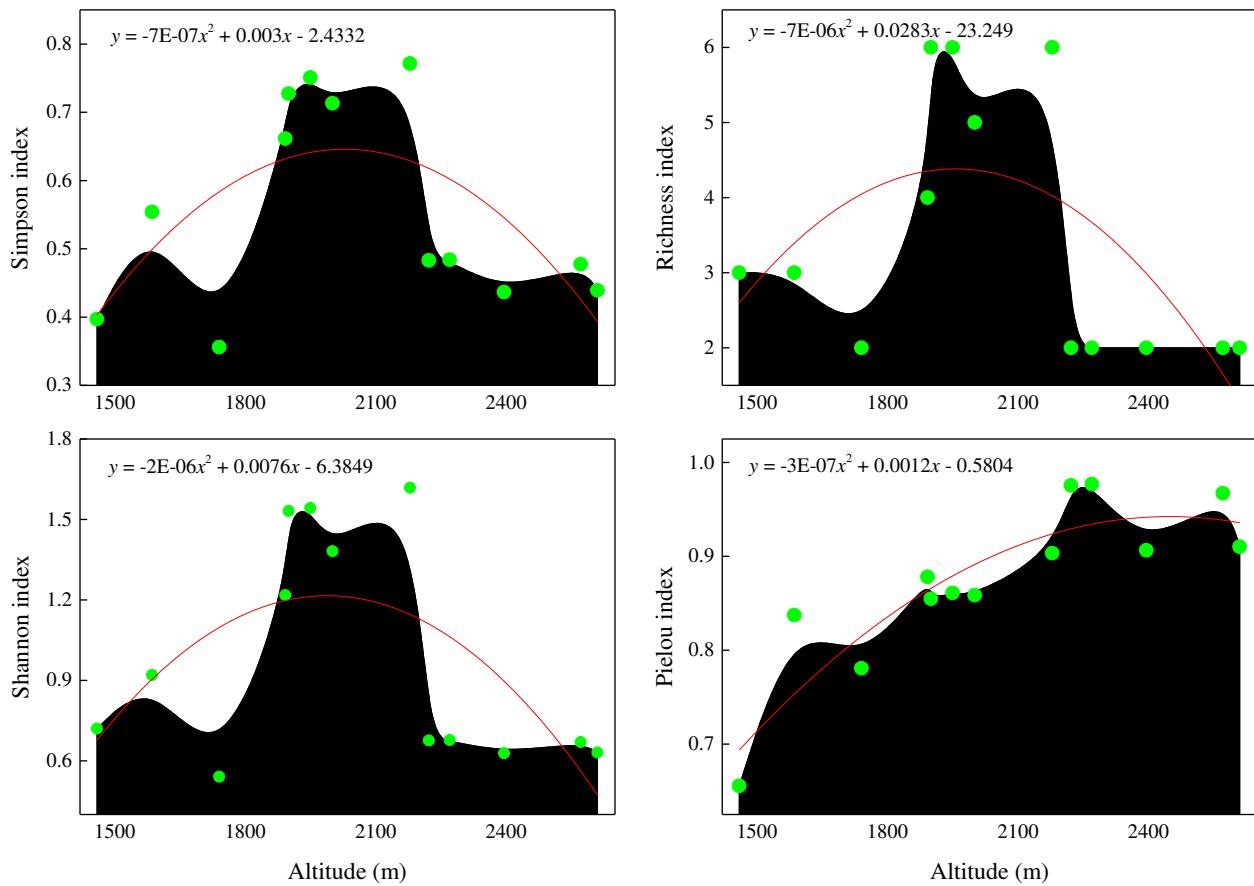| Plant type | Diversity index | Exponential function | Linear function | Logarithmic function | Quadratic polynomial function | Power function |
|---|---|---|---|---|---|---|
| Herb | Richness | 0.1568(0.161) | 0.1361(0.194) | 0.1064(0.255) | 0.3411(0.101) | 0.1295(0.206) |
| | Simpson | 0.3421(0.028) | 0.3477(0.026) | 0.3304(0.032) | 0.3549(0.022) | 0.3288(0.032) |
| | Shannon | 0.2159(0.094) | 0.1860(0.124) | 0.1859(0.124) | 0.1896(0.315) | 0.2144(0.096) |
| | Pielou | 0.4920(0.005) | 0.5095(0.004) | 0.4750(0.006) | 0.5465(0.003) | 0.4648(0.007) |
| Shrub | Richness | 0.3984(0.179) | 0.2288(0.337) | 0.1647(0.425) | 0.5678(0.284) | 0.3053(0.256) |
| | Simpson | 0.7197(0.053) | 0.6349(0.058) | 0.5671(0.084) | 0.7348(0.136) | 0.6430(0.055) |
| | Shannon | 0.6414(0.056) | 0.4965(0.118) | 0.4183(0.165) | 0.6920(0.171) | 0.5484(0.092) |
| | Pielou | 0.4200(0.164) | 0.4437(0.149) | 0.4741(0.131) | 0.5189(0.334) | 0.4522(0.144) |
| Arbor | Richness | 0.1417(0.205) | 0.0892(0.321) | 0.0621(0.412) | 0.3717(0.098) | 0.1090(0.271) |
| | Simpson | 0.0043(0.831) | 0.0094(0.753) | 0.0015(0.901) | 0.4209(0.065) | 7E-05(0.978) |
| | Shannon | 0.0626(0.410) | 0.0501(0.462) | 0.0287(0.580) | 0.3966(0.080) | 0.0391(0.517) |
| | Pielou | 0.6452(0.001) | 0.6629(0.001) | 0.7116(0.000) | 0.7975(0.000) | 0.6987(0.000) |

**TABLE 2**

| Altitude (m) | Importance value (%) | | |
|:---:|:---:|:---:|:---:|
| | Deciduous broad-leaved trees | Deciduous coniferous trees | Evergreen coniferous trees |
| 1459 | 14.048 | — | 42.976 |
| 1586 | 20.893 | — | 58.214 |
| 1740 | 50.000 | — | — |
| 1892 | 20.208 | 11.099 | 48.485 |
| 1900 | 10.729 | 11.796 | 45.290 |
| 1950 | 17.218 | 35.356 | 6.495 |
| 2001 | 16.815 | 16.160 | 33.395 |
| 2179 | 20.826 | 4.486 | 12.211 |
| 2222 | — | 59.214 | 40.786 |
| 2270 | — | 41.074 | 58.926 |
| 2395 | — | 32.196 | 67.804 |
| 2571 | — | 39.353 | 60.647 |
| 2610 | — | 32.553 | 67.447 |

**SUPPLEMENTARY TABLE**

| Life form | Species | Height (m) | Coverage | Density (m$^{-2}$) | Frequency |
|---|---|---|---|---|---|
| Herb | *Kobresia humilis* | 0.010 | 0.086 | 209.333 | 0.376 |
| | *Artemisia argyi* | 0.015 | 0.232 | 344.000 | 0.400 |
| | *Pulsatilla chinensis* | 0.005 | 0.000 | 0.200 | 0.001 |
| | *Pinellia ternata* | 0.020 | 0.014 | 26.657 | 0.071 |
| | *Sanicula chinensis* | 0.029 | 0.006 | 10.600 | 0.013 |
| | *Scutellaria scordifolia* | 0.023 | 0.005 | 10.500 | 0.013 |
| | *Astragalus scaberrimus* | 0.003 | 0.000 | 0.800 | 0.002 |
| | *Plantago asiatica* | 0.007 | 0.022 | 12.689 | 0.075 |
| | *Cirsium setosum* | 0.012 | 0.005 | 0.879 | 0.006 |
| | *Lathyrus davidii* | 0.013 | 0.001 | 2.100 | 0.004 |
| | *Bupleurum longiradiatum* | 0.015 | 0.006 | 1.143 | 0.009 |
| | *Spodiopogon sibiricus* | 0.018 | 0.001 | 0.857 | 0.009 |
| | *Speranskia tuberculata* | 0.010 | 0.001 | 0.800 | 0.001 |
| | *Sanguisorba officinalis* | 0.016 | 0.006 | 4.860 | 0.029 |
| | *Heracleum hemsleyanum* | 0.012 | 0.000 | 0.200 | 0.001 |
| | *Aconitum polyschistum* | 0.004 | 0.001 | 0.267 | 0.001 |
| | *Cynanchum chinense* | 0.019 | 0.107 | 122.667 | 0.493 |
| | *Potentilla bifurca* | 0.004 | 0.003 | 2.667 | 0.027 |
| | *Platanthera chlorantha* | 0.001 | 0.001 | 0.800 | 0.006 |
| | *Saussurea japonica* | 0.023 | 0.023 | 10.800 | 0.096 |
| | *Stachys affinis* | 0.027 | 0.017 | 2.571 | 0.023 |
| | *Heteropappus hispidus* | 0.098 | 0.013 | 30.933 | 0.032 |
| | *Rorippa indica* | 0.020 | 0.012 | 6.324 | 0.019 |
| | *Actinostemma tenerum* | 0.005 | 0.000 | 0.400 | 0.001 |
| | *Lappula myosotis* | 0.003 | 0.001 | 0.571 | 0.003 |
| | *Ainsliaea elegans* | 0.016 | 0.012 | 3.229 | 0.023 |
| | *Lycianthes biflora* | 0.007 | 0.002 | 1.000 | 0.002 |

| | | | | |
|---|---|---|---|---|
| *Saxifraga stolonifera* | 0.019 | 0.005 | 10.400 | 0.019 |
| *Polemonium coeruleum* | 0.024 | 0.007 | 1.786 | 0.013 |
| *Scutellaria baicalensis* | 0.005 | 0.000 | 0.200 | 0.001 |
| *Leontopodium leontopodioides* | 0.015 | 0.022 | 53.244 | 0.117 |
| *Sedum stellariifolium* | 0.024 | 0.004 | 2.286 | 0.017 |
| *Equisetum ramosissimum* | 0.018 | 0.003 | 1.200 | 0.012 |
| *Rubia membranacea* | 0.032 | 0.023 | 3.000 | 0.030 |
| *Viola verecunda* | 0.028 | 0.002 | 1.600 | 0.005 |
| *Cerastium arvense* | 0.012 | 0.017 | 27.516 | 0.069 |
| *Sphaerophysa salsula* | 0.162 | 0.018 | 21.067 | 0.043 |
| *Graptopetalum pachyphyllum* | 0.009 | 0.000 | 0.600 | 0.002 |
| *Oxytropis coerulea* | 0.013 | 0.017 | 10.950 | 0.067 |
| *Geranium wilfordii* | 0.024 | 0.003 | 3.379 | 0.010 |
| *Androsace henryi* | 0.005 | 0.001 | 12.800 | 0.003 |
| *Czernaevia laevigata* | 0.006 | 0.001 | 0.700 | 0.002 |
| *Agrimonia pilosa* | 0.039 | 0.002 | 1.100 | 0.003 |
| *Geum aleppicum* | 0.035 | 0.004 | 2.543 | 0.006 |
| *Pedicularis shansiensis* | 0.016 | 0.018 | 12.929 | 0.077 |
| *Ranunculus japonicus* | 0.028 | 0.001 | 0.200 | 0.001 |
| *Dracocephalum rupestre* | 0.003 | 0.003 | 0.857 | 0.006 |
| *Potentilla fragarioides* | 0.021 | 0.086 | 68.000 | 0.372 |
| *Artemisia eriopoda* | 0.014 | 0.001 | 1.400 | 0.004 |
| *Patrinia villosa* | 0.008 | 0.001 | 0.800 | 0.002 |
| *Elymus dahuricus* | 0.021 | 0.013 | 59.932 | 0.174 |
| *Taraxacum mongolicum* | 0.026 | 0.077 | 33.333 | 0.253 |
| *Rhaponticum uniflorum* | 0.014 | 0.001 | 0.200 | 0.001 |
| *Rubia cordifolia* | 0.006 | 0.002 | 0.800 | 0.002 |
| *Gentiana macrophylla* | 0.006 | 0.007 | 0.857 | 0.009 |
| *Artemisia carvifolia* | 0.021 | 0.009 | 7.200 | 0.046 |

| | | | | |
|---|---|---|---|---|
| *Avena sativa* | 0.028 | 0.006 | 7.714 | 0.054 |
| *Blumea mollis* | 0.021 | 0.001 | 3.000 | 0.006 |
| *Adenophora stricta* | 0.002 | 0.001 | 0.857 | 0.006 |
| *Allium senescens* | 0.034 | 0.001 | 2.133 | 0.003 |
| *Lathyrus quinquenervius* | 0.010 | 0.006 | 1.829 | 0.016 |
| *Ostericum sieboldii* | 0.012 | 0.001 | 1.600 | 0.003 |
| *Galium bungei* | 0.038 | 0.009 | 9.633 | 0.044 |
| *Rumex acetosa* | 0.007 | 0.001 | 0.333 | 0.002 |
| *Carex tristachya* | 0.115 | 0.104 | 332.921 | 0.307 |
| *Thalictrum aquilegifolium* | 0.011 | 0.041 | 60.387 | 0.196 |
| *Ligularia fischeri* | 0.015 | 0.002 | 1.514 | 0.007 |
| *Heteropappus altaicus* | 0.159 | 0.038 | 55.000 | 0.071 |
| *Clematis hexapetala* | 0.061 | 0.013 | 14.667 | 0.023 |
| *Chrysanthemum coronarium* | 0.010 | 0.006 | 1.143 | 0.009 |
| *Vicia unijuga* | 0.032 | 0.003 | 2.879 | 0.010 |
| *Potentilla chinensis* | 0.062 | 0.003 | 2.767 | 0.008 |
| *Aconitum carmichaeli* | 0.024 | 0.005 | 3.013 | 0.011 |
| *Galium linearifolium* | 0.010 | 0.002 | 3.600 | 0.005 |
| *Kobresia capillifolia* | 0.058 | 0.135 | 405.600 | 0.560 |
| *Potentilla longifolia* | 0.024 | 0.016 | 15.324 | 0.102 |
| *Valeriana officinalis* | 0.045 | 0.001 | 0.857 | 0.009 |
| *Rubus reflexus* | 0.018 | 0.002 | 1.800 | 0.005 |
| *Carpesium cernuum* | 0.021 | 0.002 | 1.200 | 0.003 |
| *Festuca ovina* | 0.020 | 0.000 | 3.267 | 0.005 |
| *Fragaria vesca* | 0.035 | 0.092 | 145.312 | 0.184 |
| *Allium ramosum* | 0.040 | 0.001 | 1.000 | 0.003 |
| *Deyeuxia arundinacea* | 0.019 | 0.001 | 4.758 | 0.004 |
| *Vicia sepium* | 0.018 | 0.001 | 0.633 | 0.002 |
| *Siphonostegia chinensis* | 0.093 | 0.006 | 5.667 | 0.013 |

| | | | | | |
|---|---|---|---|---|---|
| | *Polygala tenuifolia* | 0.014 | 0.001 | 1.033 | 0.002 |
| | *Viola prionantha* | 0.008 | 0.004 | 14.400 | 0.016 |
| | *Poa annua* | 0.040 | 0.003 | 4.533 | 0.012 |
| | *Stipa capillata* | 0.018 | 0.033 | 220.000 | 0.160 |
| | *Eragrostis ferruginea* | 0.043 | 0.014 | 85.400 | 0.031 |
| | *Lespedeza chinensis* | 0.022 | 0.001 | 2.133 | 0.009 |
| | *Polygonum viviparum* | 0.015 | 0.148 | 216.744 | 0.421 |
| | *Viola philippica* | 0.009 | 0.001 | 0.267 | 0.001 |
| | *Aster tataricus* | 0.010 | 0.004 | 1.600 | 0.011 |
| Shrub | *Rosa xanthina* | 1.776 | 0.137 | 0.038 | |
| | *Rosa hugonis* | 1.521 | 0.057 | 0.029 | |
| | *Daphne giraldii* | 0.700 | 0.001 | 0.001 | |
| | *Cotoneaster acutifolia* | 0.860 | 0.003 | 0.004 | |
| | *Potentilla fruticosa* | 0.310 | 0.007 | 0.049 | |
| | *Hippophae rhamnoides* | 0.738 | 0.149 | 0.167 | |
| | *Rosa davurica* | 3.383 | 0.212 | 0.012 | |
| | *Cotoneaster multiflorus* | 2.700 | 0.009 | 0.002 | |
| | *Spiraea pubescens* | 0.820 | 0.005 | 0.017 | |
| | *Pyracantha fortuneana* | 9.200 | 0.152 | 0.006 | |
| | *Potentilla glabra* | 0.511 | 0.009 | 0.024 | |
| Arbor | *Betula platyphylla* | 7.413 | 0.245 | 0.028 | |
| | *Populus tomentosa* | 8.058 | 0.509 | 0.031 | |
| | *Platycladus orientalis* | 4.250 | 0.049 | 0.006 | |
| | *Salix matsudana* | 6.500 | 0.181 | 0.003 | |
| | *Betula albo-sinensis* | 8.006 | 0.329 | 0.018 | |
| | *Larix principis-rupprechtii* | 14.476 | 0.426 | 0.018 | |
| | *Quercus liaotungensis* | 7.552 | 0.336 | 0.015 | |
| | *Koelreuteria paniculata* | 7.443 | 0.324 | 0.014 | |
| | *Acer buergerianum* | 4.167 | 0.231 | 0.014 | |

| | | | |
|---|---|---|---|
| *Crataegus pinnatifida* | 2.725 | 0.075 | 0.006 |
| *Salix pseudotangii* | 2.475 | 0.087 | 0.008 |
| *Populus davidiana* | 8.540 | 0.297 | 0.010 |
| *Populus simonii* | 11.286 | 2.107 | 0.019 |
| *Pinus tabuliformis* | 9.492 | 1.128 | 0.069 |
| *Picea asperata* | 11.120 | 1.176 | 0.060 |