

Contrasting relationships between species diversity and genetic diversity in natural and disturbed forest tree communities

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Summary

- This study aimed to reveal species–genetic diversity correlations (SGDCs) and their underlying mechanisms in natural and disturbed forests.
- A community survey and molecular analyses were carried out to compare species diversity (SD), the genetic diversity of the dominant tree species *Euptelea pleiospermum* (GD), the altitudinal patterns of SD and GD, SGDC, genetic differentiation (F_{ST}), community divergence (F_{ST-C}), effective population size (N_e), and recent migration rate between mountain riparian forests along the Yandu (natural) and Nan (disturbed) rivers.
- In natural forests, both SD and GD showed a unimodal altitudinal pattern and GD was positively correlated with SD, whereas a unimodal pattern and positive SGDC were not found in the disturbed forests. SD and F_{ST} at the natural sites were higher than those at the disturbed sites. However, there were no significant differences in GD, F_{ST-C} , N_e or recent migration rate between the natural and disturbed sites.
- A correlation between the patterns of SD and GD along a geographical gradient (e.g. altitude) is an important driver of positive SGDC. The absence of positive SGDC in the disturbed forests may result from reduced SD but unaffected GD, indicating nonparallel changes in SD and GD. This study furthermore cautions against generalizations about changes in SD and GD following disturbance.

Introduction

At regional scales, migration, drift and selection are dominant drivers of diversity patterns (Vellend & Geber, 2005). Their effects on species diversity (SD) at the community level are analogous to their effects on genetic diversity (GD) at the population level (Vellend & Geber, 2005). Therefore, a positive species–genetic diversity correlation (SGDC) is expected, and simulation and empirical studies have demonstrated such a relationship (Vellend, 2003, 2004, 2005; Wehenkel *et al.*, 2006; Lankau & Strauss, 2007; He *et al.*, 2008; He & Lamont, 2010; Odat *et al.*, 2010).

Both neutral (migration and drift) and adaptive (selection) processes are potential determinants of positive SGDC (Hubbell, 2001; Etienne & Olf, 2004; Vellend & Geber, 2005; Evanno *et al.*, 2009). When SD and GD are not correlated with habitat properties and selective processes, parallel action of neutral processes on the two levels of diversity is a possible explanation for positive SGDC (Etienne & Olf, 2004; Vellend & Geber, 2005). However, He *et al.* (2008) reported that the physical environment (e.g. dune height) rather than neutral processes was the driver of covariation between SD and GD. Systems where variation in SD is predicted largely by a single variable provide excellent opportunities to look for parallel variation in GD predicted by the same variable (Vellend, 2005).

In mountain landscapes, altitude, a property long considered to be the principal driver of species distribution patterns, is strongly related to plant diversity (Lomolino, 2001; Kreft & Jetz, 2007). Altitudinal gradients of plant diversity result from a combination of ecological and evolutionary processes (Lomolino, 2001). Hump-shaped patterns in relation to altitude are typical for both SD (Rahbek, 1995) and GD (Ohsawa & Ide, 2008). If the same altitudinal patterns of SD and GD occur at similar altitudinal ranges, a positive SGDC is expected in natural mountain forests.

Anthropogenic disturbance is considered to be one of the greatest threats to plant biodiversity (Fahrig, 2003). Construction of roads for timber transportation and recreational activity is a major disturbance in many mountain areas (Chen *et al.*, 2005; Takahashi & Miyajima, 2010). Road construction is always accompanied by the destruction and fragmentation of habitat (Balkenhol & Waits, 2009; Holderegger & Di Giulio, 2010). Habitat fragmentation is expected to reduce within-patch diversity of SD and GD as a result of decreased population abundances and reduced immigration rates (Zuidema *et al.*, 1996). However, if one level of diversity is more sensitive to such changes than the other, SD and GD may not vary in parallel over a given range of habitat patch size or isolation (Vellend, 2005). Some studies have reported that road margins act as corridors for the dispersal of seed and pollen (Byrne *et al.*, 2007; Holderegger

& Di Giulio, 2010). This role of roads may weaken the negative effect of habitat fragmentation on GD, but it cannot prevent the potential decrease of woody SD. Therefore, whether SD and GD change in parallel through time in disturbed systems is an important question in community genetics (Vellend, 2004).

SGDC was used as a measure of parallel responses in SD and GD (Cleary *et al.*, 2006). If there is a positive SGDC in undisturbed systems, the absence of the positive relationship in disturbed systems can be seen as an indicator of nonparallel responses of the two aspects of biodiversity to disturbance. Several recent studies reported that SD and GD showed similar changes and that a positive SGDC was found in habitats undergoing a disturbance (Vellend, 2004; Cleary *et al.*, 2006; Evanno *et al.*, 2009). However, the organisms investigated in these studies all have a short lifecycle. Lifecycle is an important factor in the detection of the impact of disturbance on GD (Bacles & Jump, 2011; Struebig *et al.*, 2011). Here, we were interested in whether long-lived organisms show parallel changes in SD and GD in a human-disturbed forest system.

In this study, we measured the SD of woody plant communities and the GD of *Euptelea pleiospermum* (a dominant tree species) in natural and disturbed mountain riparian forests of central China to address the following questions. Do SD and GD show similar altitudinal patterns in natural forests? Is there a positive SGDC in natural forests? If so, is this pattern also found in disturbed forests? Are SD and GD reduced in disturbed forests relative to natural forests?

Materials and Methods

Study species

Euptelea pleiospermum Hook. f. et Thoms (Eupteleaceae) is a deciduous, broad-leaved, Tertiary-relict tree species of mountain riparian forests in China. This species is distributed across wide

altitudinal ranges (720–3600 m asl) along stream sides (Fu & Jin, 1992). Mature trees can reach up to 12 m in height and 20 cm in diameter. Flowering takes place in early spring before leaf-out and flowers are wind-pollinated (Endress, 1986). Seed production is abundant and the light samara is dispersed by wind and/or water. Seed vigor decreases rapidly after > 1 yr, indicating that this species does not form a persistent soil seed bank (Wei *et al.*, 2010a).

Study sites

The study area is located in riparian forests of the Shennongjia Mountains ($31^{\circ}21'20''$ – $31^{\circ}36'20''$ N, $110^{\circ}03'05''$ – $110^{\circ}33'50''$ E) in central China (Fig. 1). The Shennongjia Mountains (3105.4 m asl) are an important part of the south-central China biodiversity hot-spot and are rich in Tertiary-relict and endemic plants (Myers *et al.*, 2000; Ying, 2001). Chinese endemic genera are limited to land below 2000 m (Shen *et al.*, 2004). Altitude is the main factor determining the distribution pattern of forest tree communities (Jiang *et al.*, 2002a; Zhao *et al.*, 2005; Wei *et al.*, 2010b), and the altitudinal pattern of plant diversity has a unimodal pattern with a peak (*c.* 1500 m) in the mixed evergreen and deciduous broad-leaved forest zone (Jiang *et al.*, 2002b; Shen *et al.*, 2004; Zhao *et al.*, 2005).

Mountain riparian zones are crucial refuges for Tertiary-relict plants in this area (Jiang *et al.*, 2002b; Wei *et al.*, 2010b). There are four main river systems in the Shennongjia Mountains: the Yandu River and Xiangxi River on the south-facing slope, which are tributaries of the Yangtze River, and the Nan River and Du River on the north-facing slope, which are tributaries of the Han River (Fig. 1). *Euptelea pleiospermum* is one of the dominant relict tree species of the riparian plant communities on this subtropical mountain (Wei *et al.*, 2008, 2010b).

The study was undertaken in riparian forests along the upper reaches of two river systems (Fig. 1). The Yandu River is

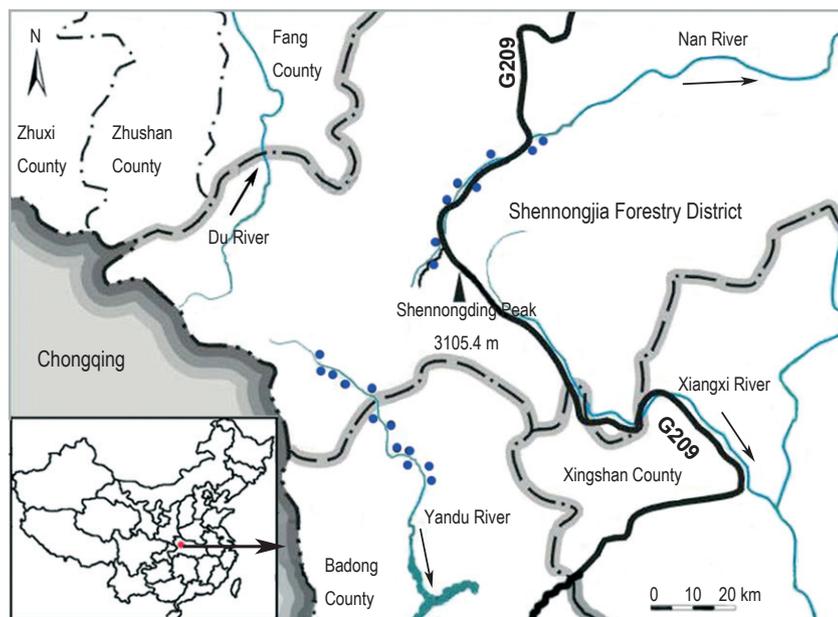


Fig. 1 Map of the study region with the locations of the 20 study sites along the upper reaches of the Nan River (eight sites) and Yandu River (12 sites) in central China. G209 (bold black line) is the No. 209 national highway of China.

relatively unaffected by human disturbance because of its inaccessibility. The Nan River, along which there is a national highway below 1700 m and a vehicle road for tourism above 1700 m, is severely disturbed by human activities. Study sites were established at roughly 100-m elevational intervals along the two rivers. The sampling range depended on the altitudinal range of *E. pleiospermum* along each river (Yandu River, 900–2000 m; Nan River, 1200–1900 m). As a result, a total of 12 and eight sites were established along the Yandu River and Nan River, respectively (Fig. 1, Table 1).

Community survey and sampling

A community survey was conducted between late July and early September of 2006. At each site, one plot (20 × 30 m) was established in a forest tree community dominated by *E. pleiospermum*. Within each plot, we recorded the species and diameter at breast height (DBH) of all living trees (DBH ≥ 2.5 cm). The nomenclature follows that of the Flora of China (Wu & Raven, 1994).

Leaf sampling was carried out in April and May 2008. Within and around each surveyed plot, we randomly (without replacement) collected several young leaves of *E. pleiospermum* individuals that were at least 30 m apart. The sampled leaves were immediately dried in a 10 × 5 cm plastic bag containing silica gel. Because of the sporadic distribution at some altitudes, sample sizes were sometimes relatively low, ranging from six to 61 per population. As a result, a total of 351 and 230 individuals were sampled along the Yandu River and Nan River, respectively (Table 1).

Table 1 Site characteristics, plant species diversity (*S*, species richness; *D*, Simpson's diversity index), genetic diversity of *Euptelea pleiospermum* (*A_R*, allelic richness; *H_E*, expected heterozygosity) and effective population size (*N_e*–ONEsAMP and *N_e*–LDNE) for the 20 sites along the Nan River (disturbed; N1–N8) and Yandu River (undisturbed; Y1–Y12)

| Site | Altitude (m) | <i>S</i> | <i>D</i> | <i>N</i> | <i>A_R</i> | <i>H_E</i> | <i>N_e</i> –ONEsAMP (prior = 2–500) | <i>N_e</i> –LDNE (<i>P_{crit}</i> = 0.05) |
|------|--------------|----------|----------|----------|----------------------|----------------------|--|--|
| N1 | 1904 | 13 | 0.815 | 36 | 3.71 | 0.622 | 36.4 (28.3–58.4) | 32.6 (17.7–80.8) |
| N2 | 1875 | 12 | 0.878 | 31 | 4.28 | 0.671 | 44.3 (32.2–79.8) | 117.7 (36.5–∞) |
| N3 | 1720 | 12 | 0.835 | 25 | 4.27 | 0.656 | 26.7 (19.8–48.1) | 33.3 (17.4–108.5) |
| N4 | 1675 | 14 | 0.859 | 30 | 4.03 | 0.613 | 35.8 (26.5–63.9) | 137.0 (40–∞) |
| N5 | 1521 | 14 | 0.811 | 37 | 4.13 | 0.611 | 40.0 (29.8–84.2) | – |
| N6 | 1410 | 16 | 0.869 | 32 | 4.24 | 0.635 | 56.7 (41.2–108.0) | 43.6 (22.6–143.1) |
| N7 | 1360 | 18 | 0.840 | 24 | 3.93 | 0.590 | 34.3 (25.3–68.6) | – |
| N8 | 1290 | 12 | 0.808 | 15 | 4.08 | 0.629 | – | – |
| Y1 | 2010 | 15 | 0.821 | 33 | 3.65 | 0.558 | 25.5 (18.2–46.0) | 7.5 (3.8–12.0) |
| Y2 | 1956 | 14 | 0.822 | 24 | 4.09 | 0.635 | 28.5 (20.4–52.8) | 26.1 (13.1–89.3) |
| Y3 | 1806 | 17 | 0.857 | 6 | 3.88 | 0.606 | – | – |
| Y4 | 1750 | 18 | 0.909 | 28 | 3.76 | 0.621 | 22.6 (17.0–39.0) | 26.2 (14.0–69.8) |
| Y5 | 1640 | 27 | 0.920 | 40 | 4.38 | 0.686 | 41.4 (30.0–81.4) | 59.4 (33.4–158.7) |
| Y6 | 1575 | 22 | 0.888 | 61 | 4.33 | 0.657 | 54.6 (39.5–102.5) | 115.3 (59.2–498.1) |
| Y7 | 1471 | 25 | 0.936 | 41 | 4.45 | 0.687 | 35.1 (24.4–76.3) | 21.3 (14.8–31.9) |
| Y8 | 1320 | 20 | 0.899 | 28 | 4.09 | 0.643 | 26.7 (20.0–52.1) | 63.9 (27.3–∞) |
| Y9 | 1270 | 18 | 0.864 | 11 | 3.80 | 0.558 | – | – |
| Y10 | 1101 | 14 | 0.847 | 10 | 3.68 | 0.575 | – | – |
| Y11 | 1005 | 17 | 0.847 | 37 | 3.79 | 0.555 | 57.6 (38.5–152.7) | 22.5 (13.5–41.7) |
| Y12 | 980 | 14 | 0.859 | 32 | 4.18 | 0.613 | 30.3 (20.9–60.7) | 28.1 (17.0–55.0) |

N, sample size; –, estimation not performed (for site with *N* < 20) or with negative value; *N_e*–ONEsAMP and *N_e*–LDNE, effective population size (*N_e*) estimates based on two different programs (ONEsAMP and LDNE; see text for details); confidence limits (95%) for *N_e* are shown in parentheses. The genetic diversity of *E. pleiospermum* (*A_R*, allelic richness; *H_E*, expected heterozygosity) was taken from a previous study (X. Wei *et al.*, unpublished data).

Microsatellite procedure

All leaf samples were stored at 4°C before DNA extraction. Total DNA was extracted from leaves using a modified CTAB (Cetyl Trimethyl Ammonium Bromide) method (Doyle & Doyle, 1987). We tested 14 nuclear microsatellite loci developed for *E. pleiospermum* (Zhang *et al.*, 2008), from which eight (EP021, EP036, EP059, EP081, EP087, EP091, EP278 and EP294) were selected as they had suitable levels of polymorphism. PCR amplification and the allele resolution procedure were performed as described by Zhang *et al.* (2008).

Statistical analysis

Two measures of SD were used: species richness (*S*) and Simpson's diversity index (*D*). The number of species per plot was taken as a measure of species richness. If the relative frequency of species *i* was *f_i* ($\sum f_i = 1$), Simpson's diversity index was estimated as $1 - \sum f_i^2$. Both measures of SD were calculated using PC-ORD 4.0 (McCune & Mefford, 1999). The measures of GD used were allelic richness (*A_R*) and expected heterozygosity (*H_E*), as they are analogous to *S* and *D*, respectively (Etienne, 2005; Evanno *et al.*, 2009). *A_R* was calculated using rarefaction analysis with FSTAT 2.9.3.2 (Goudet, 2001) and *H_E* was estimated using GENETIX 4.05 (Belkhir *et al.*, 1996–2004). FSTAT 2.9.3.2 was also used to test for deviation from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD). The significance of LD was Bonferroni-corrected for multiple comparisons (Rice, 1989). Relationships between SD (*S* and *D*) and GD (*A_R* and *H_E*) were tested using Pearson correlation.

To reveal the altitudinal patterns of SD and GD along the Yandu River, we divided sampled sites into three groups (L, low altitudes, 900–1200 m; M, middle altitudes, 1300–1600 m; and H, high altitudes, 1700–2000 m; each with four sites) and then compared mean values of diversity parameters (S , D , A_R , and H_E) among the groups. Statistical significance was determined by one-way analysis of variance (ANOVA) followed by Tukey's *post hoc* test.

To investigate whether human disturbances reduced SD and GD, we compared mean values of diversity parameters between the Yandu River and the Nan River. Statistical significance was determined by performing a paired-samples t -test. We removed sites Y1, Y10, Y11 and Y12 from the natural habitat for pairwise comparisons of species and genetic data (SD, GD, F_{ST} , F_{ST-C} , N_e , and recent migration rate) between the two rivers.

To investigate whether human disturbances increased genetic divergence and community divergence, we compared mean values (paired-samples t -test) of divergence parameters between the two rivers. Pairwise population genetic differentiation (F_{ST}) was calculated using FSTAT 2.9.3.2 (Goudet, 2001). F_{ST} was estimated as $(H_T - H_S)/H_T$, where H_T is the total expected heterozygosity, and H_S is average H_E across populations (Nei, 1977). F_{ST-C} , a direct analogue of F_{ST} , was used to measure community divergence (Vellend, 2004). By treating community as 'locus' and species as 'allele' (Vellend, 2004), we estimated the analogues of H_T and H_S at community level and then used the same formula to calculate F_{ST-C} .

To investigate whether effective population size (N_e) was reduced in human-disturbed populations, we calculated N_e for each population and then compared the mean values between the two rivers; significance was also determined via a paired-samples t -test. The contemporary N_e was calculated with ONESAMP 1.2 (Tallmon *et al.*, 2008) and LDNE 1.31 (Waples & Do, 2008). ONESAMP uses summary statistics and approximate Bayesian computation to calculate N_e estimates. The lower and upper limits of the prior distribution for N_e were 2 and 500, respectively. LDNE uses a linkage disequilibrium method to calculate N_e estimates and incorporates the bias correction from Waples (2006). We assumed a random mating model and calculated separate estimates using three threshold allele frequencies (P_{crit} : 0.05, 0.02, and 0.01) for excluding rare alleles.

To investigate whether road margins along rivers act as corridors of dispersal, we compared mean values (paired-samples t -test) of recent migration rates along the two river valleys. Recent migration rate is a measure that can be used as an indirect estimate of gene flow among populations over the last several generations. We estimated recent migration rates between populations along each river by using the program BAYESASS version 1.3 (Wilson & Rannala, 2003). The program calculates unidirectional estimates of migrant (m) for each population pair (Fraser *et al.*, 2007); this method is based on the model in which individuals are exchanged between populations over generations (Goossens *et al.*, 2005). The program was run using a Markov chain Monte Carlo (MCMC) length of 3 000 000 with a burn-in period of 1 000 000 (initial conditions of Δp = allele frequency, Δm = migration, and ΔF = inbreeding coefficient, all equal to 0.15).

Results

Species diversity

One hundred and eleven species were recorded in the 20 plots (Supporting Information Table S1). Apart from *E. pleiospermum*, the most frequently observed species were *Betula luminifera*, *Cercidiphyllum japonicum*, *Bothrocaryum controversum*, *Salix wallichiana*, and *Padus brachypoda*.

We found significant differences in SD among plant communities along the two rivers (Table 1). Compared with communities along the Yandu River, communities along the Nan River displayed a significantly lower mean (\pm SE) species richness (20.1 ± 1.5 and 13.9 ± 0.8 , respectively; $t = 4.597$, $P = 0.002$) and Simpson's diversity index (0.887 ± 0.013 and 0.839 ± 0.010 ; $t = 3.817$, $P = 0.007$).

Genetic diversity of *E. pleiospermum*

A total of 91 alleles at eight nuclear microsatellite loci were revealed across 581 individuals of the 20 populations of *E. pleiospermum*. The test for HWE found that 25 of 160 locus–population combinations were significant and no locus displayed consistent deviation from HWE across all populations. Only one (EP036 \times EP294) of 28 locus pairs showed significant LD in eight populations. No consistent genotypic disequilibrium was found between members of any locus pair across all populations, so all loci were used in further analyses.

Along the Yandu River, rarefied allelic richness ranged from 3.65 to 4.45, and expected heterozygosity varied from 0.555 to 0.687 (Table 1). Along the Nan River, rarefied allelic richness ranged from 3.71 to 4.28, and expected heterozygosity varied from 0.590 to 0.671 (Table 1). Both parameters of GD showed no significant differences between *E. pleiospermum* populations along the Yandu River and Nan River (A_R : 4.10 ± 0.10 and 4.08 ± 0.07 , respectively; $t = 0.110$, $P = 0.915$; H_E : 0.637 ± 0.015 and 0.628 ± 0.009 , respectively; $t = 0.406$, $P = 0.697$).

Altitudinal patterns of SD and GD

Along the Yandu River, altitudinal patterns of the two measures of SD (S and D) followed similar trends (L < M > H), indicating the communities at mid-altitude (M) had higher SD than lower (L) and higher (H) communities (Fig. 2a,b). Along the Nan River, this altitudinal pattern was not found (data not shown).

Along the Yandu River, altitudinal patterns for both parameters of GD (A_R and H_E) were similar to the trend (L < M > H) for SD (Fig. 2c,d). Along the Nan River, this altitudinal pattern was again not found (data not shown).

Species–genetic diversity correlation (SGDC)

In natural forests along the Yandu River, parameters of GD for *E. pleiospermum* (A_R and H_E) were positively correlated with measures of SD (S and D) (Fig. 3). By contrast, significant

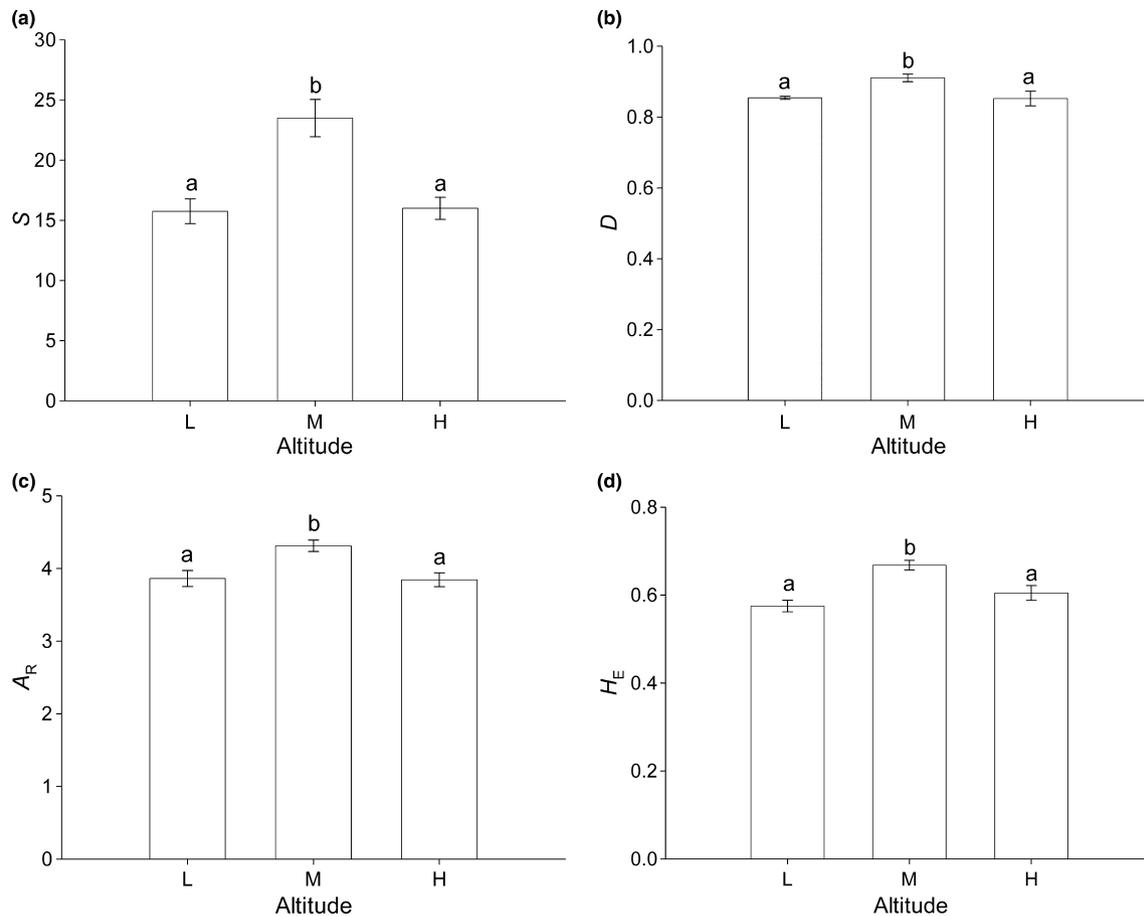


Fig. 2 Altitudinal patterns of species diversity (S , species richness; D , Simpson's diversity index) and genetic diversity of *Euptelea pleiospermum* (A_R , allelic richness; H_E , expected heterozygosity) along the Yandu River. Values are mean \pm SE. Different letters indicate significant differences ($P < 0.05$) between groups. Altitude: L, low altitudes, 900–1200 m; M, middle altitudes, 1300–1600 m; and H, high altitudes, 1700–2000 m; each with four sites.

positive correlations were not found between parameters of SD and GD in disturbed forests along the Nan River (Fig. 3).

F_{ST} , F_{ST-C} , N_e and recent migration rate

We detected significant difference in F_{ST} (0.033 ± 0.004 and 0.063 ± 0.007 , respectively; $t = -4.131$, $P = 0.000$) but not in F_{ST-C} (0.031 ± 0.003 and 0.032 ± 0.004 ; $t = -0.226$, $P = 0.823$) between the Yandu River and the Nan River (for details, see Table S2).

We found no significant difference in the effective population size (N_e -ONESAMP and N_e -LDNE) of *E. pleiospermum* populations between the Yandu River and the Nan River (N_e -ONESAMP: 34.8 ± 4.8 and 38.3 ± 4.1 , respectively; $t = 0.689$, $P = 0.522$; N_e -LDNE: 33.3 ± 8.8 and 61.6 ± 25.3 , respectively; $t = 1.688$, $P = 0.190$) (Table 1). All estimates of N_e -LDNE using the three threshold allele frequencies (P_{crit} : 0.05, 0.02, and 0.01) for excluding rare alleles produced nonsignificant results; here, we only present results for $P_{crit} = 0.05$.

For recent migration rates among within-river populations of *E. pleiospermum*, we also detected no significant difference between the two rivers, indicating that roads along the Nan River probably did not significantly increase gene flow (Yandu River:

0.030 ± 0.008 ; Nan River: 0.022 ± 0.007 ; $t = 0.891$, $P = 0.377$; for details, see Table S3).

Discussion

Positive SGDC in natural forest tree communities

Our data show a positive correlation between the SD of a natural mountain riparian forest and the GD of its dominant tree species, *E. pleiospermum* (Fig. 3). This result is consistent with earlier findings reported for herb species (Vellend, 2004; Odat *et al.*, 2010), forest trees (Wehenkel *et al.*, 2006), and plant functional groups (He *et al.*, 2008; He & Lamont, 2010). Although both we and Wehenkel *et al.* (2006) found positive SGDC in forest tree communities, our explanations are quite different. Wehenkel *et al.* (2006) ascribed the positive SGDC to the replacement of one or two climax tree species with lower GD by several pioneer tree species with higher GD. However, we developed an environmental explanation for the positive relationship.

The same altitudinal pattern of SD and GD at similar altitudinal ranges is considered to be the determinant of the detected positive SGDC. In other words, parallel effects of altitude on the two levels of diversity resulted in the significant positive

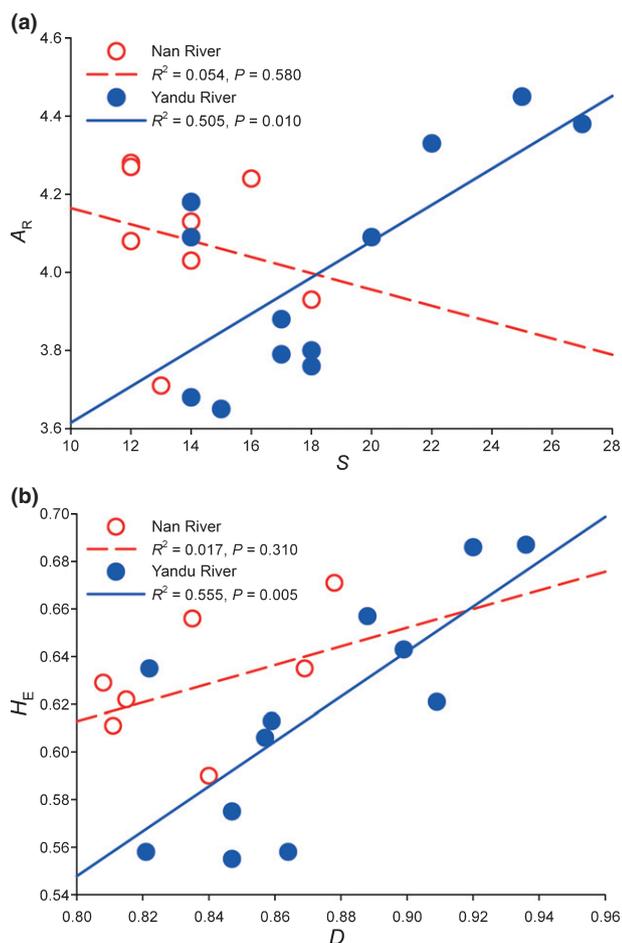


Fig. 3 Relationships between plant species diversity and genetic diversity of *Euptelea pleiospermum* along the Nan (disturbed) and Yandu (undisturbed) rivers. (a) Correlation between species richness (S) and allelic richness (A_R). (b) Correlation between Simpson's diversity index (D) and expected heterozygosity (H_E).

relationship between SD and GD. Similar to the results of Vellend (2004) and He *et al.* (2008), we have provided evidence for the hypothesis that other variables, rather than habitat area, could drive positive SGDC. Forests at mid-altitude are under optimal conditions, whereas forests at lower and upper altitudes are under suboptimal conditions. From upper or lower to mid-altitude populations, spatial distribution patterns of *E. pleiospermum* at a small scale (20 × 30 m) gradually changed from random to clumped (Wei *et al.*, 2008), indicating a gradual increase in population size and density. Therefore, more individual hypothesis, which indicate that both SD and abundance of dominant species are expected to increase at more productive sites (Srivastava & Lawton, 1998; Odat *et al.*, 2010), is probably the best explanation for the positive SGDC. Mid-altitude zones can be seen as more productive habitats, in which both the SD of communities and the GD of species are expected to increase (Srivastava & Lawton, 1998; Eckert *et al.*, 2008; Ohsawa & Ide, 2008). Furthermore, vegetation at mid-altitudes in our study area was mixed deciduous and evergreen broad-leaved forest, so SD was higher than at lower (evergreen broad-leaved forest) and upper (deciduous forest)

altitudes (Shen *et al.*, 2004; Zhao *et al.*, 2005). In peripheral habitats, small population and community sizes lead to drift, thereby reducing GD and SD (Hubbell, 2001; Vellend, 2004); limited from-and-to gene flow and founder effect can also reduce GD by promoting genetic drift (Ohsawa & Ide, 2008).

In some systems, patterns of SD and GD along geographical gradients (e.g. altitude, latitude, or longitude) are determined by the effects of environment gradients on the two levels of diversity. Vellend (2005) pointed out that it is difficult to formulate general predictions regarding covariation between SD and GD in these types of system. Because altitude is an important environmental gradient (being correlated with, for example, temperature and moisture), our results provide rarely tested empirical support for the hypothesis that a strong correlation in the patterns of SD and GD along geographical gradients is an important driver of a positive SGDC. In other words, the parallel effects of environmental gradients resulted in similar patterns of SD and GD along the geographical gradient, thereby producing a positive SGDC. At larger scales, two recent studies found no positive SGDC in vascular plant communities, because SD and GD did not respond similarly to environmental gradients or history events and their patterns along geographical gradients were different (Puşcaş *et al.*, 2008; Fady & Conord, 2010). Their findings also highlighted the importance of similar patterns of SD and GD in shaping a positive SGDC.

No positive SGDC in disturbed forest tree communities

In contrast to the positive SGDC found in the natural communities, we detected no significant correlation between the SD of a disturbed mountain riparian forest and the GD of its dominant tree species, *E. pleiospermum*. Our results demonstrated that the absence of positive SGDC may be attributable to reduced SD but unaffected GD of *E. pleiospermum* in the disturbed forest tree communities. Our results were also different from those of several previous studies which demonstrated that SD and GD displayed parallel changes following natural (Cleary *et al.*, 2006; Evanno *et al.*, 2009) or anthropogenic (Vellend, 2004) disturbances.

Two processes are likely to reduce SD in the disturbed forest tree communities. First, direct destruction of forests (e.g. cutting or damage) associated with road construction decimates many rare species (species with very low density). The decrease in species richness can be interpreted as being a consequence of the disappearance of rare species. Although the population size and density of dominant tree species may also be reduced, the most common species may be overrepresented in the disturbed forest tree communities with the disappearance of rare species. This is the reason why Simpson's diversity index (D) was reduced, corroborating the explanation of Vellend (2004) in secondary forest-herb communities. Furthermore, as *E. pleiospermum* is the dominant species in most of the surveyed communities, its overrepresentation in the disturbed habitat can explain why the community divergence along the Nan River was not increased. Secondly, road construction changes physical and chemical soil properties and makes soil-surface conditions unsuitable for the

establishment and growth of woody species. Similar negative effects of road construction have been reported in other mountain forests (Takahashi & Miyajima, 2010). In general, deforestation and poor recruitment along roadsides are the major drivers of the reduction of SD in disturbed mountain riparian forests.

Two additional hypotheses might explain why genetic erosion was not detected. First, increased gene flow may counteract the negative genetic effects of habitat destruction and deforestation caused by road construction. Because *E. pleiospermum* is a wind-pollinated tree with small, light samaras, and river valleys could act as dispersal corridors for this riparian species in the study area (X. Wei *et al.*, unpublished data), we assumed that roads along river valleys would have promoted its pollen flow or seed dispersal. However, we did not detect smaller genetic differentiation (F_{ST}), lower effective population size (N_e), or higher recent migrate rate along the Nan River compared with the Yandu River, which fails to support this hypothesis (Tables S2, S3 and Table 1). Secondly, negative genetic effects of road construction have not occurred or need time to become detectable (Holderegger & Di Giulio, 2010; Bacles & Jump, 2011). If human disturbance, especially habitat fragmentation, does not reach a threshold, its negative impact is negligible (Parker & Mac Nally, 2002). Even if fragmentation has passed the threshold, affects may lag by several hundred years (e.g. several generations for tree species) as genetic structure builds up to a detectable level in forest remnants (Bacles & Jump, 2011). Although we did not detect significant differences in effective population size and density of *E. pleiospermum* with DBH ≥ 2.5 cm (Yandu River: 14.8 ± 5.0 ; Nan River: 13.9 ± 5.0 ; paired-samples *t*-test: $t = 0.133$, $P = 0.898$; for details, see Table S1) between the two rivers in this study, we previously found that the number of *E. pleiospermum* with DBH < 2.5 cm along the Nan River is far less than that along the Yandu River (Wei *et al.*, 2008). As the road along the Nan River is less than 50 yr old (Ying *et al.*, 1999), we can speculate that the negative genetic effect will become more obvious with time. Therefore, the second hypothesis has the most support.

To our knowledge, this is the first study that provides evidence for nonparallel responses of SD and GD in disturbed systems. This finding is different from those of several other studies with short-lifecycle organisms, for example, forest-herb communities (Vellend, 2004), butterflies (Cleary *et al.*, 2006) and freshwater gastropods (Evanno *et al.*, 2009). As discussed above, lifecycle differences between the studied organisms may be the best explanation for this discrepancy. In general, our study cautions against generalizations about changes of SD and GD in disturbed systems.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Field survey data for the 20 forest tree communities along the Nan and Yandu rivers

Table S2 Genetic differentiation (F_{ST}) and community divergence (F_{ST-C}) among sites along the Nan and Yandu rivers

Table S3 Recent migration rates between *Euptelea pleiospermum* populations along the two rivers obtained using the program BAYESASS version 1.3

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