

## LETTER

# Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest

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### Abstract

How extraordinary numbers of species can coexist in hyper-diverse communities remains unresolved. While numerous hypotheses have been proposed based on observational and theoretical investigations, little is known about which mechanisms are truly active in forest communities and less is known about their relative contributions to community assembly. In this study, generalized linear mixed models with crossed random effects were used to assess the relative contributions of density dependence and habitat association to community-level diversity maintenance. Species habitat associations were classified based on soil nutrients, topography and species composition. Local neighbourhood effects were also addressed with spatially explicit models of seedling survival. The results shown here reveal that local- and community-level seedling dynamics were consistent with density-dependent predictions, although habitat association played a more important role in shaping short-term seedling survival. We conclude that density dependence could promote species coexistence on the premise of habitat partitioning.

### Keywords

Borrowing strength, community compensatory trend, crossed random effects, density dependence, generalized linear mixed models, Gutianshan, habitat association, Janzen–Connell hypothesis, seedling survival, species coexistence, subtropical broad-leaved forest.

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### INTRODUCTION

Numerous hypotheses have been proposed to explain patterns of diversity both at local and larger spatial scales in plant communities. It is increasingly recognized that one of the critical challenges in community ecology is to evaluate the respective contributions of different mechanisms and to determine the main processes promoting species coexistence (Barot & Gignoux 2004; Carson *et al.* 2008). Density dependence has been hypothesized as one of the most prominent mechanisms in the maintenance of diversity, and several hypotheses invoke density-dependent predictions in community assembly (Janzen 1970; Connell 1971; Hooper 1998; Chesson 2000; Volkov *et al.* 2005). In temperate and tropical forests, density dependence has been found to be an important explanation for patterns of survival on very local

scales (Augspurger 1984; Condit *et al.* 1992; Schupp 1992; Gilbert *et al.* 2001; HilleRisLambers *et al.* 2002; Brook & Bradshaw 2006; Freckleton & Lewis 2006). However, surprisingly few studies have examined the community-level consequences of density-dependent processes in species-rich plant communities. In such communities, local-scale density dependence is hypothesized to result in a community compensatory trend (CCT; Connell *et al.* 1984) in which rare species exhibit a higher per capita survival rate than abundant species as a result of frequency-dependent processes. Accordingly, rare species could be rescued from competitive exclusion and common species would never achieve mono-dominance.

Empirical tests of the CCT hypothesis have traditionally examined whether species' vital rates were negatively correlated with species' abundance in the community (e.g.

Connell *et al.* 1984; Welden *et al.* 1991; Webb & Peart 1999; Wright 2002; Queenborough *et al.* 2007; Comita & Hubbell 2009). The underlying assumption of such tests is that, when density dependence is active, the short-term dynamics that occur over the length of a typical study should indicate poor performance where a species is abundant and better performance where the species is rare. However, this pattern would not be evident if a species is abundant because it is in its preferred habitat, or rare because it is in a marginal habitat. In fact, we might well observe positive density dependence in cases where species exhibit strong habitat preferences (Wright 2002). Given that species habitat associations have been observed in numerous plant communities worldwide (Harms *et al.* 2001; Itoh *et al.* 2003; Valencia *et al.* 2004; Aiba & Nakashizuka 2007; Lai *et al.* 2009), tests for community-level consequences of density dependence must account for habitat associations. Furthermore, variation among species in habitat preferences is also hypothesized to promote species coexistence in forest communities. Thus, simultaneous evaluation of both density dependence and habitat associations would shed light on the relative contribution of these two mechanisms to diversity maintenance in species-rich communities.

Furthermore, from the perspective of the traditional CCT tests, it is necessary to incorporate rare species into analyses so that comparisons between rare species and common species can be made for the whole community (Connell *et al.* 1984). However, tests of CCTs in most previous studies were limited in several analytical aspects. First, previous studies utilized species-based regression in which species' performance (e.g. survival, growth and recruitment) and population size were represented by a single point (i.e. the estimate of performance was based on the average over individuals of the species), and it was difficult to assign species' performance for most species due to limited sample sizes. Second, traditional methods for calculating species' performance in CCT tests fail to take into account the spatial structure of sampling units, and may therefore be biased due to spatial autocorrelation in seedling survival. Meanwhile, in addition to the potentially confounding effects of habitat associations, differences among species in life history strategy may prevent the detection of a density dependence driven CCT (Comita & Hubbell 2009) or may result in a spurious CCT (Wright 2002; Queenborough *et al.* 2007).

Following these lines of reasoning, an appropriate analytical method is essential for a complete understanding of density dependence. Unlike traditional species-based CCT tests, we used individual-based generalized linear mixed models (GLMMs) with crossed random effects to account for the sampling spatial structure of the dataset, species identities, and to control for other factors (e.g. habitat associations and seedling height) for a credible CCT

test (Quene & van den Bergh 2008). Moreover, we assessed the relative importance of density dependence compared to habitat association in shaping seedling survival patterns using variance component analyses (Bryk & Raudenbush 1992; McMahon & Diez 2007). In addition, local-scale density dependence was investigated with varying-slope mixed models that allow for the assessment of local neighbourhood effects for all species in the community, including the rarest species.

In this study, we provide convincing evidence that density dependence is prevalent in seedling survival both at local and larger spatial scales, consistent with several community-wide studies (Wills *et al.* 1997, 2006; Harms *et al.* 2000). Our results also reveal that when controlling for the influence of species differences (e.g. habitat association and seedling height), a CCT was apparent and explained a significant portion of the variation among species in survival rates, which implicitly indicates an important role for density dependence at the community level. We further conclude that density-dependent effects were critical in the regulation of seedling survival and could maintain species coexistence in conjunction with habitat associations.

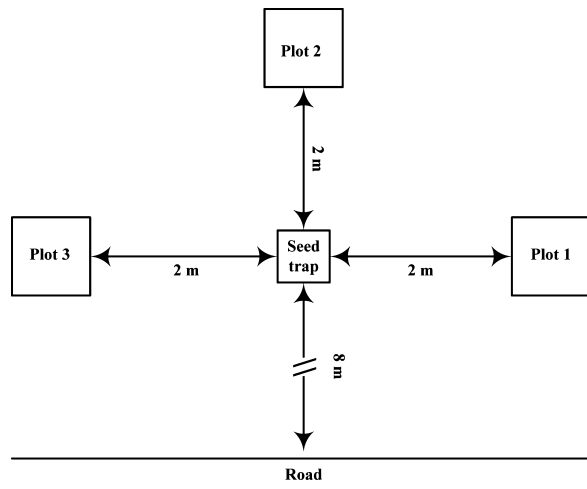
## MATERIAL AND METHODS

### Study site

This study was based on the 24 ha Gutianshan (GTS) permanent subtropical forest dynamic plot (FDP) located in GTS Forest Reserve, Zhejiang province, China. This plot is a part of the Chinese Forest Biodiversity Monitoring Network, which has sponsored four large FDP that cover a range of typical vegetations spanning temperate, subtropical and tropical forests (Legendre *et al.* 2009). The climate at GTS is seasonal, with two typical dry seasons (from July to August and from October to February; Lai *et al.* 2009). Detailed descriptions of climate, topography and flora can be found in Legendre *et al.* (2009). During 2005, all trees and shrubs  $\geq 1$  cm d.b.h. (diameter at breast height, 1.3 m above ground) in the plot were tagged, measured, mapped and identified to species (Lai *et al.* 2009; Legendre *et al.* 2009).

### Seedling census

To monitor seed rain and seedling dynamics in the 24-ha FDP, a network of census stations was established in a stratified random design along the trails (Figure S1). Each station consisted of a 0.5-m<sup>2</sup> litter trap for collecting flowers and seeds, and three 1-m<sup>2</sup> seedling plots for monitoring seedling dynamics. These three seedling plots were placed 2 m away from each of three sides of each seed trap (Fig. 1). In May 2006, we erected 130 stations with a mean distance ( $\pm$  SD) of  $19.36 \pm 2.9$  m between nearest-neighbour



**Figure 1** Census station layout.

stations. In each 1 m<sup>2</sup> seedling plot, all woody plants ≤ 1 cm d.b.h. have been tagged and identified to species. Survivors were checked in subsequent censuses and new recruits were tagged and identified. We recensused seedling plots three times a year (May, August and November) in 2006 and 2007, and twice a year (May and August) since 2007. To avoid complications caused by the ice storm in February 2008, the analyses presented here only use the first 1.5 years of seedling data (May 2006–November 2007).

## Analytical methods

### Model structure

The sampling design allows us to take the three 1 m<sup>2</sup> seedling plots as replicates of each station, and the state of the focal seedlings was assigned unity (alive) or zero (dead) from May 2006 to November 2007. Consequently, the seedling census data has a simple hierarchical structure: individual seedlings (level 1) were nested within each of the three 1 m<sup>2</sup> seedling plots (level 2), which are in turn nested within the 130 census stations (level 3) in the 24 ha FDP. This spatial structure of the seedling dynamic data can be appropriately analysed using GLMMs, which facilitate quantification of the relationships between the binary response variable and covariates at different scales. In this study, we also included species identity as a crossed random factor, such that the species adopted in the analysis can be thought of as being randomly sampled from all species in the community, providing a convenient framework for evaluating multi-scale density dependence and habitat association. The GLMMs with crossed random effects can be specified as:

$$y_{ijk} \sim \text{binomial}(p_{ijk})$$

$$\begin{aligned} \pi_{ijk} &= \log\left(\frac{p_{ijk}}{1-p_{ijk}}\right) \\ &= [\beta_0]_{\text{fixed-part}} + [u_{\text{species}} + u_{jk} + u_k]_{\text{random-part}}, \end{aligned} \quad (1)$$

where  $y_{ijk}$  was the binary response (alive or dead) for seedling  $i$  in plot  $j$  and station  $k$  in November 2007, and  $p_{ijk}$  describes the predicted survival probability for each seedling. The first set of brackets in eqn 1 above includes the fixed portion of the model, where  $\beta_0$  denotes the fixed intercept. The second set of brackets includes the random portion of the model, where  $u_{jk}$  and  $u_k$  refer to plot-specific (level 2) and station-specific (level 3) random intercepts, respectively, which were used to characterize the survival autocorrelation within the same plot and census station. The variation among species was characterized by  $u_{\text{species}}$ . All notation follows West *et al.* (2007). In this study, eqn 1 is considered as the unconditional model, and provides a baseline against which more complex models can be compared.

### Testing for a community compensatory trend and habitat associations

Based on the unconditional model eqn 1, we then began with the inclusion of species-level variables, specifically population size. Thus, our first conditional model, in which seedling survival was expressed as a function of population size ( $x_p$ ), can be written as:

$$\begin{aligned} \pi_{ijk} &= \log\left(\frac{p_{ijk}}{1-p_{ijk}}\right) \\ &= [\beta_0 + \beta_1 x_p]_{\text{fixed-part}} + [u_{\text{species}} + u_{jk} + u_k]_{\text{random-part}} \end{aligned} \quad (2)$$

Notice that the only difference between the unconditional model (eqn 1) and the conditional model (eqn 2) is the inclusion of an extra fixed effect, which in this case is population size. Two measures of population size (abundance and basal area of stems ≥ 1 cm d.b.h.) were calculated at the 24 ha scale based on the initial FDP census data. Values of population size were standardized by the mean and standard deviation before being added into eqn 2.

In the mixed framework, random effects can be estimated through variance components. In eqn 1, as there were no predictors, the estimated random effects were unconditional components, while for eqn 2 these were conditional components. One important way of calculating how much of the variation among species can be explained by population size is to compute the diminished variance among species between eqns 1 and 2, which is referred to as variance component analyses (Bryk & Raudenbush 1992). For these analyses, the explanatory power ( $R^2$ ) differs slightly from that of the traditional  $R^2$  statistic in that it is only a measure of the percentage of explained variation by

predictors at a certain scale. Details of variance component analysis can be found in McMahon & Diez (2007).

With the expectation that habitat association would be prevalent if habitat partitioning is important in species coexistence, multivariate regression tree methods (De'ath 2002) were used to divide the plot into habitats based on soil variables and topography and indicator species analysis (Dufrene & Legendre 1997) was then used to detect significant species habitat associations based on the distribution of trees (d.b.h.  $\geq 1$  cm). To control for intrinsic differences among species and evaluate the relative contributions of CCT compared to habitat association at community level, we classified all sampled seedling species into different habitat association guilds. We then included habitat associations as a species-level categorical variable in eqn 2. Habitat association was included as a fixed effect (similar to population size), and was set equal to the number of the habitat type with which the species was associated or to zero for species not associated with a habitat. Additionally, the CCT tests were also conducted separately for each group of species with the same habitat association (for groups with  $\geq 5$  species), and variance component analysis was also used to quantify the variation explained by CCT as described above. Meanwhile, we controlled for seedling height in all community-level tests (added as a fixed effect) as seedling height was usually significantly and positively correlated with seedling survival, which can cause a spurious CCT pattern, if rare species have higher mean seedling height than common ones (Queenborough *et al.* 2007).

#### *Tests of local-scale density dependence*

To test whether a CCT pattern was driven by local-scale density dependence, we used the mixed-model framework described above to construct a varying-slope model by adding by-species random slopes to the coefficients for local neighbourhood variables at different scales. In this framework, local neighbourhood compositions (i.e. seedling density within the 1-m<sup>2</sup> seedling plot and basal area of surrounding saplings and trees) can be added into models together or separately, and species-by-species coefficients of density-dependent effects can be estimated even for the rarest species by taking advantage of the borrowed strength from other species in the analysis (Gelman & Pardoe 2006). For simplicity, we first think about what the model looks like when adding only one local neighbourhood composition predictor ( $x_{local}$ ). This random slope model can be defined as:

$$\begin{aligned} \pi_{ijk} &= \log\left(\frac{\hat{p}_{ijk}}{1 - \hat{p}_{ijk}}\right) \\ &= [\beta_0 + \beta_1 x_{local}]_{\text{fixed-part}} + [\gamma_{\text{species} \times \text{local}} + \mu_{\text{species}} \\ &\quad + \mu_{jk} + \mu_k]_{\text{random-part}}, \end{aligned} \quad (3)$$

where  $\beta_1$  represents the mean coefficient value of the local variable across all species and  $\gamma_{\text{species}}$  denotes the random slope term for each species (i.e. variation among species in the coefficient of the  $x_{local}$ ). Compared to the unconditional model (eqn 1), this model (eqn 3) contains an additional fixed effect ( $\beta_1 x_{local}$ ) and an additional random term ( $\gamma_{\text{species} \times \text{local}}$ ). Under this definition, we not only assume that the local neighbourhood compositions were related to seedling survival, but we also allow the relationship between local neighbourhood compositions and seedling survival to vary across species. For simplicity, we can also stipulate that the coefficients of local neighbourhood compositions did not vary across species by eliminating the random slope term ( $\gamma_{\text{species} \times \text{local}}$ ) from eqn 3.

In this document, local neighbourhood compositions were defined at both plot and station levels for each of the 1259 seedlings in the May 2006 census. The seedling density of total, conspecific and heterospecific neighbours was calculated in the 1-m<sup>2</sup> seedling plot (level 2). The stem basal area of total, conspecific and heterospecific neighbours were calculated within a 20-m radius from the seed trap of each station (level 3), as previous analyses have shown that basal area performs better than stem density (Comita & Hubbell 2009) and effects of neighbours are typically negligible beyond 20 m (Hubbell *et al.* 2001). The relative conspecific seedling density (proportion of conspecifics in the 1-m<sup>2</sup> plot) and relative conspecific basal area of adult trees (within 20 m radii) were also calculated.

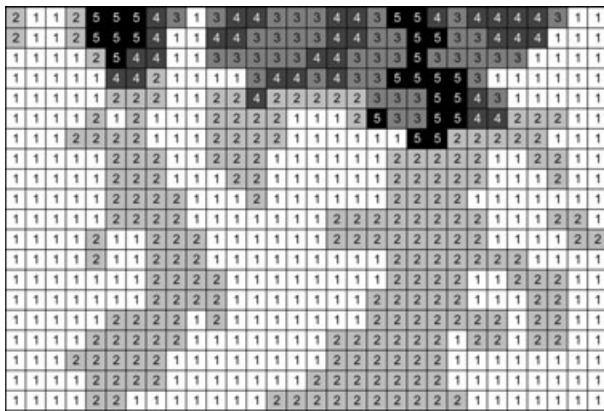
All analyses were conducted in R 2.9.1 (R Development Core Team 2009). The multivariate regression tree and indicator species analysis was computed based on the 'mvpart' library (De'ath 2006) and the 'labdsv' library (Roberts 2006). Mixed models with crossed random effect were fitted by the lmer() function of the 'lme4' package with the recommended Laplace method (Bates *et al.* 2008; Bolker *et al.* 2009). Likelihood ratio (LR) tests were used to assess the significance of random effects, and the fixed effects were tested by Wald Z tests (Bolker *et al.* 2009). Odds ratios (OR) were obtained by taking the exponential of parameters of fixed effects and were used to describe the partial effects of variables on the odds of survival (Hubbell *et al.* 2001).

## RESULTS

### Habitat associations

Three variables, altitude (alt), total phosphorus (T.P) and available calcium (A.Ca), were selected by the MRT (multivariate regression tree) procedure and a tree with five habitat categories was selected as the best one after 1000 cross-validation trials (Figure S2). Based on these three variables, the whole 24 ha FDP was classified into five habitat categories with 20 × 20 m cells (Fig. 2 and Figure S3)





**Figure 2** Map of five habitat types classified by 20 × 20 m cells with multivariate regression tree analysis: low valley (type 1), low ridge (type 2), mid-slope (type 3), high slope (type 4) and high ridge (type 5).

that correspond to the following categories: low valley (type 1), low ridge (type 2), mid-slope (type 3), high slope (type 4) and high ridge (type 5). Thirty-six species were identified as indicator species, meaning that they were significantly associated with one of the five habitat types, and 27 of those species were also represented in the seedling data. Of those species with seedling data, 11 species were associated with habitat type 1, two species with habitat type 2, and 14 species with habitat type 5 (Table S1). The remaining 43 seedling species did not exhibit clear habitat associations, and were assigned a habitat association of type 0.

**Community level analyses of seedling survival**

Of the initial seedling cohort tagged in May 2006, 313 out of 1259 seedlings of 70 species died by November 2007. Seedling mortality rate varied across species, ranging from 0.04 to 1.0, and the mean mortality rate for all seedlings was 0.25.

Individual-based mixed models with crossed random effects were utilized to quantify the variation of seedling survival at different levels. After controlling for seedling height, a significant variance component among species ( $\sigma^2_{\text{species}}$ ) was identified (Table 1). The spatial term ( $u_{jk}$ ) for the 1-m<sup>2</sup> plot scale was not significantly different from zero, whereas the station-level random term,  $u_k$  ( $\sigma^2_{\text{station}}$ ; Table 1), was apparent and indicated that seedling survival was strongly auto-correlated within the same census station. To compare the relative contributions of CCT and habitat association, conditional models that included two measures of population size were constructed. Contrary to expectation, population size (abundance and basal area of stems  $\geq 1$  cm d.b.h.) of species was not significantly associated with seedling survival in the full data set ( $P = 0.13$  and  $P = 0.97$  for abundance and basal area, respectively) and

only a small fraction of variance (9 and 0.1% for abundance and basal area, respectively) can be explained, which is much less than that explained by habitat association (17.7%; Table 1a). In the subset of habitat-associated species, basal area (but not abundance) was negatively correlated with seedling survival, indicating a CCT, and explained 13.8% of the variance among species in seedling survival (Table 1b). In comparison, habitat association explained 34.6% of the variance among species in seedling survival for those species (Table 1b). For species associated with habitat type 1, only population size based on basal area exhibited a significant negative correlation with seedling survival and explained 50.5% of the variance among species (Table 1c). Although there was no significant negative correlation between population size (abundance or basal area: d.b.h.  $\geq 1$  cm) and seedling survival for species associated with habitat type 5, population size based on abundance of trees  $\geq 5$  cm d.b.h. had significant negative effect on seedling survival (Table 1d) and more interestingly, this typical subtropical forest community was saturated with trees  $\geq 5$  cm d.b.h. ( $\rho = 1483$  trees per ha; Hubbell 2001). For species without clearly defined habitat association (type 0), tree abundance  $\geq 1$  cm positively influenced seedling survival (Table 1e), but population size expressed as basal area did not have a significant effect.

**Local-scale density dependence**

With all 70 species combined, seedling height had a consistent positive effect on focal seedling survival (OR = 1.05–1.07,  $P < 2e-16$ ). Conspecific tree basal area (level 3) had a significant negative effect on focal seedling survival (OR = 0.52,  $P = 0.01$ ) and the relative conspecific seedling density (level 2) and basal area (level 3) also exerted strong negative effects on community-wide seedling survival (OR = 0.34,  $P = 0.00$  and OR = 0.04,  $P = 0.02$ , Table 2). In contrast, heterospecific seedling density and total seedling density (level 2) showed positive effects on focal seedling survival (OR = 1.09,  $P = 0.02$  and OR = 1.05,  $P = 0.07$ ; Table 2). Odds ratios for total basal area, heterospecific tree basal area and conspecific seedling density were not significantly less than one (Table 2). When the significant density-related variables at the two different scales (plot scale: heterospecific seedling density and relative conspecific seedling density; station scale: conspecific tree basal area and relative conspecific tree basal area) were combined in a single model, these models showed a better fit to the dataset than adding them separately. For the two best fitted combined models, the mean coefficients for local density-dependent factors across all species were in accordance with models including a single density-dependent variable (Table 2 scales combined models: A, B). Based on LR tests, we eliminated the random slope term for conspecific

**Table 1** Parameter estimates and variance predictions in mixed models with crossed random effects used to test for effects of population size and habitat associations on seedling survival at the community level

Models	Parameters		Population size		Habitat association	
	$\sigma^2_{\text{station}}$	$\sigma^2_{\text{species}}$	Estimate ( <i>P</i> -value)	$R^2$	<i>P</i> -value	$R^2$
(a) All species ( $N = 1259$ , species = 70)						
Unconditional model	0.34436	1.35868				
Conditional model 1 (abundance: d.b.h. $\geq 1$ cm)	0.34689	1.24197	0.25 (0.13)	9%		
Conditional model 2	0.34683	1.11886			0.02	17.7%
(b) Habitat-associated species ( $N = 615$ , species = 27)						
Unconditional model	0.36893	1.21159				
Conditional model 1 (basal area: d.b.h. $\geq 1$ cm)	0.37069	1.04419	-0.4 (0.08)	13.8%		
Conditional model 2	0.35659	0.79254			0.006	34.6%
(c) Type 1 ( $N = 365$ , species = 11)						
Unconditional model	0.14999	0.71472				
Conditional model (basal area: d.b.h. $\geq 1$ cm)	0.13841	0.35391	-0.64 (0.045)	50.5%		
(d) Type 5 ( $N = 217$ , species = 14)						
Unconditional model 2	0.94985	0.38332				
Conditional model 2 (abundance: d.b.h. $\geq 5$ cm)	0.89695	0	-0.24 (0.046)	100%		
(e) Species without clear habitat association ( $N = 644$ , species = 43)						
Unconditional model 1	0.51828	1.42558				
Conditional model 2 (abundance: d.b.h. $\geq 1$ cm)	0.51200	0.87369	0.4 (0.02)	38.7%		

(a) All species: the full seedling dataset; (b) habitat-associated species: a subset of species with well-defined habitat associations; (c) type 1: species significantly associated with habitat 1 (low valley); (d) type 5: species significantly associated with habitat 5 (high ridge); (e) species without clear habitat association: a subset of species without clear habitat associations. The analyses for the remaining three habitat types were not calculated due to limited sample sizes.  $\sigma^2_{\text{station}}$  = variance among stations;  $\sigma^2_{\text{species}}$  = variance among species;  $R^2$ , the explanatory power of the species-level covariates, not the traditional  $R^2$  (McMahon & Diez 2007).

All the models were analysed using a partial correlation analysis in which the controlling effects of seedling height on seedling survival were removed. Population size was standardized by the mean and standard deviation prior to entering into the analysis.

basal area, relative conspecific basal area (station scale: within 20 m radius;  $P = 0.99$  and  $P = 0.99$ , respectively) and relative conspecific seedling density (1 m<sup>2</sup> plot scale;  $P = 0.41$ ) in the two scales combined models (Table 2 scales combined models: A, B), which indicates that the survival of all 70 species was unanimously negative in response to these three density variables. In contrast, the random term for heterospecific seedling density (1 m<sup>2</sup> plot scale) in scales combined model B (Table 2) was marginally significant ( $P = 0.07$ ), indicating variation among species in the effect of heterospecific seedling density on survival. Thus, the coefficients were also estimated individually for each species by taking advantage of the 'borrowing strength' effect of mixed models. The coefficients for 67 of the 70 species showed a positive pattern with this variable, except for three species (*Rhododendron ovatum*, *Rhododendron simsii*, *Lespedeza formosa*; Table S2).

## DISCUSSION

Our results confirmed that, at both local and community scales, rarer species were favoured over commoner species

in this subtropical forest. After taking into consideration differences among species in habitat associations and seedling height, species' abundance in the community had a significant negative correlation with seedling survival, which was consistent with a CCT. Moreover, the results from local-scale analyses are also consistent with the hypothesis that the observed CCT results from local neighbourhood effects. In addition to detecting signatures of negative density dependence at different scales, our study also provides new insight into the explanatory power of density dependence in determining spatial patterns of seedling survival and the relative importance of density dependence compared to habitat association, another mechanism proposed to explain species coexistence in diverse plant communities.

## Community compensatory trend and habitat association

Intrinsic differences among species have been regarded as essential for species coexistence, except in the random ecological drift model (Hubbell 2001). Unlike life history traits alone, habitat association is the consequence of the

**Table 2** Summary of the odds ratios for covariates in the analyses of local-scale density dependence in a subtropical forest, China

Scale	Seedling survival against seedling height	Parameter estimate				
		Odds ratio	Pr(>  z )	AIC	BIC	logLik
1 × 1 m <sup>2</sup> plot scale	Total seedling density	1.05	0.07	973.2	998.9	-481.6
	Conspecific seedling density	0.93	0.31	976.2	1009	-483.1
	Heterospecific seedling density	<b>1.09</b>	<b>0.02</b>	<b>966.3</b>	<b>992</b>	<b>-478.2</b>
	Relative conspecific seedling density	<b>0.34</b>	<b>0.00</b>	<b>964.2</b>	<b>984.7</b>	<b>-478.1</b>
Station scale (radius ≤ 20 m; d.b.h. ≥ 1 cm)	Total tree basal area	0.95	0.38	971.8	992.4	-481.9
	Conspecific tree basal area	<b>0.52</b>	<b>0.01</b>	<b>968.8</b>	<b>999.6</b>	<b>-478.4</b>
	Heterospecific tree basal area	0.96	0.38	974.8	1001	-482.4
	Relative conspecific tree basal area	<b>0.04</b>	<b>0.02</b>	<b>972.4</b>	<b>998</b>	<b>-481.2</b>
Scales combined models						
A	Conspecific tree basal area	<b>0.61</b>	<b>0.04</b>	<b>962.2</b>	<b>987.9</b>	<b>-476.1</b>
	Relative conspecific seedling density	<b>0.37</b>	<b>0.00</b>			
B	Relative conspecific tree basal area	<b>0.02</b>	<b>0.01</b>	<b>960.9</b>	<b>991.7</b>	<b>-474.4</b>
	Heterospecific seedling density	<b>1.10</b>	<b>0.01</b>			

Covariates at different scales and seedling height were regressed against focal seedling state (lived or died) for all species combined.

Odds ratios < 1 indicate negative effects on seedling survival and odds ratios > 1 indicate positive effects on seedling survival.

Bold values denote significant odds ratios at  $\alpha = 0.05$  level.

interaction between species life history strategy and habitat filtering, thus it is more credible and efficient to adopt this integrative criterion to characterize differences among species in the same community. In this study, the whole 24 ha plot can be classified into five habitat types in light of topography and soil properties. Unlike a recent study only utilizing topography data (Legendre *et al.* 2009), we found more species (36 species) were significantly habitat associated at the Sidak-corrected 5% significance level, consistent with the results from Harms *et al.* (2001) and Lai *et al.* (2009). Of the five habitat types, the type 4 and type 5 habitat were more inclined to be disturbed by lightning strokes since they were higher up on the mountain and mainly composed of pioneer tree species, whereas the other three types contained representative subtropical evergreen broad-leaved forest vegetation, which comprises about 91% area of the 24 ha plot.

Like most previous CCT tests, this study focused on the seedling stage, which is considered the most vulnerable stage in the tree life cycle and the stage at which negative density dependence should be most apparent. To know how important density dependence was in determining seedling survival patterns, the relative effect of CCT was assessed compared to habitat association. For all species combined, the relationship between species abundance and survival was positive, and only 0.1–9% of the variation among species in seedling survival was explained. In contrast, habitat association was a significant predictor of seedling survival and explained 17.7% of the variation among species (Table 1a). When we added species abundance and habitat association in a single model, habitat association also explains more variation than species abundance. For species with signifi-

cant habitat associations, habitat association still explained a larger portion of the variation in species' seedling survival rates than species abundance (Table 1b). However, after ruling out the impact of habitat associations, CCTs were apparent and species abundance explained most of the seedling survival variation among species (Table 1c, d). These patterns suggest that CCT was a main process in driving seedling dynamics, even though density dependence seems to be less important than habitat partitioning in determining short-term seedling survival patterns.

For species without clear habitat association, we did not find a CCT and potential explanations for the opposite trends were that: First, the influence of intrinsic differences (e.g. species' shade tolerance) have not been ruled out in our analyses (Comita & Hubbell 2009); second, indicator species analyses are a conservative method for identifying species habitat associations, so species without significant habitat association may actually have habitat preferences. In addition, CCT patterns will only be detectable in communities, where the negative effects of density dependence are not cancelled out by habitat filtering. Alternatively, because most species without clear habitat association in the indicator species analyses are relatively rare species, they likely encounter lower densities of conspecific neighbours, therefore reducing our ability to detect negative effects of increasing conspecific density or frequency.

### Local neighbourhood effects

An array of factors, both biotic and abiotic, may influence seedling survival and may alter species composition in later

life stages. Our study first focused on overall mean biotic neighbourhood effects across all species on seedling survival, and results in Table 2 provide strong evidence for local density-dependent effects. We found a significant positive correlation between seedling survival and heterospecific seedling density at the 1-m<sup>2</sup> plot scale. In contrast, the negative effect of conspecific seedling density on seedling survival was not apparent, but relative conspecific seedling density (i.e. frequency) was negatively correlated with seedling survival. Similar patterns were apparent at the station scale: conspecific tree basal area had a significant, negative impact on seedling survival, and seedling survival decreased with the increasing proportion of conspecific tree basal area. The results provided here were observational and are insufficient to distinguish among several mechanisms that may be responsible for the density-related patterns. The observed frequency-dependent mortality was consistent with the Janzen–Connell hypothesis (Janzen 1970; Connell 1971), which attributes such patterns to host-specific natural enemies, such as pathogens and herbivores. Seedling–seedling competition is less likely to be responsible for density-dependent patterns, and it has been shown to be relatively unimportant in some tropical forests (Paine *et al.* 2008; Svenning *et al.* 2008). Our results are also consistent with the species herd protection hypothesis (Wills 1996; Peters 2003), which posits that increasing heterospecific neighbours would facilitate the focal seedling survival by depressing the encounter probability with its species-specific pests and pathogens. However, when a permutation test (9999 times) was used to check the relationship between heterospecific seedling density and relative conspecific seedling density, we found a significant negative correlation between the two variables (coefficient = -8.3,  $P$ -value < 0.0001). Thus, the positive effect of heterospecific seedling density may simply be due to the fact that relative conspecific seedling density is lower in plots with more heterospecific seedlings. Carefully designed experiments are needed to distinguish between potential hypotheses concerning the effect of heterospecific neighbour density.

In contrast to auto-regression models (Hubbell *et al.* 2001), our approach not only controls for spatial autocorrelation in survival, but also allows for estimates of density effects for rare species. The mixed models with crossed random effects can ‘borrow strength’ from other species in order to produce ‘indirect’ estimates for rare species. This approach is based on the rationale of the exchangeability of all species in the same community (Hubbell 2001) and thereby allows us to model the random coefficients across species. Nonetheless, confidence in species-specific estimates for rare species is low in some specific conditions, since the estimates for species with small sample sizes will be pulled towards the overall mean across all species, and

rare species will appear to be more similar to abundant species than they may truly be. In our case, for conspecific tests, the random slope term tested by LR tests for conspecific basal area, relative conspecific basal area and relative conspecific seedling density were not significant. Thus, we can confirm that density/frequency dependence is prevalent in the community and further infer that all species respond in the same way statistically to these density-dependent variables. On the contrary, because the coefficient for heterospecific seedling density was marginally significantly varying across species ( $P = 0.07$ ), ‘borrowing strength’ was used to estimate the coefficients for each species (Table S2) and this may be problematic for species with limited samples (< 3–5 individuals). However, these conclusions are conservative because the benefits of species herd protection will only be evident using the analysis presented in this study when the benefits of species herd protection outweigh the negative effects of high heterospecific density resulting from resource competition and generalist pests (Peters 2003). For the three species that did not show survival pattern consistent with species herd protection (*R. ovatum*, *R. simsii*, *L. formosa*), their leaves were covered with vellus hair that suggest a higher resistance to pathogens or herbivores. As a result, the benefits of species herd protection were less important compared to interspecific competition for species with high resistance to enemies. Furthermore, density dependence is not restricted to only the seedling stage, and it may play a continuous role in regulating survival patterns across several stages of tree life cycle (Uriarte *et al.* 2004; Wright *et al.* 2005; Wills *et al.* 2006). Indeed, the density-dependent pattern has also been confirmed in GTS for saplings and adult trees (Zhu *et al.* 2010). Thus, the role of density dependence has been underestimated in this short-term seedling dynamic study, and long-term research is clearly necessary for assessing the full scope of density dependence in community assembly.

In summary, our novel approach has provided strong evidence for density dependence at our diverse, subtropical forest site. The scaling of density dependence from the local to community level suggests that density dependence is an important mechanism for community diversity maintenance. Our results also indicate that niche differentiation with respect to edaphic and topographical habitat variables also contributes to species coexistence in this forest. However, since multiple species were associated with each habitat, the observed species’ habitat associations are not sufficient to explain the coexistence of all species in this hyper-diverse community (Wright 2002). Thus, we conclude that, through effects on seedling survival, both density dependence and habitat association likely contribute to the maintenance of diversity in this subtropical forest.



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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** The census network of seedling stations in Gutianshan forest dynamic plot.

**Figure S2** Multivariate regression tree of the Gutianshan (GTS) 24 ha plot.

**Figure S3** Map of habitat types classified by 20 × 20 m cells overlay with topography.

**Table S1** Indicator species that are significant indicators of different habitat types at the Sidak-corrected 5% significance level.

**Table S2** The specific coefficients of heterospecific seedling density (1 m<sup>2</sup> plot scale) for all 70 species in Table 2 scales combined model B.

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