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Genetic tracking of density-dependent adult recruitment: A case study in a subtropical oak

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Abstract

1. Density-dependent recruitment is fundamental to understanding species diversity and community dynamics in plants. Although there is compelling evidence that seeds and seedlings die from conspecific negative density dependence (CNDD) as predicted by the Janzen–Connell hypothesis, characterising adult recruitment remains a challenge for long-living trees. Previous studies have used the decrease in fine-scale spatial genetic structure (FSGS) across life stages to indicate CNDD; however, this has not been tested rigorously.
2. We addressed these challenges by integrating dispersal kernels and FSGS. To establish links between density dependence and FSGS, we simulated seedlings based on the estimated dispersal kernels from parentage analyses, and further simulated adults under various seedling-to-adult recruitment scenarios, using an individual-based spatially explicit model. We tested this method in an isolated *Cyclobalanopsis glauca* population on China's Dajinshan Island.
3. We detected significant FSGS in the seedlings and weaker, though also significant, FSGS in the adults. As expected, the observed FSGS of seedlings was well predicted by the simulated seedlings, with observations falling inside the 95% confidence envelopes over all distance classes. However, the simulations showed that CNDD enhanced the FSGS while positive density dependence dampened it during the seedling-to-adult transition. The adult FSGS of our population was therefore explained by positive rather than negative density-dependent adult recruitment.
4. *Synthesis*. Our study demonstrates that the change of FSGS in conjunction with dispersal-based model tests can offer a valuable insight into density-dependent adult recruitment. The results indicate that the transitions from seedlings to adults in *C. glauca* are dominantly regulated not by Janzen–Connell effects, but by processes of positive density dependence. More broadly, the findings may provide a caution against extrapolations of widespread Janzen–Connell effects in seeds and seedlings to adult recruits, underscoring a critical gap between mechanisms at early stages and long-term population and community dynamics.

KEYWORDS

adult recruitment, conspecific density dependence, *Cyclobalanopsis glauca*, effective dispersal kernel, Janzen–Connell hypothesis, plant population and community dynamics, spatial genetic structure

1 | INTRODUCTION

Since Hutchinson (1961) proposed the famous paradox of the plankton, understanding the maintenance of diversity in plant communities has been an enduring Herculean task for ecologists (Chesson, 2018). Hypotheses explaining species coexistence usually consider the effects of neighbours, especially conspecific neighbours, on demographic patterns (Ellner et al., 2019; Wright, 2002). For example, the Janzen–Connell hypothesis predicts that conspecific negative density dependence (CNDD) occurs where specialised natural enemies (e.g. pathogens and herbivores) depress recruitment in the vicinity of conspecific adults, freeing ecological space for other species, thereby maintaining local diversity (Connell, 1971; Janzen, 1970; Johnson et al., 2012; LaManna et al., 2017; Levi et al., 2019). Intraspecific competition suppressing the growth of conspecific neighbours may also lead to CNDD (Terborgh, 2012). Alternatively, conspecific positive density dependence (CPDD) can arise as a result of benefits from accumulated host-specific ectomycorrhizal fungal mutualists (Bennett et al., 2017; Merges et al., 2020), localised predator satiation (Tong et al., 2017) and/or habitat preferences (Zhu et al., 2015).

Strong evidence of CNDD has been found at early life stages from seeds, to seedlings, and saplings in various tree species (Brown et al., 2020; Comita et al., 2014; Harms et al., 2000; Liang et al., 2016; Umana et al., 2018; Wang et al., 2019). However, it remains poorly understood whether adult recruitment is negatively or positively density-dependent, or neutral (Kellner & Hubbell, 2018; Steinitz et al., 2011). Seedlings can often establish with relatively high density (tens per square metre), yet only a few of them can grow to maturity (usually no more than hundreds per hectare); therefore, a process promoting the diversity of seedlings does not necessarily translate into the enhanced diversity of adult trees (Freckleton & Lewis, 2006). Consequently, assessing adult recruitment is a critical step towards better understanding the degree to which density dependence permits species coexistence and contributes to the maintenance of tree diversity at the mature stage (Kellner & Hubbell, 2018; Schupp & Jordano, 2011).

Obtaining enough data across various ontogenetic stages to characterise adult recruitment is by no means an easy task, especially for long-lived trees. This may explain why the studies that have tested density dependence in adults are so rare (Kellner & Hubbell, 2018). An alternative way to understand long-term recruitment is through the lens of changes in spatial patterns of individuals across different ontogenetic stages, with the principle that aggregation will subside through ontogeny under CNDD and will increase if CPDD dominates (Bagchi et al., 2011). Nevertheless, simulations have shown that CNDD may also lead to an increase in aggregation with size-class in some cases (Murrell, 2009). More importantly, spatial patterns generated by environmental filtering and by limited dispersal remain difficult to distinguish, even though many ameliorations have been made in both spatial statistics and spatial point process modelling (Brown et al., 2016). Genetic data should be useful with respect to this difficulty because pollen and seed movement can be quantified using parentage analysis on genotyped individuals (Moran & Clark, 2011; Thompson & Meagher, 1987).

An approach to infer density dependence from genetic data is based on the mode shift in the seed dispersal kernel estimated for dispersed seeds, seedlings and later stages (Figure 1, yellow

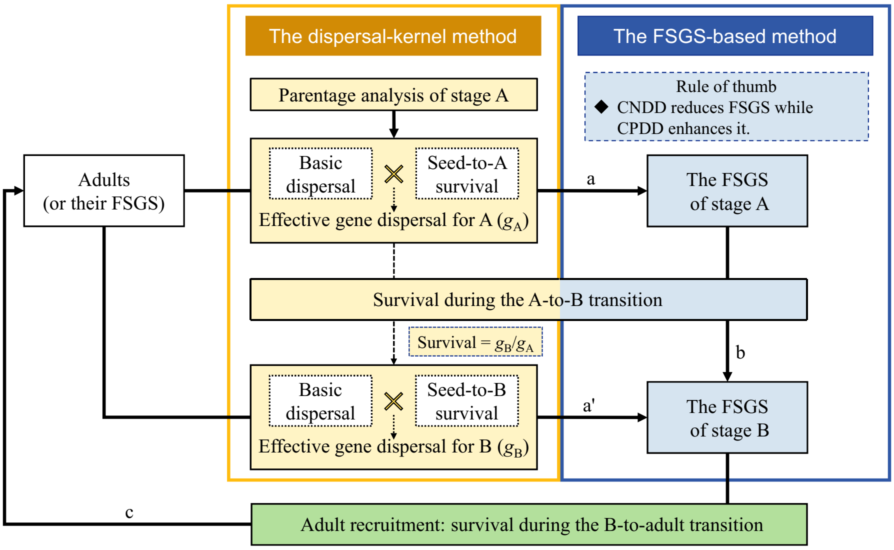


FIGURE 1 Framework of genetic approaches to infer density dependence in recruitment. One traditional method invokes dispersal kernels (yellow box). For any stage A (or B), the effective dispersal kernel g_A (or g_B) is the product of seed dispersal kernel and survival during the seed-to-A (or seed-to-B) transition. The survival curve during the A-to-B transition can be estimated by dividing g_B by g_A. A second traditional method (blue box) takes advantage of fine-scale spatial genetic structure (FSGS) to distinguish between conspecific negative density dependence (CNDD) and positive density dependence (CPDD). Given the pros and cons of each method (see the Introduction for details), we evolve an integrative approach (bold lines). It re-enacts the FSGS of a stage using the effective dispersal kernels (a, a'), and then models how density-dependent recruitment affects the FSGS of the next stage (b, c)

box), with effective dispersal describing the movement of seeds that lead to successful establishment rather than that of all seeds (Klein et al., 2013; Schupp et al., 2010). CNDD is expected to shift the effective dispersal kernel in late stages away from maternal trees while CPDD tends to shape reverse patterns (Bontemps et al., 2013; Gonzalez-Martinez et al., 2006; Murphy et al., 2017). Even more directly, the survival curves may be extracted by dividing the effective dispersal kernel of the later stage by that of the earlier stage (Steinitz et al., 2011; Tautenhahn et al., 2012). This method is appropriate for isolated maternal trees (i.e. single point source models), allowing seed dispersal and post-dispersal survival to be disentangled at any ontogenetic stage. However, in the more realistic cases of the complex spatial arrangement of several maternal trees, it may fail because seed shadows overlap and thereby all offspring are impacted by neighbouring adults irrespective of their origins (Tautenhahn et al., 2012), unless the neighbourhood effects are highly related to genotype similarity (Eck et al., 2019; Tito de Morais et al., 2020). Additionally, estimating the effective dispersal kernel can be technically difficult for adults, impeding the inference of adult recruitment with this method (but see Steinitz et al., 2011).

Another method uses the change of fine-scale spatial genetic structure (FSGS), that is, the non-random distribution of alleles within plant populations, to inform density dependence (Choo et al., 2012; Chung et al., 2003; Hardesty et al., 2005; Jones & Hubbell, 2006; Figure 1, blue box). The tenet is similar to that of the non-genetic method (Bagchi et al., 2011): limited gene dispersal builds the fundamental FSGS and, with this as a template, site-specific or random mortality processes act and shape patterns for later life stages (Kalisz et al., 2001; Wang et al., 2011). A common rule of thumb is that CNDD weakens the genetic structure while CPDD enhances it (Zhou & Chen, 2010). However, the spatial genetic signals of density-dependent recruitment have not been substantiated explicitly, and the effects of limited dispersal and those of other recruitment processes are not well disentangled. Other factors that can impact FSGS, such as population density (Vekemans & Hardy, 2004) and generation overlap (Jones & Hubbell, 2006), should be accounted when interpreting the demographic changes of FSGS.

Following the above lines of reasoning, neither method has enough accuracy or power in revealing recruitment especially for adults. Nevertheless, the dispersal kernel method can help disentangle the effects of recruitment processes on FSGS from those of dispersal, while in turn FSGS is a stable outcome of multiple-point-source interactions and can be used instead of effective dispersal kernel as the response variable. In light of this complementarity, we have evolved an integrative method (Figure 1, bold lines) to test density dependence in recruitment.

The integrative method establishes the direct link between recruitment and spatial genetic patterns by modelling FSGS based on the empirical dispersal kernels and different hypothesised recruitment types. More specifically, the processes that underlie effective gene dispersal also shape FSGS and *vice versa*, making it possible to re-enact the FSGS of a development stage from the corresponding effective dispersal kernels (Figure 1a,a'). Therefore, modelling how the survival/mortality of that stage impacts the FSGS of the next stage under different hypotheses of density dependence allows for detecting the spatial genetic signals of density-dependent recruitment. This approach can not only inform recruitment of seedlings, saplings or juveniles (Figure 1a,b), where three stages (A, B and adults in Figure 1) will be required but also applies to adult recruitment (Figure 1a',c), which requires two stages (B and adults in Figure 1). Here, we illustrate the integrative approach by investigating density dependence during the seedling-to-adult transition in a subtropical oak population.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling protocol

The study was conducted in the evergreen broad-leaved forest on Dajinshan Island of Shanghai, China (30°41′N, 121°25′E; *c*. 0.23 km^2; Figure S1). This island is a nature reserve, and had never been open for visiting. We focused on *Cyclobalanopsis glauca* (=*Quercus glauca*), a dominant species in the forest. It is a wind-pollinated monoecious oak and thought to be self-compatible (Chen & Song, 1997). Rodents are primarily responsible for the secondary seed dispersal after seed fall by gravity. The population genetic structure is likely to be stable because the forest has been almost free from anthropogenic disturbances for at least several hundred years. Importantly, the long distances (at least 50 km) between this population and other *Cyclobalanopsis* populations almost preclude the possibilities of either pollen- or seed-immigration, providing a suitable condition for an accurate estimation of dispersal kernels.

To maximise the accuracy of parentage inference, we mapped and collected fresh leaves from all the potentially reproductive trees of *C. glauca* over the whole island (Figure S1, $n = 202$). The diameters at breast height (DBH) were measured. We mapped and collected a random sample of seedlings ($n = 416$), which is usually enough for accurately estimating spatial genetic structure (Cavers et al., 2005). Compared to other schemes (e.g. exhaustively sampling within a plot or along transects), random sampling of seedlings over the whole island both improves our ability to capture the kernel tail and better reflects the whole population. Clonal ramets of adults and seedlings were avoided to the best of our ability.

2.2 | Genotyping and data pre-analyses

DNA was extracted from samples using a Plant Genomic DNA Kit (Tiangen), and genotyped with nine microsatellite loci developed for *C. glauca* (Tong et al., 2012). To assess genotyping error rate, we re-conducted a part of the experiment, including PCR, fragment size scoring, and allele binning and calling; in total, 726 alleles were re-genotyped. More details of the experiment are described in

Appendix S1. Based on multilocus genotypes, we found three clonal ramets in the seedlings (Appendix S2) and excluded them in further analyses. Null alleles were tested and found in six loci, where we made the most conservative correction for them by recoding all apparent homozygotes as heterozygotes consisting of the detected allele and a null allele (Appendix S3).

2.3 | Parentage assignments and estimation of dispersal kernels

Both maternal and paternal relationships were reconstructed simultaneously, with selfing allowed, under a maximum likelihood framework implemented in the cervus program (Marshall et al., 1998). Mutations and genotyping errors were allowed to occur at a rate of 0.01 in the analysis, according to our regenotyping controls. In further analyses, we used only biparental assignments that had high confidence (>80%) and were at least two times more likely than any other trio involving the same offspring (i.e. unambiguous).

Due to the biparental inheritance of microsatellites, we were unable to distinguish maternal from paternal parent using our genetic data. Since the seed dispersal of oaks is greatly limited relative to pollen dispersal (Chybicki & Burczyk, 2010; Petit et al., 2005), we assumed that the nearer parent was maternal and the more distant one was paternal. This assumption is common in other parentage analyses of plants with seed fall by gravity (Choo et al., 2012; Dow & Ashley, 1996; Nakanishi et al., 2009), though it potentially biases downwards estimates of seed dispersal distance, which will be more of an issue in species where the distance of seed dispersal approaches or exceeds the distance of pollen dispersal.

We used six distribution families, that is, the Gaussian, exponential, exponential power, Weibull, geometric and 2Dt families, following Austerlitz et al. (2004), to fit the pollen dispersal kernel, $f(r)$, and seed dispersal kernel, $g(r)$. Parameters were estimated separately for each family with a maximum likelihood method, and the best families were chosen based on the Akaike information criterion (AIC) for $f(r)$ and $g(r)$, respectively.

2.4 | Characterisation of FSGS

After confirming the absence of genetic discontinuities in the population with the Bayesian cluster approach in geneland (Guillot et al., 2005), we assessed the FSGS for adults and seedlings, respectively. Pairwise genetic coancestry was quantified using Nason's kinship coefficient F_{ij} (Loiselle et al., 1995), since it is statistically robust (Gapare & Aitken, 2005). To visualise FSGS, F_{ij} values were averaged over a set of distance classes, which were twenty 10-m intervals up to 200 m, then ten 50-m intervals up to 700 m and >700 m. These distance classes represent an effective compromise between resolution (making distance classes small enough to detect FSGS) and power (having enough pairs within each class). Standard errors of F_{ij} were estimated by bootstrapping 10,000 times. To test for FSGS, we randomly permuted multilocus genotypes among locations 10,000 times. The above analyses were conducted in the software spagedi (Hardy & Vekemans, 2002). Differences in FSGS between seedlings and adults were tested using the heterogeneity test in genalex 6.5 (Peakall & Smouse, 2012).

2.5 | Inference of density dependence during the seedling-to-adult transition

To infer density dependence in adult recruitment, we modelled the FSGS of adults through the a'–c pathway of Figure 1 (i.e. stage B = seedlings). We first simulated seedlings using the estimated mating system and dispersal kernels from parentage analysis (Figures 2i–iv). These simulated seedlings should have the same FSGS as the real seedlings (Figure 2v). Adult recruitment was then simulated under different scenarios of density dependence (Figure 2vi), thereby providing the null distributions of adult FSGS under different hypotheses of adult recruitment. Specifically, we simulated seedlings (n = 10,000) and adult recruitment within each time frame of 20 years (corresponding to the average reproductive age of *C. glauca*), using an individual-based spatially explicit model as follows.

2.5.1 | Selecting maternal trees

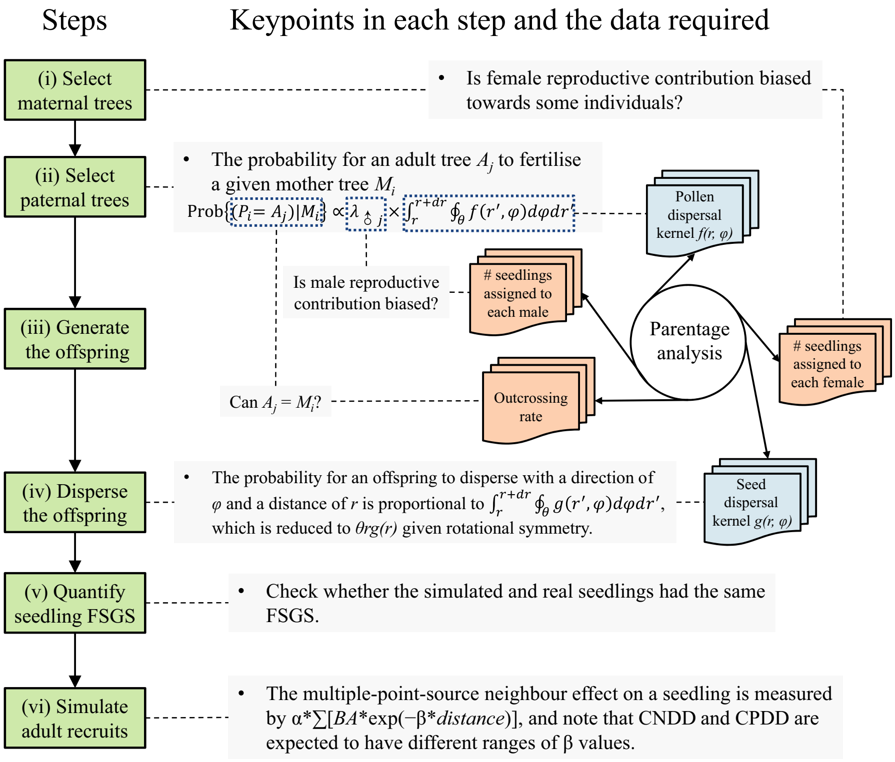
Female reproductive contribution may be highly biased towards some individuals (e.g. Schnabel et al., 1998; Sezen et al., 2005), so we used the number of seedlings assigned to a given mother tree in the parentage analysis as a proxy for female fertility, and checked its distribution with a chi-square test. It showed a Poisson distribution ($\chi^2 = 54.0$, $df = 48$, $p = 0.26$), suggesting that all adult trees had an equal expectation of maternal reproductive success (Kimura & Crow, 1963). Thus, maternal trees $\{M_1, M_2, \ldots, M_n\}$ were determined by randomly sampling from all adult trees with replacement.

2.5.2 | Selecting pollen donors

For each maternal tree M_i, we sampled for the paternal tree P_i. Since no self-fertilisation was found by the parentage analysis, it was assumed in our simulation that $P_i \neq M_i$. The probability for any adult tree A_j to fertilise M_i, in general, depends on the male fertility ($\lambda_{♂j}$) of A_j (e.g. the quantity and quality of pollen), and the direction (φ) and distance (r) of A_j relative to the spatial position of M_i, which can be described as:

$$\mathrm{Prob}\{(P_i = A_j) \mid M_i\} \propto \lambda_j \int_{r}^{r+\mathrm{d}r} \oint_{\theta} f(r', \varphi)\,\mathrm{d}\varphi\,\mathrm{d}r', \tag{1}$$

FIGURE 2 Scheme for modelling the spatial genetic structure of adults. An individual-based spatially explicit model is used, and the steps and key points are shown. The mating system (orange box) and effective dispersal kernels (blue box) estimated from parentage analysis provide the foundation for modelling the spatial genetic structure of seedlings (i–v). Density dependence is then modelled for the transition from seedlings to adults (vi)



where θ is the subtending arc angle and $f(r, \varphi)$ is the pollen dispersal kernel. Male reproductive success, with the number of seedlings assigned to a given paternal tree in the parentage analysis as the proxy, showed a Poisson distribution in the study population ($\chi^2 = 35.0$, $df = 30$, $p = 0.24$), suggesting an equal expectation of male fertility for all adult trees. Given that pollen dispersal did not display any directional preference in this population, Equation (1) could be reduced to:

$$\mathrm{Prob}\{(P_i = A_j)|M_i\} \propto rf(r), \tag{2}$$

where $f(r)$ was the direction-independent pollen dispersal kernel (Clark et al., 1999). We determined paternal trees $\{P_1, P_2, \ldots, P_n\}$ by sampling from all adult trees with replacement according to Equation (2).

2.5.3 | Breeding seeds

A seed was reproduced by each pair of M_i and P_i. The multilocus genotype of the seed was inherited from its parents following the Mendelian rule at each locus and the random combination rule among loci.

2.5.4 | Dispersing the seeds

Similar to 'selecting pollen donors', the probability for a seed S_i dispersing over distance r was parameterised as:

$$\mathrm{Prob}\left(M_i \overset{r}{\Rightarrow} S_i\right) \propto rg(r), \tag{3}$$

where $g(r)$ was the estimated seed dispersal kernel. Based on Equation (3), we sampled from 0 to 550 m (a bit farther than the maximum of the observations) as seed dispersal distances. Since both the seed dispersal syndrome of *C. glauca* and the actual seed dispersal pattern (Figure S2) suggested isotropy of seed dispersal in the population, we randomly sampled dispersal angles from 0 to 2π. To make the simulated seed distribution close to reality (e.g. no seed fell into the sea), no seed was allowed to fall outside the convex hull of all real samples; otherwise, we would re-disperse that seed.

2.5.5 | Checking the FSGS of seedlings

All dispersed seeds survived to become seedlings, because the pollen and seed dispersal kernels used in this model were determined by parentage analysis of seedlings, and thereby represented the effective rather than raw dispersal. We randomly chose 413 individuals from the 10,000 simulated seedlings and characterised their FSGS using the same method as in section 2.4, to check whether the simulated and real seedlings had the same pattern of FSGS.

2.5.6 | Simulating adult recruitment

We modelled adult mortality and the same number of new recruits from the simulated seedlings to the adult population. The proportion of adult mortality could be assumed to approximate $20/(L - 20)$, where L was the average life span of the species. We used values of

0.5 and 0.25, which translated into annualised rates of 2.5% per year and 1.25% per year, respectively, for adult recruitment. As a comparison, Kellner and Hubbell (2018) reported a value of 3.03% per year in a Neotropical canopy tree species, *Handroanthus guayacan*. We sampled the adults for death with probabilities proportional to their DBH values.

To model density-dependent adult recruitment, an exponential decay of neighbour effect with distance was assumed following Comita et al. (2010) in the form of α*∑[*BA**exp(−β**distance*)], where *BA* denotes the basal area of an adult and β determines the spatial scale of neighbour effects. The parameter α was used to ensure that the number of adult recruits balanced the number of adult deaths, thus controlling for potential impact of population density on the strength of spatial genetic structure. When modelling CNDD, we assumed $\beta = 0.05$, 0.10, 0.20, 0.40 and 0.80, given that negative neighbour effects typically occur within tens of metres (Comita et al., 2010; Zhu et al., 2018). This parameterisation is similar to that of a recent CNDD model (Stump & Comita, 2018; $\beta = 0.20$). The probability of a seedling recruiting into the adult population was negatively related to the total neighbour effect it suffered; hence, lower β values represent stronger CNDD effects. In contrast, the ecological processes underlying positive density dependence, such as predator satiation and environmental filtering, mostly act at a larger spatial scale (Kraft & Ackerly, 2010; Nathan & Casagrandi, 2004). Lower β values (0.001, 0.005, 0.010, 0.050 and 0.100) were therefore assumed in the modelling of CPDD recruitment. The survival probability of a seedling was positively related to the total neighbour effect it suffered. Thus, higher β values indicate stronger CPDD effects. Additionally, density-independent survival was modelled by assuming $\beta = 0$.

To reduce the carry-over effect of original adult members on the simulated genetic structure, all steps (i–vi) were repeated until all original members had been replaced. The adult FSGS was then measured using the same method as in Section 2.4. For each of the hypothesised scenarios of adult recruitment, we performed 200 independent runs of simulation and determined the 95% confidence envelopes of predicted FSGS of adults. All simulations were conducted using R 3.1.1 (R Core Team, 2014).

3 | RESULTS

All seedlings were successfully assigned to at least one parent, with the majority (409/413) assigned at least one parent pair. Approximately one-half of the seedlings (208/413) had biparental assignments with high confidence (>80%), most of which ($N = 164$) were unambiguous. The 164 parent–offspring trios were used to estimate the mating system and dispersal kernels. They involved 136 adult trees with 97 and 94 individuals donating pollen and female gametes, respectively, without any selfing events. The average dispersal distance of pollen was 179.9 ± 16.3 m (*M* ± *SE*), with 46% of the pollen dispersed beyond 100 m and the furthest up to 754.3 m (Figure 3a). Pollen dispersal distances were best fit by the Weibull distribution ($\Delta AIC_{min} = 3.5$, Figure 3a). The mean distance of seed dispersal was 31.1 ± 6.5 m, with only 15% of the seeds dispersed beyond 30 m and nearly a half (81/164) of the seeds were assigned to the nearest conspecific adult. Nevertheless, we found some seeds that were dispersed several hundred metres (up to 516.1 m), indicating the presence of long-distance seed dispersal. Seed dispersal distances were best fit by the 2Dt model ($\Delta AIC_{min} = 13.7$, Figure 3b).

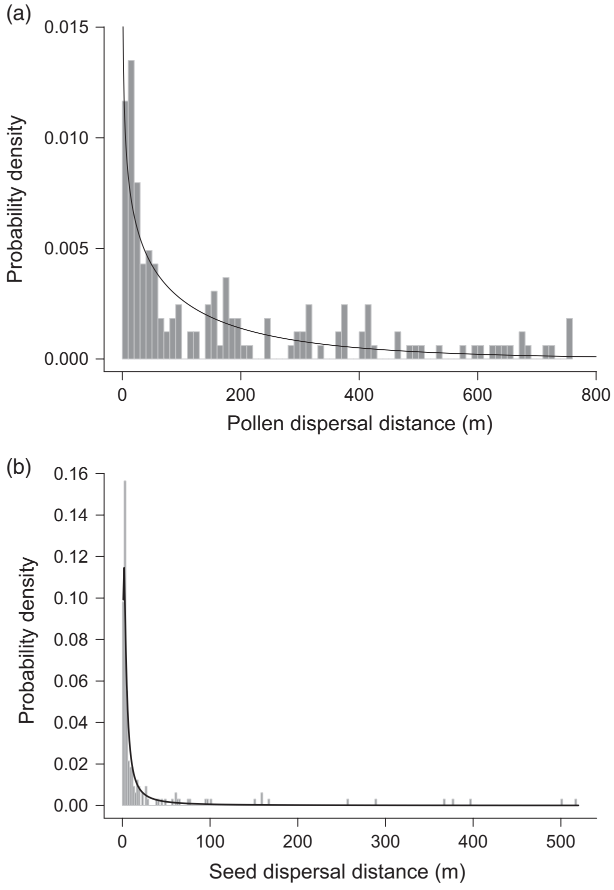


FIGURE 3 Effective dispersal distances within the *Cyclobalanopsis glauca* population estimated by parentage analysis. Curves are the best fitted dispersal kernels of (a) a Weibull distribution for pollen dispersal and (b) a 2Dt distribution for seed dispersal

The FSGS of the seedlings was characterised by local pedigree structure, as indicated by significantly higher pairwise kinship than expected by chance within 0–70 m (all $p < 0.001$). The kinship decreased approximately linearly with the logarithm of geographical distance, with a slope of −0.0069 ± 0.0013. The genetic patterns were well predicted by our model, as the 95% confidence envelopes of predicted kinship covered the observations at all distance classes (Figure 4). Moreover, the predicted kinship decayed with log(distance) at a rate (−0.0063 ± 0.0007) comparable to the empirical rate. Hence, the processes shaping the FSGS of seedlings had been fully accounted for by incorporating dispersal kernels into the model, allowing for testing the effect of the seedling-to-adult transition on FSGS alone.

Local pedigree structure was detected in the adults only at the smallest distance interval, suggesting a weaker FSGS in the adults than in the seedlings (heterogeneity test: $\omega = 109.9$, $p < 0.0001$). Post-hoc single-interval tests further revealed significantly decreased kinship between adults relative to that between seedlings at the intervals of 10–20 m ($t^2 = 11.7$, $p = 0.001$) and 30–40 m ($t^2 = 9.7$, $p = 0.001$; Figure 5a). The changes of FSGS from the seedlings to the adults were not well explained in either density-independent or negative density-dependent adult recruitment scenarios, where the observed kinship coefficients fell below the lower limit of the 95% confidence envelopes at 0–10 m, 10–20 m and 30–40 m (Figure 5b,c). Furthermore, when negative density dependence became stronger

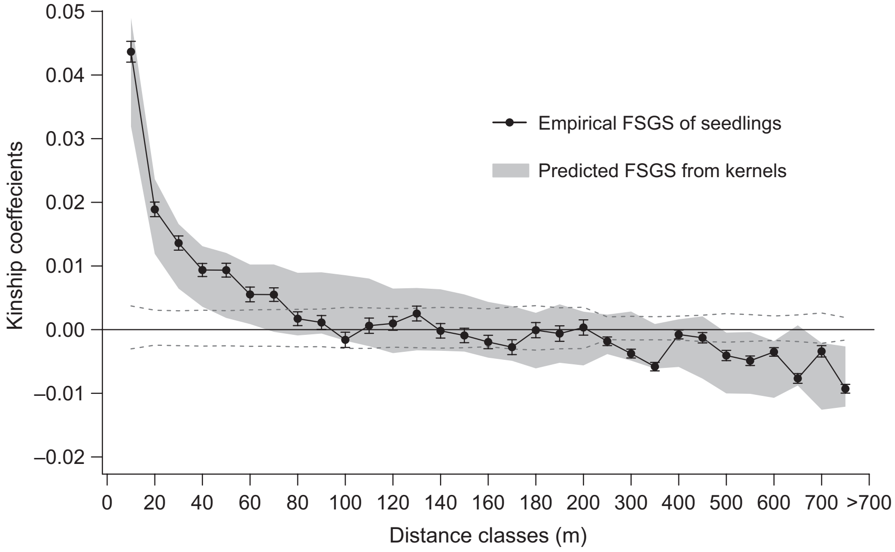


FIGURE 4 Empirical and predicted fine-scale spatial genetic structure (FSGS) in the seedlings of *Cyclobalanopsis glauca*. The empirical FSGS is shown by the average kinship coefficients and the standard errors. Dashed lines represent the 95% confidence envelopes of predicted kinship under the null hypothesis of no FSGS. The grey area is the 95% confidence envelopes of predicted FSGS by the modelling of seedlings based on the effective dispersal kernels

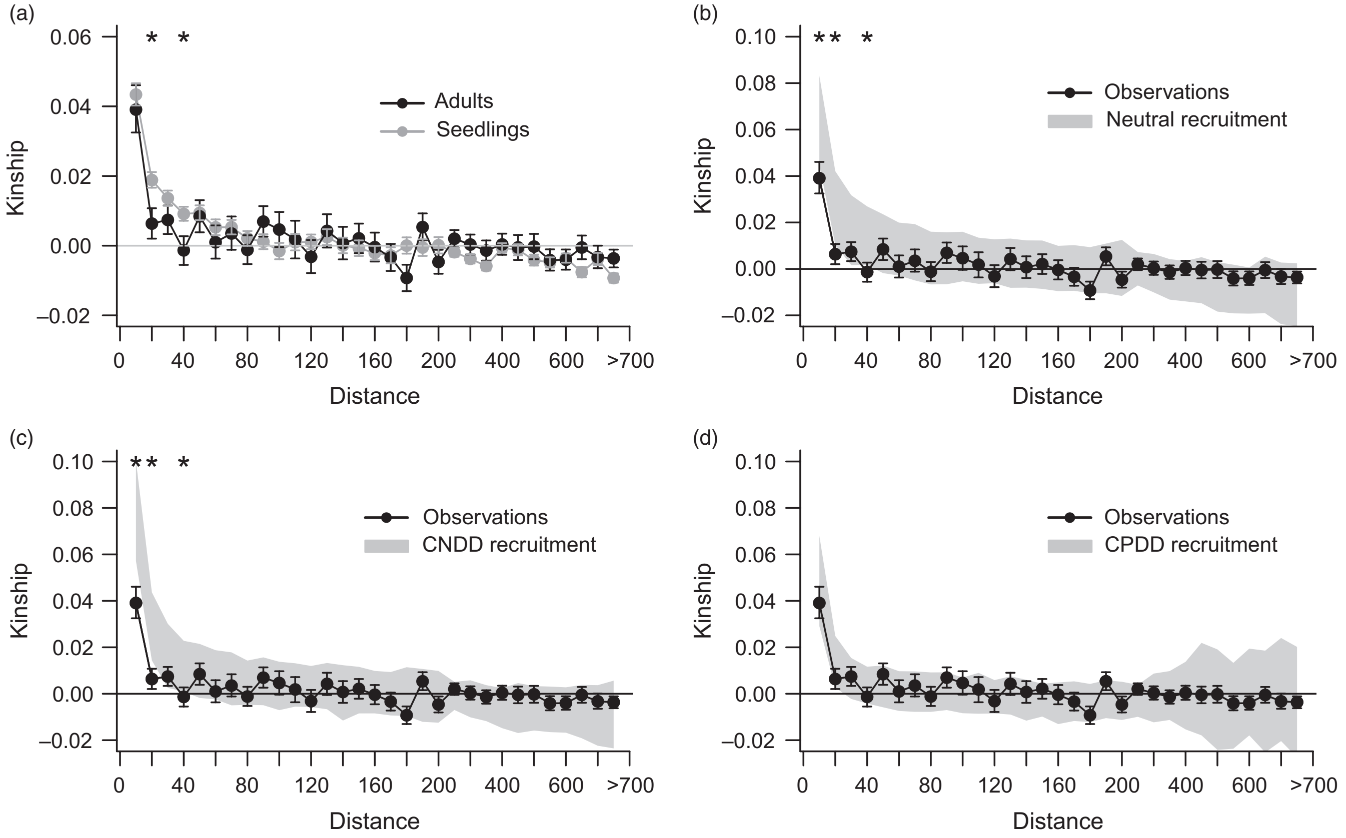


FIGURE 5 Empirical and predicted fine-scale spatial genetic structure (FSGS) in the adults of *Cyclobalanopsis glauca*. (a) Differences in FSGS between seedlings and adults. Under the hypotheses of (b) neutral and (c) conspecific negative density-dependent adult recruitment (using $\beta = 0.2$ as the example), the empirical kinship values fall outside the 95% confidence envelopes (grey areas) at several intervals. All significant differences are denoted by asterisks. (d) When adult recruitment is positively density-dependent ($\beta \geq 0.005$), the observations are well within the 95% confidence envelopes of predicted FSGS. The model with $\beta = 0.005$ is presented

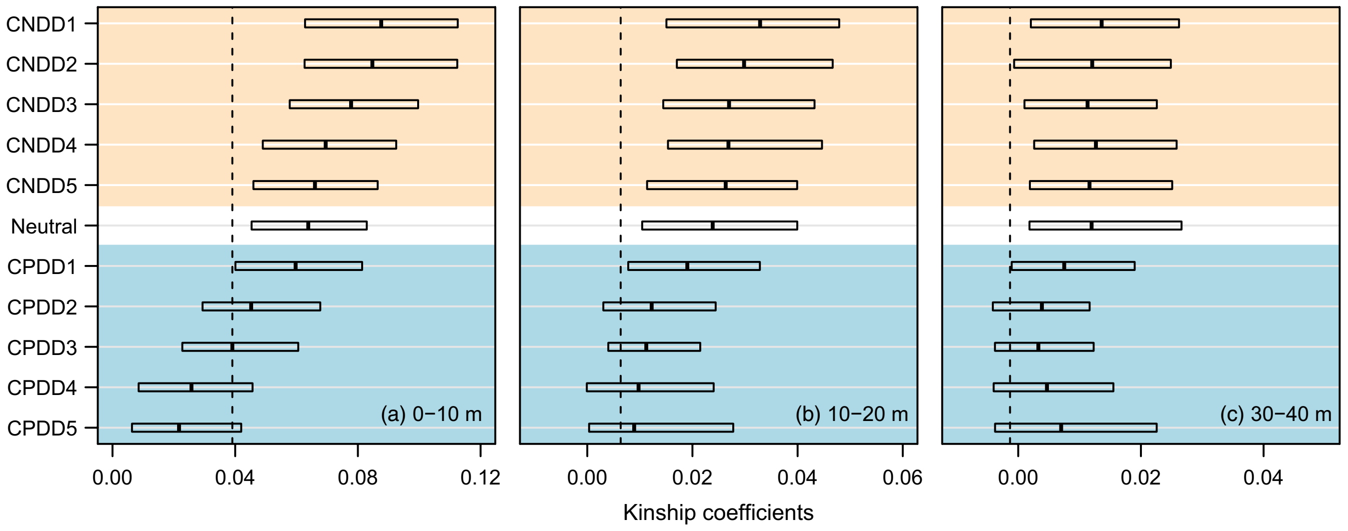


FIGURE 6 Predicted pairwise kinship coefficients under different hypotheses of density dependence in adult recruitment. The scenarios differ in the parameterisation of the spatial scale of neighbour effects (β). Conspecific negative density dependence (CNDD) scenarios 1–5 assume $\beta = 0.05$, 0.1, 0.2, 0.4 and 0.8, respectively. Conspecific positive density dependence (CPDD) scenarios 1–5 assume $\beta = 0.001$, 0.005, 0.01, 0.05 and 0.1, respectively. Note that lower β values represent stronger effects in CNDD models, while stronger CPDD is characterised by higher β values. The neutral scenario assumes $\beta = 0$. The median and the 95% confidence intervals of predicted kinship are shown for three distance intervals under each scenario. The observed values are denoted by dashed line for comparisons

(lower β), an increase in local kinship (<20 m) suggestive of enhanced FSGS was predicted (Figure 6). In contrast, in the positive density dependence scenario ($\beta \geq 0.005$), the observed adult FSGS was well within the 95% confidence envelopes of predicted FSGS over all distances (Figure 5d). As positive density dependence became stronger (higher β), the pairwise kinship decreased, particularly at the smallest distance interval (Figure 6).

4 | DISCUSSION

Although negative density dependence has been widely studied for decades, our understanding of the extent to which the mechanism can explain species coexistence and the diversity of mature trees remains in flux. This is at least partly due to the lack of information on recruitment at late life stages, particularly for adults (Kellner & Hubbell, 2018). We integrated the two traditional genetic (i.e. dispersal-kernel and FSGS-based) methods, and established explicit links between recruitment processes and spatial genetic patterns while accounting for pollen and seed movement. We found that the attenuation of FSGS from the seedling stage to adults in a *C. glauca* population was well predicted by positive, not negative or neutral, density dependence in adult recruitment.

It has been widely presumed that negatively density-dependent recruitment weakens FSGS and positive density dependence enhances it (Jones & Hubbell, 2006; Zhou & Chen, 2010), whereas our models revealed the opposite pattern. The rationale behind the conventional rule of thumb is probably that (1) nearby pairs (both adult-seedling and seedling-seedling) usually have higher genetic relatedness than relatively distant pairs and (2a) negative density dependence tends to eliminate nearby pairs and thereby reduces genetic relatedness, whereas (2b) positive density dependence is apt to retain more nearby pairs. This would be reasonable if considering only a single maternal tree, or under a uniform distribution of maternal trees. However, when maternal trees are heterogeneously distributed, the seedlings in the neighbourhood of clustered adults should be subject to stronger density-dependent effects than those near low-density adult trees. Owing to the increased overlap of seed shadows, the seedlings near clustered adults are also expected to have lower probabilities of sharing the same parent(s) and lower genetic relatedness than those near low-density adult trees (Gapare & Aitken, 2005; Hamrick et al., 1993). Such density-mediated spatial heterogeneity in the strengths of both density dependence and FSGS may reverse the consequences of negative/positive density dependence on FSGS: negative density dependence selects for the seedlings near low-density adult trees and thereby augments the FSGS, while positively density-dependent recruitment more favours the seedlings in the neighbourhood of clustered adults, generating a weaker FSGS. This is very likely in our study, as the kinship coefficients at the smallest distance interval (0–10 m) between the seedlings near low-density adults are much higher than those between the seedlings near clumped adults (0.059 vs. 0.028, Figure S3). Our findings suggest that the link between density dependence and FSGS may be more complex than previously thought, and establishing this link is necessary for FSGS-based inferences of recruitment.

Our results also highlight the necessity to incorporate late life stages when assessing the contribution of negative density dependence as a diversity-promoting mechanism. Indeed, it is consistent with the prediction that negative neighbour effects will diminish through ontogeny due to declining susceptibility to asymmetric competition and/or increasing defence and tolerance to natural enemies

(Terborgh, 2012). For example, Janzen–Connell effects are pervasive in seedlings across almost all the tree species on Barro Colorado Island (BCI; Comita et al., 2010; Harms et al., 2000), but only found in saplings and juveniles for less than half of the species (Bagchi et al., 2011; Hubbell et al., 1990). Furthermore, the strength of negative conspecific neighbour effects was found to become weaker at later life stages (Zhu et al., 2015, 2018). This trend of declining CNDD through ontogeny on BCI has also been found in other forests (Luo et al., 2012; Zhang et al., 2009). Nevertheless, our results are inconsistent with the few studies that have investigated density dependence of adult recruitment (Kellner & Hubbell, 2018; Steinitz et al., 2011). Those discrepancies may be attributable to the different analytical approaches employed, where Steinitz et al. (2011) used the dispersal kernel method, and Kellner and Hubbell (2018) used remote sensing to obtain dynamic data. Moreover, the study population of Steinitz et al. (2011) was expanding quickly over the recent decade, probably accentuating the negative conspecific neighbour effects.

Positively density-dependent adult recruitment is revealed in the *C. glauca* population. Similar patterns have been reported in the BCI forest, where conspecific density showed a positive effect on adult survival in most of the studied species (Zhu et al., 2015). Habitat preference is a likely explanation for positive density dependence (Kupers et al., 2019), as seeds may arrive and seedlings are able to establish in sites with suboptimal environmental conditions (e.g. edaphic factors), but adult trees survive better and occur at higher densities in more suitable habitats. However, we cannot rule out other mechanisms (e.g. intraspecific facilitation or predator satiation) only from genetic data, and further studies are needed to elucidate the underlying ecological processes.

We assume in this study that heterospecific neighbours have minor effects on recruitment and thereby quantify survival by a function of distance from only conspecific neighbours. According to modern coexistence theory, only when plants have a greater negative impact on conspecifics than on heterospecifics, can species coexistence be stabilised and diversity be maintained (Chesson, 2018; HilleRisLambers et al., 2012). It has been empirically demonstrated in many plant species that seedlings are much more negatively affected by conspecific than heterospecific neighbours (Comita et al., 2010; Johnson et al., 2012; Zhu et al., 2015). A similar asymmetry between conspecifics and heterospecifics has also been documented for some positive neighbour effects on seedlings derived from feedback with mycorrhizas (Bennett et al., 2017; Klironomos, 2002). Nevertheless, heterospecific effects may become stronger at later life stages due to the increased requirement of resources. It is thus premature to conclude that heterospecific neighbours play a limited role during adult recruitment. Expanding our approach to encompass interspecific interactions may be required.

To conclude, we have presented a new method to identify density dependence in adult recruitment by integrating dispersal kernels and FSGS. Simulation analyses showed that adult FSGS intensified when adult recruitment was negatively density-dependent, but weakened by positive density dependence. Applying this method in an island *C. glauca* population, we found that the adult FSGS was best explained by positive rather than negative density-dependent adult recruitment. These results preclude the dominant role of Janzen–Connell effects in regulating the transitions from seedlings to adults in *C. glauca*. Our findings highlight a critical gap between prevalent evidence for Janzen–Connell effects in seeds and seedlings and diversity maintenance in mature trees. Going beyond early ontogenetic stages to incorporate adult recruitment should be a goal of future studies and will benefit understanding of long-term population and community dynamics.

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AUTHORS' CONTRIBUTIONS

X.-Y.C. and X.T. conceived and designed the study; Y.-Y.D. and X.T. carried out the experiments; X.T., X.-Y.C. and J.D.N. analysed the data and drafted the paper. All authors edited the paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data from this study, including the genotypes and R codes, are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.cz8w9gj2w (Tong et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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