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Neighbourhood density and genetic relatedness interact to determine fruit set and abortion rates in a continuous tropical tree population

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Tropical trees may show positive density dependence in fruit set and maturation due to pollen limitation in low-density populations. However, pollen from closely related individuals in the local neighbourhood might reduce fruit set or increase fruit abortion in self-incompatible tree species. We investigated the role of neighbourhood density and genetic relatedness on individual fruit set and abortion in the neotropical tree *Jacaranda copaia* in a large forest plot in central Panama. Using nested neighbourhood models, we found a strong positive effect of increased conspecific density on fruit set and maturation. However, high neighbourhood genetic relatedness interacted with density to reduce total fruit set and increase the proportion of aborted fruit. Our results imply a fitness advantage for individuals growing in high densities as measured by fruit set, but realized fruit set is lowered by increased neighbourhood relatedness. We hypothesize that the mechanism involved is increased visitation by density-dependent invertebrate pollinators in high-density populations, which increases pollen quantity and carry-over and increases fruit set and maturation, coupled with self-incompatibility at early and late stages due to biparental inbreeding that lowers fruit set and increases fruit abortion. Implications for the reproductive ecology and conservation of tropical tree communities in continuous and fragmented habitats are discussed.

Keywords: positive density dependence; *Jacaranda copaia*; Barro Colorado Island; forest fragmentation; spatial genetic structure; pollen limitation

1. INTRODUCTION

Negative density dependence slows competitive exclusion within diverse communities and therefore promotes and maintains species diversity (Janzen 1970; Wright 2002). In tropical trees, negative density-dependent recruitment (Harms *et al.* 2000; Wright *et al.* 2005), survival (Hubbell *et al.* 2001) and growth (Uriarte *et al.* 2004) have been found at most demographic stages examined. The strong role of density dependence in determining the spatial distribution of individuals and the maintenance of diversity has highlighted the importance of the local neighbourhood context for plant fitness and demography. Nonetheless, relatively little is known about density-dependent patterns in tree reproduction, another critical component of plant fitness.

Neighbourhood models of plant reproduction in experimental populations have shown that fecundity can be negatively density dependent due to increased competition for limited resources (Silander & Pacala 1985, 1990). However, if pollen or pollinators are in short supply, self-incompatible plants might be expected to show positive density dependence in fecundity. Positive density dependence, a *per capita* fitness increase with increasing density (Courchamp *et al.* 1999), could occur by reducing pollen limitation (Ghazoul *et al.* 1998; Ashman *et al.* 2004). Tropical trees are prime candidates for positive density-dependent reproduction. Most rely upon insects for pollination, are largely outcrossed and self-incompatible (Bawa 1974; Bawa *et al.* 1985; Ward *et al.* 2005; Dick *et al.* 2008). In the absence of pollinators or apomixis, low-density self-incompatible trees are likely to show lowered fruit set owing to the mismatch between low pollen availability and high flower abundance (Burd 1994). Conversely, trees at high local densities with small nearest neighbour distances would be expected to show greater fruit and seed set owing to the attraction of positive density-dependent insect pollinators and a subsequent increase in pollen quantity realized through increased visitation of flowers (Levin & Kerster 1969; Silander 1978).

The strength of density-dependent reproduction may also depend upon the quality, or relatedness, of available pollen. Limited seed dispersal creates neighbourhoods in which focal plants are surrounded by relatives, which creates positive spatial genetic structure locally (Loveless & Hamrick 1984; Epperson 2003; Vekemans & Hardy 2004). Although spatial genetic structure has been widely documented in plants, we know comparatively little about the effects of neighbourhood genetic structure and relatedness on individual fitness within populations. High conspecific genetic relatedness and localized pollination in a neighbourhood

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are hypothesized to lower the relative quality of pollen available to self-incompatible species and increase levels of biparental inbreeding (Souto *et al.* 2002; Elam *et al.* 2007). This could decrease fruit set or increase fruit abortion through late acting self-incompatibility (Byers 1995), thereby lowering fitness.

Fruit abortion is a widespread phenomenon in plants (Stephenson 1981). The role of environmental uncertainty, in terms of resource availability, pollinator abundance and their effects on the quantity and quality of pollen has been frequently invoked to explain widespread fruit abortion (Janzen 1978; Bawa & Webb 1985). At present, it is unclear whether increased local conspecific density does in fact increase fruit set and maturation in tropical trees and the extent to which density interacts with neighbourhood relatedness to determine fecundity (Aizen & Harder 2007). Owing to its central role in determining plant fitness, population growth and regeneration, understanding density-dependent effects on tree fecundity is essential to understanding current and future population dynamics and community structure, particularly in the light of current trends of habitat fragmentation and changes in pollinator abundances (Ashman *et al.* 2004). However, conducting controlled ecological experiments with adult reproductive trees in natural populations is often intractable and requires other approaches.

This difficulty can be overcome within mapped forest census plots by using neighbourhood modelling techniques (Canham & Uriarte 2006). Plant fecundity is determined by tree size (Thomas 1996; Clark *et al.* 2004; Wright *et al.* 2004), habitat associations (Janzen 1978; Queenborough *et al.* 2007), competition with lianas (Stevens 1987; Wright *et al.* 2005) and inter- and intraspecific competition (Silander & Pacala 1985). Neighbourhood models of the effects of conspecific density and genetic relatedness on reproduction should jointly consider the contribution of these variables to individual fecundity. Here, we adopt a neighbourhood dynamics approach similar to those used previously to analyse density-dependent tree recruitment, growth and mortality (Hubbell *et al.* 2001; Uriarte *et al.* 2004). We use spatial, environmental and population genetic data to test for density-dependent fruit set and abortion and the interaction between density and relatedness in *Jacaranda copaia* (Aub) D. Don, a common neotropical tree.

We measured total fruit set and abortion over 3 years for most individuals within a completely mapped and genotyped population of *J. copaia* within a forest dynamics plot (FDP) in central Panama. We used multilocus microsatellite genotypes of all individuals in the study to quantify the relatedness between all trees (Jones & Hubbell 2006). We evaluate models and make predictions using a multiple working hypotheses approach along with maximum-likelihood parameter estimation and model selection procedures (Burnham & Anderson 2002). After considering the covariates of tree diameter, soil nutrient concentrations, topography and liana competition, we ask (i) is fruit set and abortion density dependent in *J. copaia* and, if so, is it positive or negative? and (ii) does genetic relatedness within a neighbourhood interact with density and fecundity to determine fruit set and fruit abortion?

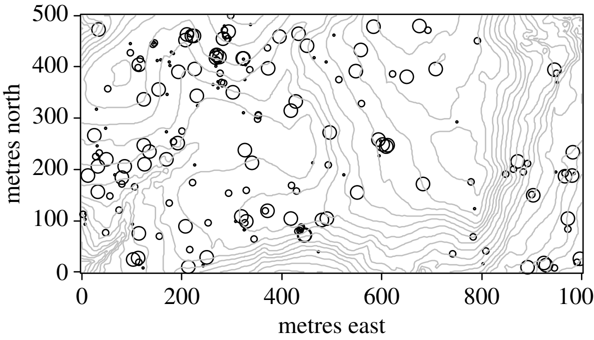

Figure 1. Map of reproductive-sized *J. copaia* trees in the 50 ha plot on BCI, Panama. Circle size corresponds to mean annual fruit set of the individual during the 3 year study period (small circles, 10 fruits or less per year; medium circles, more than 10 and 100 fruits or less per year; large circles, more than 100 fruits per year). Lines are 5 m topographic intervals.

2. MATERIAL AND METHODS

(a) *Site and species*

We conducted our research within the 50 ha FDP of Barro Colorado Island (BCI), Panama (Hubbell & Foster 1983). The FDP was established in 1980 and consists of a standing number of approximately 213 000 mapped stems 1 cm or above in diameter at breast height (DBH) of approximately 300 species (http://ctfs.si.edu/datasets/bci/). The FDP has been recensused five times since 1980. We used information from the 2000 census to locate 199 reproductive-sized *J. copaia* adults within the plot in 2000 through to 2003.

Jacaranda copaia is a canopy-emergent, wind-dispersed tree that is strongly shade intolerant and requires large tree fall gaps to regenerate. It ranges from Bolivia to Belize and is a common pioneer tree in neotropical forests. It exhibits a ‘cornucopia’ strategy of flowering by synchronously producing large numbers of flowers over periods of weeks (Gentry 1974), which are pollinated by large bees (Degen & Roubik 2004). Mating system studies using genetic markers have shown that *J. copaia* is a predominantly outcrossed species and probably self-incompatible (James *et al.* 1998), although the stage at which this incompatibility occurs is unknown. The minimum reproductive size is estimated at 20 cm DBH (Wright *et al.* 2005) on BCI.

Within the BCI forest, *J. copaia* has a highly clumped distribution (figure 1) owing to limited seed dispersal and strong gap dependence at the seedling stage for recruitment and survival. On the FDP, *Jacaranda* adults and seedlings show weak habitat and soil nutrient associations (Harms *et al.* 2000; John *et al.* 2007). *Jacaranda copaia* flowers during the dry season, from February to April. Seeds are produced in a large woody capsule that has two locules, each of which contains approximately 250 seeds (S. J. Wright 2008, personal communication). Seed dispersal occurs in late August and September when fruits dehisce and seeds are released. After dehiscence the flat, dry and woody halves of each fruit (10–15 cm) fall to the ground beneath the tree. Aborted fruit are smaller than mature fruit (less than 10 cm), have not dehisced and have not released seeds. Predispersal seed predators for the species include beetles and wasps (F. A. Jones 2000, unpublished data). Predated fruit also fall to the forest floor and can readily be distinguished from aborted and mature fruit because predated fruit shows evidence of galling by wasps or holes bored by beetles.

Measuring individual variation in fruit set is typically difficult for forest trees; however, the fact that whole *J. copaia* fruit are not eaten and dispersed by animals but rather fall directly beneath the tree crown after dispersal makes it feasible to quantify fruit set for individuals of this species.

Positive fine-scale spatial genetic structure, measured by the pairwise relatedness between individuals, exists in the reproductive-sized *J. copaia* population on BCI at distances up to 100 m. This structure is created by limited seed dispersal and gap dependence (Jones *et al.* 2005; Jones & Hubbell 2006). On average, the nearest conspecific neighbours of *Jacaranda* are half siblings: they share one parent.

(b) *Fruit set estimation*

To estimate individual fruit set and abortion, we established transects in each cardinal direction (north, south, east and west) beneath the canopy of each reproductive-sized *J. copaia* individual (DBH 20 cm or more) in November and December of 2000, 2002 and 2003. Few capsules were produced in 2001, so we did not measure fruit set in that year. For each tree, we established a transect from the base of the trunk to the edge of the tree's canopy in each direction. At 1 m intervals, we laid a 0.5 m^2 PVC frame on the ground and counted the total number of mature dehisced fruit, immature non-dehisced woody fruit and insect predated fruit. We also recorded presence or absence of lianas in the crown of each tree.

In each year, we estimated the total fruit set of each individual by calculating the mean fruit set (per m^{-2} sampled area) of that individual (all mature, immature and insect predated fruit) and multiplied it by the total canopy area of the individual as determined from the lengths of the four transects beneath each tree. For our analysis of fruit abortion, we calculated the proportion of non-aborted fruit out of the total number of fruit. Fruit predated by insects were considered non-aborted because in the absence of predation, these fruit would have presumably matured. Neighbourhood analyses of predispersal distance and density-dependent seed predation will be presented separately (F. A. Jones 2008, unpublished data).

(c) *Soil nutrients*

Tree density and fruit production might be determined by a common underlying factor and therefore obscure density-dependent patterns. For example, high densities and high individual fruit set might be expected to occur in highly favourable resource areas. In order to control for potential effects of soil resource availability and neighbourhood density on fruit production and abortion rates, we included data on soil nutrients in our neighbourhood models. Thirteen macro- and micronutrients were measured across the FDP by John *et al.* (2007). We collapsed the complexity of these soil resources, which are often strongly correlated, into independent orthogonal axes through a principal component analysis (PCA) on measurements taken for each 20×20 m grid point. We then assigned axis scores to individual trees within each 20×20 m quadrat. The first four axes, which accounted for 99.6 per cent of the variation in nutrients, were used in the neighbourhood analyses of fruit production and abortion. In addition, we included slope as a covariate in the models, since soil moisture concentrations vary with topography on BCI (Daws *et al.* 2002).

(d) *Neighbourhood indices*

We calculated a conspecific neighbourhood fecundity index (NFI), which sums the effect of the fecundity of neighbouring conspecific trees j, within a radius of 100 m of the focal individual i, and is weighted by distance between i and j:

$$\mathrm{NFI} = \sum \frac{\mathrm{total}_j^{\alpha_1}}{\mathrm{dist}_{ij}^{\delta_1}},$$

where total_j is neighbour j's mean total fruit set. We also calculated a similar index in which the effects of neighbours are conditioned on their genetic relatedness to the focal individual. This neighbourhood relatedness index (NRI) takes the form

$$\mathrm{NRI} = \sum \frac{\mathrm{total}_j^{a2} \times r_{ij}^{\chi}}{\mathrm{dist}_{ij}^{\delta 2}},$$

where r_{ij} is the pairwise genetic relatedness between focal trees i and j, described below, and dist_{ij} is the Euclidean distance between focal trees i and j. The exponents α, χ, and δ are fitted parameters.

Genetic relatedness around each focal tree i was determined from an analysis of pairwise genetic relatedness r_{ij} between tree i and the neighbouring *J. copaia* tree j using Loiselle *et al.*'s (1995) pairwise index of relatedness r_{ij}, for six polymorphic nuclear microsatellite loci. Jones & Hubbell (2003, 2006) contain detailed descriptions of these data. In short, r_{ij} can range from -1 to $+1$ with an average relatedness scaled to 0. We rescaled r_{ij} to range from 0 to 1 such that this value can now be interpreted as a genetic distance between two individuals relative to the entire population. In the NRI, as the relatedness of a neighbour increases, it decreases the neighbour's effective fecundity in the index. We choose a maximum radius of 100 m for our analyses because this is the scale at which reproductive-sized individuals show significant pairwise relatedness above that expected at random (Jones & Hubbell 2006).

Where individuals were less than 100 m from the plot edge, we corrected for edge effects by assuming that the portion of the circle located outside of the plot had the same average neighbourhood index value (per unit area) as the portion within the plot. Thus, we adjusted index values by dividing the observed index by the proportion of the total circular area located inside of the plot.

(e) *Model description and parametrization*

For each focal individual, total fruit set was averaged over the 3 years. For 18 out of the 197 reproductive-sized *J. copaia* trees (DBH more than 20 cm) encountered in the 50 ha plot during the study, estimates of fruit set were available for only 1 or 2 years, due to individual mortality during the study period or missing data. Therefore, these individuals were not included as focal individuals in the analysis, but were included in the calculation of neighbourhood indices. Values of mean fruit set across 3 years were log transformed after first adding 1 to normalize residuals.

We included tree size, liana infestation, slope and the first four principal component axes from the soil analysis as covariates in our models of neighbour effects. Log-transformed values of DBH were used as the measure of tree size. Liana infestation was calculated as the proportion of years in which lianas were observed in the canopy. All covariates were recentered on 0 by subtracting the mean of each variable from each value to allow for more straightforward interpretation of

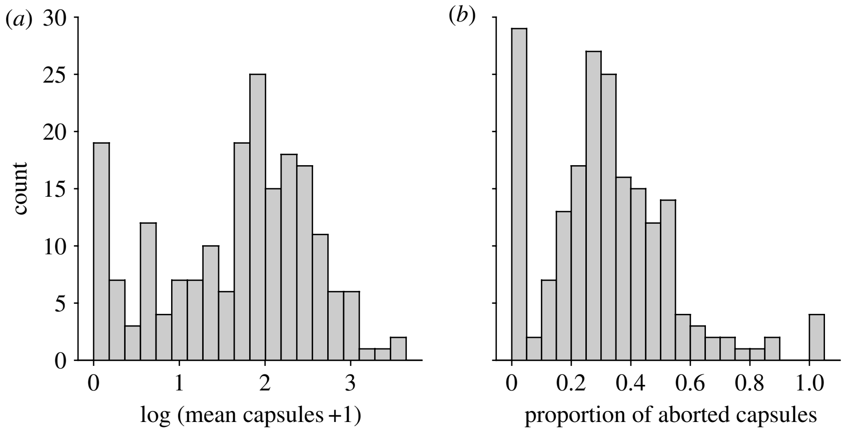

Figure 2. Frequency histograms of (*a*) log mean total *J. copaia* capsule production + 1 and (*b*) proportion of fruit aborted for 3 years within the FDP on BCI.

Table 1. Minimum, maximum, median and mean values of dependent and independent variables used in modelling the total mean fruit and mean viable fruit set of *J. copaia*.

variable	min	max	median	mean
total fruit per year	0	4433.67	79	288.91
total proportion of aborted fruit	0	1.0	0.30	0.31
diameter at breast height mm (DBH)	211	916	467	485.44
conspecific neighbours within 100 m	0	42	13	15.75
estimated neighbourhood fruit set (100 m)	0	8689	2508.33	2981.9
neighbourhood genetic relatedness index	0.1842	0.5327	0.4682	0.4616

the effects of density and relatedness on fruit set and abortion. In detailed preliminary analyses, we also included a term that took into account the effect of heterospecific tree size and distance on focal *Jacaranda* fruit set and abortion. Heterospecific neighbourhood had no effect on *Jacaranda* fruit set or abortion rates and was therefore excluded from subsequent analyses (see Papaik & Canham 2006).

For models of (natural log transformed) total fruit set, we assumed that residuals approximated a normal distribution. We then compared three models in our analyses. Model 1 only included the main covariates and no effect of density:

$$\ln(\text{fruit} + 1) = \beta_0 + \beta_1 \ln(\text{DBH}) + \beta_2 \text{ liana} + \beta_3 \text{ slope} + \beta_{4\ldots7}\text{PCA}_{1\ldots4} + \varepsilon.$$

Model 2 included the NFI:

$$\ln(\text{fruit} + 1) = \beta_0 + \beta_1 \ln(\text{DBH}) + \beta_2 \text{ liana} + \beta_3 \text{ slope} + \beta_{4\ldots7}\text{ PCA}_{1\ldots4} + \beta_8 \text{ NFI} + \varepsilon.$$

Model 3, the full model, included the interaction between fecundity and relatedness:

$$\ln(\text{fruit} + 1) = \beta_0 + \beta_1 \ln(\text{DBH}) + \beta_2 \text{ liana} + \beta_3 \text{ slope} + \beta_{4\ldots7}\text{ PCA}_{1\ldots4} + \beta_9 \text{ NRI} + \varepsilon.$$

For models of the proportion of mature fruit, we used the same equations above, but assumed binomial errors. We used the raw numbers of fruit set (total and non-aborted) summed over all 3 years to calculate proportion of mature fruit set relative to the total.

Parameter optimization was carried out in the R operating environment (R Development Core Team 2008). We used linear regression to determine maximum-likelihood parameter estimates in the basic model for log-transformed total fruit set. Since models including neighbourhood indices were nonlinear, we used an optimization procedure, L-BFGS-B, a quasi-Newton method with box constraints, to determine the maximum-likelihood parameter values for the models of total fruit set ('optim' function in R). For the mature fruit set model, we used a generalized linear model with binomial errors to determine parameter values for the basic model. For the NFI and NRI models, we again used the 'optim' function, but with the optimization procedure of Nelder and Mead, which we found worked better for these models since it does not fail when the likelihood function returns values that are not finite. To reduce parameter trade-offs, fitted exponents of the neighbourhood indices were constrained to values between 0 and 3.

To compare the goodness-of-fit of various models to data, we calculated Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson 2002). To quantify the strength of evidence for the best-fit model relative to other models, we normalized likelihood values according to Akaike weights. Akaike weights provide the relative weight of evidence for each model and are interpreted as the probability that a model is the best model, given the observed data and the set of candidate models (Burnham & Anderson 2002).

3. RESULTS

Estimated total fruit set per tree ranged from 0 to more than 4000 (figure 2*a*). Averaged across 3 years, mean total fruit set was estimated at 288.9 fruit per tree (table 1). The proportion of aborted fruit ranged from 0 to 1, with a mean of 0.30 (figure 2*b*). The mean, median and ranges of dependent and independent variables are listed in table 1.

Initial analyses revealed that DBH, liana occupancy, slope and PCA axes had large enough effects on the dependent variables, based upon AIC_c values, to be included in each of the models for fruit set and abortion.

Table 2. Parameter values and model selection criteria for models used to investigate total fruit and total proportion of mature fruit set in *J. copaia*. (The best-fit models, based on AIC$_c$ values, are marked in italics. Model 1 includes no density terms, model 2 includes a density-dependent effect, and model 3 includes an interaction term between fecundity and genetic relatedness of neighbours. See text for model equations.)

	total fruit set			proportion non-aborted fruit		
variable	model 1	model 2	*model 3*	model 1	model 2	*model 3*
intercept	4.062	3.571	*3.603*	1.577	1.428	*1.511*
ln(DBH)	3.425	3.656	*3.640*	0.012	0.180	*0.0862*
liana	−0.926	−0.994	*−0.991*	−0.148	−0.089	*−0.160*
slope	−0.130	−0.118	*−0.124*	−0.049	−0.046	*−0.052*
soil PCA 1	−0.00058	−0.00058	*−0.0006*	−0.00012	−0.00015	*−0.00018*
soil PCA 2	−0.00177	−0.00171	*−0.0017*	-2.7×10^{-5}	-2.7×10^{-5}	-5.8×10^{-5}
soil PCA 3	−0.0006	−0.00133	*−0.0014*	−0.00055	−0.00067	*−0.00052*
soil PCA 4	−0.00484	−0.0032	*−0.0030*	−0.00487	−0.0045	*−0.00463*
neighbourhood effects						
total effect		0.320	*0.53*		0.004	*0.013*
fecundity exponent		0.422	*0.416*		0.885	*1.170*
distance exponent		1.279	*1.349*		1.126	*2.704*
relatedness exponent			*0.335*			*1.534*
AIC$_c$	648.99	634.86	*633.50*	1620.40	1563.87	*1548.82*
w_i	0.00029	0.336	*0.662*	2.86×10^{-16}	0.00054	*0.999*

Fruit set and proportion of mature fruit increased with increasing tree diameter. Liana occupancy had a negative effect on both total and mature fruit set. For both total fruit set and proportion of mature fruit, the full model (model 3) that included an interaction between density and relatedness (NRI) was more strongly supported than those that did not. In both cases, density had a positive sign, indicating positive density dependence (table 2) in fruit set and fruit maturation. Akaike weights (w_i) were very low for model 1 (i.e. no density effect) in both instances, and in each case we found stronger support for model 3, which incorporated a neighbourhood density effect with a genetic relatedness interaction. For mean fruit set, uncertainty exists in terms of which is the most parsimonious model when model 3 ($w_i=0.662$) is compared with model 2 ($w_i=0.336$). Model weights (w_i) are comparable to probabilities that a model of interest represents the best model given the set of other models. Akaike weights higher than 0.90 represent strong support for a particular model (Burnham & Anderson 2002). However, an examination of the proportion of variance explained by model 3 ($r^2=0.52$) was greater than that for model 2 ($r^2=0.50$) and model 1 ($r^2=0.45$). Figure 3 shows the predicted joint effect of relatedness and distance of neighbouring individuals on focal tree fruit set based on best-fit parameter values for model 3 and shows how decreased density, increased isolation (distance) and increasing relatedness act to lower fruit set.

We found support for an interaction between density and genetic relatedness of the neighbourhood (NRI) on the proportion of mature fruit (table 2). The high Akaike weight for model 3, $w_i=0.999$, indicated strong support for this model over the others. Best-fit parameter values for this model indicate that, as with total fruit production, increasing density increases the proportion of mature fruit, but the effect is conditioned on the relatedness of neighbours, with increasing relatedness resulting in higher abortion rates. Despite the much greater support for model 3, an examination of predicted versus observed values revealed that most of the variation in fruit abortion rates is left unexplained by our model.

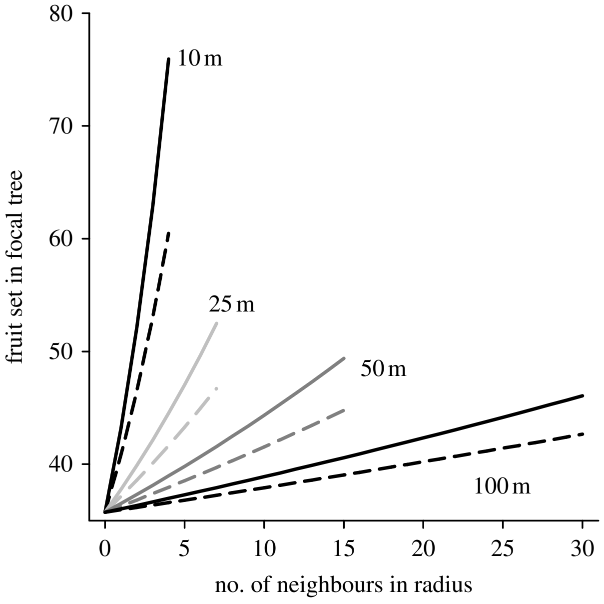

Figure 3. Model predictions for effects of neighbourhood density, relatedness and distance on mean focal tree fruit set for *J. copaia*. Lines represent the predicted effect of adding neighbours at increasing distances from the focal individual. Dashed and solid lines represent the maximum and minimum observed neighbourhood genetic relatedness, respectively.

4. DISCUSSION

Our neighbourhood analysis of reproduction in *Jacaranda* provides evidence for positive density-dependent fruit set and for an interaction between local density and genetic relatedness in determining levels of fruit set and abortion across a large continuous tree population. Below we discuss our results in light of what is currently known about plant reproduction and the importance of gene dispersal distances in continuous and fragmented landscapes. Finally, we address the implications of our study for the maintenance of species and genetic diversity within tree communities and suggest future avenues for research.

(a) *Size, lianas and soil resource effects on fruit set*

Most of the variation in fruit set and abortion was explained by tree size, liana infestation in the canopy and soil resources. We found strong evidence for the role of diameter in determining patterns of total fruit set in *J. copaia*. Because tree size and growth potential are correlated with exposure to full sunlight above the canopy (Wyckoff & Clark 2005), this finding is not unexpected. Most models of individual plant fecundity and critical reproductive size are deterministic allometric models (Thomas 1996; Wright *et al.* 2004) with predictions of annual seed and fruit set based solely on tree size. However, fruit set can vary significantly within diameter size classes (Clark *et al.* 2004). Our results demonstrate that some of the within-size-class variation in fruit set for *Jacaranda* can be explained by the biotic and abiotic neighbourhood of the focal plant.

We also found a negative effect of liana infestation on both the total fruit set and the proportion of mature fruit, consistent with the result that lianas limit tree growth and fecundity (Stevens 1987; Schnitzer & Bongers 2002), and increase the minimum reproductive size threshold of trees (Wright *et al.* 2005). Soil micro- and macronutrients also played a role here in determining individual fruit production (Kaspari *et al.* 2008) and abortion.

(b) *Positive density-dependent fruit set*

Jacaranda adult density is ultimately determined by the location of tree fall light gaps, the dispersal of seeds to those gaps, and the recruitment and survival of seedlings to adult trees. Owing to its strong requirement for high light as seedlings, few seedlings survive in the shaded understorey (Wright *et al.* 2003). While high soil resource levels might be expected to increase neighbourhood density and fruit production concomitantly, previous studies have shown weak habitat associations or specialization to soil resources for *Jacaranda* on BCI (Harms *et al.* 2001; John *et al.* 2007). We control for the potentially confounding effects of soil resources on density and reproduction by including the soil nutrient PCA axes in our analysis.

A proportion of the variation in total and mature fruit set was explained by neighbourhood conspecific density. The influence of each conspecific neighbour also increased with its fecundity, suggesting that the positive relationship between fruit set and local density may be due to a decrease in pollen limitation in high-density neighbourhoods or near highly fecund neighbours. Neighbourhood floral displays can increase individual reproductive success by attracting density-dependent pollinators (Levin & Kerster 1969; Schall 1978). Pollinators may choose areas of high floral density to reduce foraging effort by decreasing the flight time between trees. This increases the transfer of pollen between individuals and increases the number of fruit set. Conversely, our results demonstrate that isolated individuals show reduced reproductive output presumably due to increased pollen limitation.

Very early floral or fruit abortion, before carpels become woody and can be counted, is not considered in this analysis. Therefore, we have probably underestimated both the true levels of fruit set and abortion in our analyses. Nonetheless, our results show that high-density neighbourhoods show lowered fruit abortion and that models which included a density term were much more strongly supported than those that did not. That fruit abortion is lower in high-density areas implies that pollinators are attracted to high-density areas and that they may carry over pollen potentially from unrelated neighbours. Fruit abortion is a common feature of tropical trees and most plants (Bawa & Webb 1985), yet mechanisms behind it remain largely unknown. Here, we show that fruit abortion rates are not only influenced by size, soil resources and liana infestation, but also by neighbourhood effects, yet much of this variation still remains to be explained.

(c) *Effect of neighbourhood genetic relatedness*

We found a negative effect of genetic relatedness on fruit set and the proportion of mature fruit produced. In self-incompatible plants, fruit set would be expected to be lower when most mating is local and occurs between related individuals (Ishihama *et al.* 2006). In this forest, *Jacaranda* neighbouring individuals within a 50 m radius are, on average, half siblings (Jones & Hubbell 2006). At longer distances, neighbours tend to be less related; however, their effect on a focal plant also tends to decrease with distance and density (figure 3). Given limited dispersal and local genetic structure, the negative interaction between density and relatedness implies that biparental inbreeding may reduce ovule fertilization and lower total fruit set, and suggests that fruits sired by related individuals may be selectively aborted. However, we did not directly test for this by examining levels of inbreeding in aborted seeds. Aborted seeds of *Jacaranda* are extremely small, precluding genotyping of aborted embryos to definitely determine levels of inbreeding in aborted fruit. However, Hufford & Hamrick (2003) in a study of the large seeded tropical legume *Platypodium elegans* on BCI determined that aborted fruits were more inbred than mature fruit and established seedlings suggesting a potential mechanism for results presented here. High relatedness of neighbours can contribute to pollen limitation by reducing the effective number of mates, the quality of available pollen and the proportion of successful matings. Both lowered fruit set and increased rates of abortion lead to increased seed limitation, which has been proposed as a mechanism that promotes species coexistence.

(d) *Selection for gene dispersal distances*

Our results imply a fitness advantage for locally dispersed seed, as individuals that are dispersed locally are more likely to have available mates, although there is a cost to mating with relatives (figure 3). In *Jacaranda*, detailed genetic studies of seed dispersal have documented that while most dispersal is local, a significant fraction of seeds move distances greater than 100 m (Jones *et al.* 2005; Jones & Muller-Landau 2008). Our results predict a fitness advantage for *J. copaia* individuals that are able to recruit in neighbourhoods of unrelated individuals, implying a fitness advantage as adults of long-distance seed and pollen dispersal. However, our results also predict a cost to long-distance seed dispersal because individuals may disperse to neighbourhoods where conspecifics are locally rare and therefore they are isolated from mates.

Most studies of density dependence in forest tree reproduction have been conducted in forest fragments (Ghazoul *et al.* 1998). Fragmented or altered habitats may experience greater effects of density dependence owing to lowered overall adult density and pollen availability and altered disperser and pollinator assemblages. Wang *et al.* (2007) in a marker-assisted study of seed dispersal in the African tree *Antrocaryon klaineanum* showed that seed dispersal was lower in heavily hunted forests than in forests with intact disperser assemblages. This would be expected to increase the level of spatial genetic structure in the population over time. Our results imply that greater genetic structure which would arise from such a scenario could have a negative impact on tree reproduction and regeneration due to increased mating among relatives and lowered realized fruit set if plants experience inbreeding depression.

Positive density dependence in fruit and seed set has a variety of implications for population and community dynamics. It may be a contributing factor, along with dispersal limitation and habitat associations, to the ubiquitous spatial aggregation of tree species within tropical forests (Condit *et al.* 2000). However, positive density-dependent reproduction results in a decrease in species diversity in neutral models (Zhou & Zhang 2006) without a stabilizing mechanism. We suggest that lowered fruit set in related high-density neighbourhoods along with negative density dependence at other stages and lowered fitness of inbred offspring can act as stabilizing influences. Clearly, additional studies that examine complex and often contradictory density-dependent neighbourhood effects across all life stages of plants would provide further insight into these stabilizing mechanisms.

We predict that the interaction between density and genetic relatedness on fecundity may be more pronounced in high-density populations of shade-tolerant, self-incompatible trees, particularly for species with pollinators or seeds that do not travel long distances. Limited seed movement increases high local conspecific density, which in turn lowers intermate distance and acts to decrease the extent of pollen movement (Stacy *et al.* 1996; Hardy *et al.* 2006). Our results suggest that local pollination among relatives may lower seed set and lead to increased fruit abortion. However, some species may be more tolerant to inbreeding than others (Latouche-Halle *et al.* 2004). We suggest that paternity analyses concerned with pollen dispersal distances should also quantify fruit set and abortion, and the influence of local densities in determining patterns of dispersal, and if possible, examine pollen movement distances for aborted fruits and seeds.

This study demonstrates the usefulness of combining spatially explicit multivariate neighbourhood models with population genetic data to examine ecologically relevant processes in complex natural communities. Future studies should progress beyond the description of the correlation of alleles in space and attempt to understand the interaction between spatial genetic structure and other demographic parameters. Given the increasing destruction of forest habitats, predicted loss of genetic diversity and the restriction of movement imposed by fragmentation on pollen and seed dispersal vectors, the interactions between seed and pollen dispersal distances, pollinator behaviour, the local genetic neighbourhood and tree population dynamics is a topic worthy of greater exploration.

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