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Spatial patterns of tropical forest trees in Western Polynesia suggest recruitment limitations during secondary succession

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Abstract: Spatial analysis can be used to relate the patterns of tree species to their regeneration syndromes – pioneer to late-successional – and is a first step in refining hypotheses about the species traits and biotic and abiotic factors that give rise to forest community dynamics. This study examines the spatial pattern of the most abundant trees in three 0.45-ha plots in species-poor lowland rain forests on oceanic islands in Tonga, Western Polynesia, that experience frequent natural disturbance and have a 3000-y history of shifting cultivation. We contrast secondary vs. remnant late-successional forest, with particular attention paid to the spatial dispersion and clustering of tree species, and the presence of spatial dependence in the density of seedlings and saplings. Shade-tolerant species were not strongly clustered at any scale. They did not appear to be dispersal limited, in late successional forest, and only some showed patterns consistent with density-dependent mortality (more clumped when small). Shade-tolerant species were more clumped in secondary forest, and may be dispersal-limited there because vertebrate dispersers prefer primary forest. Shade-intolerant species were clumped in gaps in late-successional forest, but some were also clumped in secondary forest, indicating that they too may be dispersal limited during secondary succession. We also compared the species composition of seedlings and saplings in the centre of plots with trees in the surrounding area and inferred that active dispersal (by vertebrate frugivores) contributed as much as 50% to site species richness.

Key Words: autocorrelation, density dependence, dispersal, Moran's I, point pattern, Polynesia, recruitment, Ripley's K, spatial dependence, spatial regression, Tonga, tropical forest

INTRODUCTION

Spatial analysis has long been used in plant ecology to infer the processes that have given rise to an observed pattern (Diggle 1983, Fortin & Dale 2005, Ripley 1981), and one of the most widely observed patterns is that individuals in a plant population are clustered when small or young and have a more random or regular pattern when large or old. The clumped pattern of propagules or juveniles could arise from limited dispersal and/or environmental heterogeneity (Palmiotto *et al.* 2004), while an increasingly regular pattern of larger or older plants (Condit *et al.* 2000) would result from density- or distance-dependent juvenile mortality due to predation (Connell 1971, Connell *et al.* 1984, Janzen 1970) or competition (Barberis & Tanner 2005, Kenkel 1988, Stoll & Bergius 2005). A bivariate pattern whereby juveniles are found near adults less frequently than expected by chance would be additional evidence of density dependence (Clark & Clark 1984). Studies addressing the processes that maintain high species richness in tropical tree assemblages have found, however, that most species showed clustered patterns at all spatial scales examined, and/or did not show reduced density of juveniles near conspecific adults, when dozens to hundreds of species were examined (Aiba *et al.* 2004, Condit *et al.* 1992, 2000, Okuda *et al.* 1997, Webb & Fa'aumu 1999). Even in studies of relatively species-poor tropical forest, where density dependence would be expected to be more prevalent because plants are more likely to be near conspecific neighbours (Uriarte *et al.* 2005), many species are clustered (Debski *et al.* 2000). Studies that evaluate recruitment stages provide more direct evidence that density-dependent recruitment promotes tree diversity in tropical forests (Harms *et al.* 2000, Webb & Peart 1999, Wills *et al.* 1997, Wright *et al.* 2005).

Many of these studies have been conducted at lowland, low latitude old-growth (late-successional) sites unaffected by frequent natural disturbance such as

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hurricanes or landslides, e.g. dominated by small-scale gap dynamics. Most species investigated have been the shade-tolerant ones that predominated in late-successional forest. Owing to both ancient and recent deforestation (for agriculture and forestry), secondary tropical forest (Brown & Lugo 1990, Corlett 1995), and forest fragments (Laurance & Bierregaard 1997, Turner & Corlett 1996) are becoming more extensive worldwide. There is mounting evidence that tropical rain forests everywhere, even those once thought to be pristine, have been subjected to human disturbances, including clearing for shifting cultivation, for centuries to millennia, and that the ecological effects of previous deforestation are long lasting (Clark 1996, Fernandes & Sanford 1995, Foster *et al.* 1999, Horn & Kennedy 2001). Therefore it is important to examine the dynamics of secondary succession (Laurence 2004).

Spatial analysis can be used to relate the patterns of species to their regeneration syndromes (modes of dispersal, shade tolerance, establishment, survival and growth; Gitay *et al.* 1999) – pioneer to late-successional (Forget *et al.* 1999, McDonald *et al.* 2003, Toriola *et al.* 1998, Webb & Fa'aumu 1999). Spatial pattern analysis alone is limited in its power to test predictions about forest dynamics (Clark & Clark 1984) or succession (Rejmánek & Leps 1996), but is a vital first step in developing hypotheses about the species traits and biotic and abiotic interactions that give rise to forest community dynamics (Levin 1992).

This study examines the spatial pattern of the most abundant trees (all bird- and bat-dispersed) in species-poor lowland rain forests on oceanic islands in Tonga, Western Polynesia, that experience frequent natural disturbance and have a 3000-y history of shifting cultivation. By focusing on small remote islands as a model system the spectrum of dispersal syndromes examined can be constrained (Carlquist 1967), and few species means a large number of individuals can be studied in a small area. We contrast secondary vs. remnant late-successional forest, with particular attention paid to spatial dispersion and clustering of tree species, as well as the presence of spatial association in the density of seedlings and samplings. We classified species along a continuum of regeneration strategies from shade tolerant and shade establishing to gap establishing and pioneer, and evaluated these predictions:

(1) Shade-tolerant tree species will not show evidence of compensatory recruitment, e.g. small trees clustered in space and distant from larger trees that are randomly or regularly distributed, in late-successional forest. Rather, tree species will be clustered for all size classes and scales (Debski *et al.* 2000) owing to dispersal limitations. Further, shade-tolerant species will be more clustered in secondary than in late-successional forest, because of greater long-distance dispersal limitations and distances to seed sources (Laurence 2004).

(2) Light-demanding tree species will be clustered in late-successional forest at the scale of gaps (Pearson *et al.* 2003), and less clustered in secondary (previously cultivated) forests because of greater dispersal ability (e.g. smaller seeded and therefore greater availability of dispersers) (Whitmore 1998), greater homogeneity of light availability and potentially a soil seed bank at the time of agricultural abandonment (Bazzaz & Pickett 1980, but see Dalling *et al.* 1998).

(3) Density of seedlings and saplings of shade-tolerant species will show a negative association with light availability (due to lower survivorship, Balderrama & Chazdon 2005, or lower competitive ability in gaps), positive association with juveniles of other species (clumped in productive sites or where there is space on the forest floor), and positive association with the abundance of conspecific adults (large seeded, few dispersers); further, the association with conspecific adults will be stronger in secondary than in late-successional forest (where most dispersers prefer to be).

(4) Density of seedlings and saplings of light-demanding species will show positive spatial association with light in late-successional forest where they are expected to have established in gaps. There will be no association in secondary forest where it is expected that there was a more homogeneous distribution of propagules and resources when they established following shifting agriculture.

(5) Active seed dispersal (i.e. by extant frugivorous vertebrates) contributes to stand-level diversity in secondary and late-successional forest, but plays a lesser role in these Western Polynesian forests than has been found in tropical forests with higher tree diversity and fewer extirpations of dispersers (Webb & Peart 2001).

MATERIALS AND METHODS

Study area

The Kingdom of Tonga comprises about 170 islands totalling 700 km^2 of land spread across 600 000 km^2 of the south-west Pacific Ocean. They are mainly low limestone islands from < 1–10 million y old (Dickinson *et al.* 1999) where andesitic tephra has been deposited and weathered to rich soils (Orbell *et al.* 1985). The study took place in the Vava'u island group (18.7°S, 174.0°W), a cluster of > 60 islands (total area ∼125 km^2). The climate

Table 1. Summary information for forest plots. Location: island area is given in parentheses. Trees = number of trees mapped in large plot; Regeneration = Number of seedlings, saplings and trees < 5 cm dbh in main plot (600 m^2). Large tree loss = number of trees ≥ 10 cm dbh uprooted or snapped from Cyclone Waka 2 y prior to this study. Small tree loss = same for trees 5 to < 10 cm (E23 not surveyed post-cyclone).

Plot	U2	V8	E23
Location	Vava'u Island (96 km^2), E of Utula'ina	Vakae'itu Island (0.85 km^2)	'Euaiki Island (0.24 km^2)
Latitude	18°34′28.4″ S	18°43′27.3″ S	18°45′56.5″ S
Longitude	173°56′40.5″ W	174°5′54.3″ W	174°01′10.3″ W
Slope angle	1°	15°	33°
Aspect (slope direction)	270°	290°	10°
Elevation	40 m	25 m	20 m
Forest type	Late successional	Secondary	Late-successional
Large plot size	75 × 60 m (4500 m^2)	75 × 60 m (4500 m^2)	90 × 50 m (4500 m^2)
Trees	545	645	557
Regeneration	2837	2497	1506
Large tree loss	9	5	Unknown
Small tree loss	9	7	Unknown

is humid tropical with annual rainfall of 2255 mm, two-thirds falling between November and April, and monthly mean temperature ranging from 23.3–26.9 °C (Thompson 1986). Forest types include littoral, coastal and lowland rain forests (Mueller-Dombois & Fosberg 1998, Whistler 1992). These islands have experienced impacts from subsistence-related human activities for about three millennia (Fall 2005) and are subjected to frequent disturbance from tropical cyclones (Woodroffe 1984), with an estimated return interval of 33 y for major hurricanes (Franklin *et al.* 2004). Remnant late-successional forest (as defined in Franklin *et al.* 1999) is currently restricted to steep escarpments and isolated terraces and patches can be as narrow as 50–100 m down-slope but several km across-slope, while secondary forest comprises small (1 to several ha) patches interspersed with active cultivation.

The data

Trees were mapped in three 0.45-ha plots in July–August 2004. They were located on Vava'u Island (plot U2), Vakae'itu Island (V8) and 'Euaiki Island (E23). U2 and E23 are both late-successional lowland rain-forest sites – U2 is flat and covered with soil, while E23 is steep with many limestone boulders outcropping (Table 1). Both are dominated by *Chionanthus vitiensis* (Seem.) A.C. Sm. (Oleaceae), *Maniltoa grandiflora* (A. Gray) Scheffer (Caesalpiniaceae), *Pleiogynium timoriense* (DC.) Leenh. (Anacardiaceae) and *Pouteria grayana* St. John (Sapotaceae). It is assumed that neither has been cleared for cultivation in recent centuries, if ever, because of their steepness (E23) or remoteness (U2). In contrast, V8 is a secondary forest site, estimated to be 30–40 y since cultivation ceased (Franklin *et al.* 1999), which is gently sloping and soil-covered. The most abundant trees are *Cryptocarya turbinata* Gillespie (Lauraceae), *Arytera brackenridgei* (A. Gray) Radlk. (Sapindaceae) and *Rhus taitensis* Guillemin (Anacardiaceae). All of Vava'u was uniformly impacted by Cyclone Waka (category 3) 2.5 y prior to the 2004 survey. The number of trees whose stems were uprooted or snapped during Cyclone Waka gives a measure of canopy loss (Table 1) and was about 15 trees (≥10 cm dbh) ha^{-1} in the late-successional forest and 8 ha^{-1} in the secondary forest (where there are fewer large trees; Franklin *et al.* 2004) out of 1200–1400 trees ha^{-1} (Franklin *et al.* 1999). The area of an average tree crown (see below) is about 50 m^2. Although 25% of stems were severely damaged by the hurricane, in late-successional forest most were resprouting and tree mortality was only 6%, but impact was greater in secondary forest (>33% damage and >10% mortality).

Each 0.45-ha site ('large plot') encompassed a 30 × 20-m 'main plot' corresponding to an area originally surveyed in 1995 (Franklin *et al.* 1999, Steadman *et al.* 1999) and extended 20 m down slope, 10–20 m up slope, 30 m to the left (when facing down slope) and 15–30 m to the right (Table 1). Neither stem locations nor densities of seedlings and saplings were mapped in the previous survey. In the large plot every tree ≥ 5 cm dbh at 1.3 m height was given x,y coordinates, accurate to at least 0.5 m, using measuring tapes and a laser rangefinder (Impulse, Laser Technology Inc., Inglewood, CO, USA). Species and dbh were recorded for each tree. The main plot was divided into 24 5 × 5-m subplots, and in each subplot the densities (counts) of small seedlings (< 10 cm tall), seedlings and small saplings (10 cm – 2 m tall) and saplings (> 2 m tall but < 5 cm dbh) were recorded by species. This scale of spatial aggregation was chosen as a compromise between practical constraints and data requirements given the small size and high density of individuals relative to other tropical forests. Each plot comprised > 500 trees and > 1500 regenerating individuals (Table 1), yielding sufficient observations for the spatial analysis.

Point pattern analysis

Point pattern analysis was conducted for tree locations of each of the most abundant species in each large plot to evaluate the pattern (clustered, random or regular) of small (5 to < 10 cm dbh) and large (≥ 10 cm dbh) trees. Ripley's K(d) was calculated for 1-m increments (d) integrated to 25 m distance ($< 1/2$ the shortest plot dimension). Ripley's K (Ripley 1976) compares the observed number of points separated by distance less than d to the expected number of points under the null hypothesis of complete spatial randomness (CSR), conditioned on the average density of points in the sample. Bivariate Ripley's K was used to evaluate the distribution of small trees relative to conspecific large trees, e.g. the hypothesis of independence (Goreaud & Pelissier 2003). The range 1–25 m corresponded to scales examined in other rain-forest studies, and allowed sufficient observations in each plot to estimate significance by Monte Carlo simulation ($n = 500$) using the R (R Development Core Team 2004) package splancs (Rowlingson & Diggle 1993).

Spatial regression analysis

Spatially explicit regression methods (Keitt *et al.* 2002, Lichstein *et al.* 2002) were used to examine patterns of recruitment vs. factors related to dispersal limitations, density dependence and the physical environment (Lichstein *et al.* 2004). We hypothesized distance-dependent or neighbourhood effects of several explanatory variables. Therefore our approach was to test the dependent variable (seedling and sapling density) for spatial dependence (autocorrelation), estimate models by ordinary least squares (OLS) that included spatially lagged explanatory variables, and then test the model residuals for spatial dependence. For cases that showed residual spatial dependence the appropriate autoregressive model (lag vs. error) was estimated by maximum likelihood.

Regeneration of each abundant species was tested for autocorrelation by calculating Moran's I (Moran 1948) for seedling and sapling density (count) at lags of 1–3 subplots (e.g. 5–15 m) in each main plot using the spdep package (Bivand 2002). Spatial multiple regression models (Anselin *et al.* 2004), where density of seedlings and saplings was the dependent variable, were developed in R, using spdep to calculate spatial weight matrices and lagged variables, for each species in each main plot. Independent variables included: the density of seedlings and saplings of the other common species (Other Regeneration) in the subplot, the abundance (basal area) of conspecific trees ≥ 5 cm dbh in the subplot (Adult), at lag 1 (the total basal area inclusive of first order neighbouring subplots), and lag 2 (Adult lag_n); the abundance (basal area) of all trees in the subplot (All Trees), and at lags 1 and 2 (All Trees lag_n); and, two measures of the light environment of each subplot (Light_a and _b). The lagged variables for Adult and All Trees were calculated by aggregating the mapped tree locations from the large plot into 5×5-m subplots in the main plot and for two lags (10 m) surrounding it.

The abundance of conspecific trees (Adult) was included to test for the positive or negative spatial association of juveniles with adults at several scales (lags). The All Trees variable represents competition (for space, light and other resources) at those same scales. Other Regeneration could represent competition in the understorey environment (negative association), or favourable sites for seedling establishment (positive association). Two measures of the light environment, per cent total transmission and canopy openness, were calculated from digital hemispherical photos (Coolpix 4500 with FC-E8 fisheye converter, Nikon, Tokyo, Japan) taken at nine locations, 15–20 m apart, in the main plot and estimated for subplots using bilinear interpolation with the akima package in R. Gap Light Analyzer (Frazer *et al.* 1999, 2001) software was used to estimate these quantities from the hemispherical photos and because cloudiness index and spectral fraction values were unavailable for Tonga, the default values of 0.5 and 0.45 were used. In hindsight, light measurements should have been made in each subplot so that their resolution was consistent with the rest of the analysis, therefore their inclusion in the models is merely exploratory and meant to guide future studies. Light measurements from U2 were corrupted and light variables could not be tested for this site.

For all linear models, several diagnostics for spatial dependence were evaluated, including the classic Lagrange Multiplier tests for spatial error and spatial lag dependence (Anselin & Rey 1991) and robust versions of these tests (Anselin *et al.* 1996). These tests are designed to detect the presence of spatial dependence in model residuals. More specifically, they can distinguish between spatial error dependence (due to boundary and scale mismatches between measurements of the dependent and independent variables, or an omitted explanatory variable) and spatial lag dependence (due to an omitted spatial lag of the dependent variable).

Assumptions of all spatial analyses are that the processes generating observed patterns are homogeneous throughout the site (although there are methods to correct for density inhomogeneity; Couteron *et al.* 2003), and that the resolution of the analysis is commensurate with the processes of interest. Subareas of 5×5 m and the lags considered in this study were hypothesized to be adequate to detect relationships between adult and juvenile pattern and differentiate active and passive dispersal. Tongan overstorey trees are relatively short (tall canopy trees 16–18 m in these plots)

Table 2. Tree species characteristics and spatial pattern for small (5 to <10 cm dbh) and large (≥ 10 cm dbh) trees at lags of $d = 1$ m to 25 m based on Ripley's K, and association of small with large trees based on bivariate Ripley's K at lag distances given. Number of small and large trees in parentheses. Regeneration types: shade tolerant (A); establishes in shade but associated with gaps as saplings (B); establishes in gaps but can survive in shade as saplings (C); pioneer species (D); assignment follows Franklin (2003).

Species – regeneration type	Extant dispersers[a]	Fruit size[a] (mm)	Site status	Small	Large	Association
Chionanthus vitiensis (A)	Bird, Bat	33 × 19	Late (E23)	Random[1] (151)	Random[1] (201)	None
Chionanthus vitiensis (A)	“	“	Late (U2)	Clustered (36)	Random (109)	None[6]
Maniltoa grandiflora (A)	Bat?	60 × 35	Late (E23)	Random (10)	Random (67)	Positive 1–9 m
Maniltoa grandiflora (A)	“	“	Late (U2)	Random[2] (40)	Random (54)	None
Pouteria grayana (A)	Bat	34 × 37	Late (U2)	Random[2] (17)	Random[2] (22)	None
Syzygium clusiifolium (A)	Bird, Bat	35 × 26	Late (U2)	Random (30)	Random (42)	None
Arytera brackenridgei (B)	Bird?, Bat?	13 × 10	Secondary (V8)	Random[3] (109)	Clustered[4] (49)	None
Cryptocarya turbinata (B)	Bird	13 × 13	Secondary (V8)	Clustered (139)	Clustered (95)	Positive 1–6 m
Pleiogynium timoriense (C)	Bird, Bat	34 × 23	Secondary (V8)	Clustered (31)	Random (49)	None
Rhus taitensis (D)	Bird	7 × 6	Secondary (V8)	–	Random[5] (38)	–

[a] Sources: Banack 1998, McConkey & Drake 2002, McConkey *et al.* 2004, Meehan *et al.* 2002, Steadman & Freifeld 1999.
[1] Clustered at lags >10 m maybe due to site heterogeneity at that scale. [2] Clustered at some lags, ~7–17 m. [3] Clustered at 12+ m. [4] Clustered at 3–5 m, 10–12 m. [5] Only 7 small trees, so pattern was analysed for all trees ≥ 5 cm dbh. [6] Slightly positive association 5 m.

with correspondingly smaller crown widths than would be expected for taller trees in rain forests elsewhere, e.g. average 7.6 m for trees in Vava‘u (McConkey & Drake 2006).

Regeneration functional types

There were sufficient numbers of observations to evaluate nine species that occurred in the overstorey (≥ 30 trees, ≥ 10 per size class) or understorey (as seedlings or saplings in > 3 subplots) of one or more plots. Although they represent 7–15% of tree species richness, they comprise 64–75% of the individuals in each plot. Those species were classified into regeneration functional types (Table 2) as defined in Clark & Clark (1999, see also Swaine & Whitmore 1988) based on inferred light requirements (Franklin 2003). Those types: (1) are shade tolerant – establish and grow in dark forest; (2) establish in shade but are associated with gaps as saplings (shade establishing); (3) establish and grow in gaps but can survive as saplings in closed forest (gap establishing); and (4) require gaps for establishment and juvenile growth (pioneer). These represent a continuum of shade tolerance and are consistent with theoretical trade-offs between high-light growth rates and survival in low light in forest communities (Baraloto *et al.* 2005, Bloor & Grubb 2003, Pacala *et al.* 1996, but see Balderrama & Chazdon 2005). Light levels required for germination and optimal growth, and most other aspects of ecophysiology, are unknown for these species, as is true for most rain-forest trees in the world (Grubb & Metcalfe 1996).

Further, pioneer (versus shade-tolerant) species frequently have associated traits, such as smaller seed size, greater dispersal distance, and greater seed longevity (Gitay *et al.* 1999, Whitmore 1998). All of the species examined are bird- and/or bat-dispersed, and although the pioneer species *R. taitensis* does have the smallest fruits among those included in this study (Table 2), nothing is known about seed longevity for any of these species. It is known that extirpations of vertebrate frugivores disproportionately impacted dispersers of large seeds (Meehan *et al.* 2002, Steadman 1993), that introduced rats are primarily seed predators (McConkey *et al.* 2003, Meehan *et al.* 2005), and it is speculated that native seed and seedling predators may be less abundant than in other tropical forests (Meehan *et al.* 2005, Webb & Fa‘aumu 1999).

Active dispersal

A complete species list of seedlings and saplings in each main plot was compared with the trees in the main plot plus a 15-m buffer. Species that occurred as regeneration but not as trees were considered to have been actively dispersed by vertebrate frugivores. This is a conservative estimate of the importance of active dispersal, but more sophisticated approaches (Webb & Peart 1999) were not warranted by the data.

RESULTS

Patterns of trees and regeneration

Point patterns of shade-tolerant species were random at most scales examined for small and large trees. Clustering, where it did occur, was usually found at distance scales of 10 m or greater. Only one shade-tolerant species in a late-successional plot was clumped when small and more random when large (Table 2). In no cases were small trees negatively associated with (repelled by) locations of large trees. In only one case were locations

Table 3. Summary of spatial association (based on Moran's I at lag of one subplot; total number of individuals in the main plot shown in parentheses), and spatial linear models for regeneration of tree species (Table 2) in 24 5 × 5-m subplots in late-successional (Late) or secondary (2°) forest plots (Table 1). +SA = positive spatial association (variance of I calculated under the assumption of randomization), Random = not significantly different from CSR. Sign (positive or negative) and P-values of estimated coefficients for significant ($P < 0.1$) predictors in the multiple regression models are given; n.s. = not significant. The best model if $R^2 > 0.14$ is presented, even when not significant, for illustrative purposes.

			Spatial model predictors							
Species	Site	Spatial association	Other regen.	Adult	Adult lag	All trees	All trees lag^{1}	Light	R^2	P
Chionanthus vitiensis (A)	Late (E23)	+SA (968)	+ (0.003)	n.s.	n.s.	n.s.	+ lag2 (0.033)	+ (a) (0.057)	0.51	0.006
Chionanthus vitiensis (A)	Late (U2)	Random (172)	n.s.	+ (0.072)	n.s.	+ (0.067)	+ lag2 (0.062)	NA	0.14	0.168
Maniltoa grandiflora (A)	Late (E23)	Random^{2} (51)	+ (0.009)	n.s.	n.s.	n.s.	n.s.	− (a) (0.030)	0.23	0.078
Maniltoa grandiflora (A)	Late (U2)	+ SA (885)	+ (0.005)	n.s.	n.s.	n.s.	+ lag2 (0.082)	NA	0.35	0.023
Syzygium clusiifolium (A)*	Late (U2)	+ SA (175)	− (< 0.001)	+ (0.007)	n.s.	n.s.	n.s.	NA	–*	–*
Cryptocarya turbinata (B)	Late (U2)	Random^{2} (936)	+ (0.003)	n.s.	n.s.	n.s.	n.s.	NA	0.19	0.042
Cryptocarya turbinata (B)	2° (V8)	+SA (857)	n.s.	n.s.	− lag2 (0.098)	n.s.	+ lag2 (0.043)	− (b) (0.017)	0.43	0.018
Arytera brackenridgei (B)	2° (V8)	Random^{3} (298)	n.s.	+ (0.016)	n.s.	n.s.	n.s.	n.s.	0.23	0.120
Pleiogynium timoriense (C)	Late (U2)	+SA (42)	n.s.	n.s.	n.s.	+ (0.088)	− lag2 (0.009)	NA	0.22	0.089
Pleiogynium timoriense (C)	Late (E23)	+SA (29)	n.s.	n.s.	− lag1 (0.009)	n.s.	n.s.	+ (b) (0.068)	0.17	0.142
Pleiogynium timoriense (C)	2° (V8)	+SA (41)	n.s.	n.s.	+ lag2 (0.017)	n.s.	n.s.	+ (a) (0.040)	0.24	0.109
Rhus taitensis (D)†	Late (E23)	+SA (24)	+ (< 0.001)	NA	NA	n.s.	− lag2 (< 0.001)	− (a) (0.034)	−†	−†

Note: *Vavaea amicorum*, a shade-tolerant tree, showed randomly distributed regeneration in late-successional U2 (n = 83), and positive SA in secondary V8 (n = 352); shade-tolerant *Pouteria grayana* had randomly distributed regeneration in U2 (n = 178) but no significant models were fit in these three cases. [1]lag1 = variable at spatial lag of one subplot of 5 × 5 m; lag2 = variable at lag of two subplots; (a) canopy transmission; (b) canopy openness. [2]Positive spatial association at lag 2 (10 m); [3]Positive spatial association at lag 3 (15 m). *OLS residuals showed error dependence. Result shown for spatial autoregressive error model estimated by maximum likelihood. For λ P = 0.06, AIC = 137 vs. 139 for OLS model. † OLS residuals showed lag dependence. Result shown for spatial autoregressive lag model estimated by maximum likelihood. For ρ P = 0.021 (likelihood ratio test), AIC = 87 vs. 91 for OLS model. No residual autocorrelation (P = 0.842, Lagrange Multiplier test for error dependence).

of small trees positively associated with conspecific large trees: *Maniltoa grandiflora* was less abundant in one of the late-successional plots (E23), and although the respective patterns of small and large trees did not deviate from CSR, small trees were attracted to big trees there. This positive association did not occur in U2 where it was more abundant. Shade-establishing species were clustered in the secondary forest plot, including the abundant *Cryptocarya turbinata* which was strongly clustered in all size classes (Tables 2 and 3) and small trees were weakly attracted to large there (Figure 1).

Seedlings and saplings of shade-tolerant species tended to be positively autocorrelated at a lag of 1 (5 m) in those late-successional sites where they were extremely abundant and randomly distributed where they were sparser. In three of six cases juveniles of a shade-tolerant or shade-establishing species were positively associated at lag 1 and showed a random pattern as trees in a late-successional plot (compare Tables 2 and 3) – they were *Chionanthus vitiensis*, *Maniltoa grandiflora* and *Syzygium clusiifolium* (A. Gray) C. Muell.

Seedlings and saplings of gap-associated and pioneer species were positively spatially autocorrelated in late-successional sites while most showed random point patterns as trees in the secondary forest site (Table 2); however, seedlings and saplings of *Pleiogynium timoriense* showed positive spatial association (Table 3) and small trees were also clustered there (Table 2).

Spatial regression of seedling and sapling density

In late-successional plots, seedling and sapling density of shade-tolerant and shade-establishing species was positively associated with total basal area of all trees at lag 2 (to 10 m) in three of seven cases (species in sites), and negatively associated with the light variables in two of four cases where light was measured (Table 3). In other words, the predicted negative relationship with light was only found in about half the cases. Regeneration of these species tended to be positively associated with regeneration of other abundant species

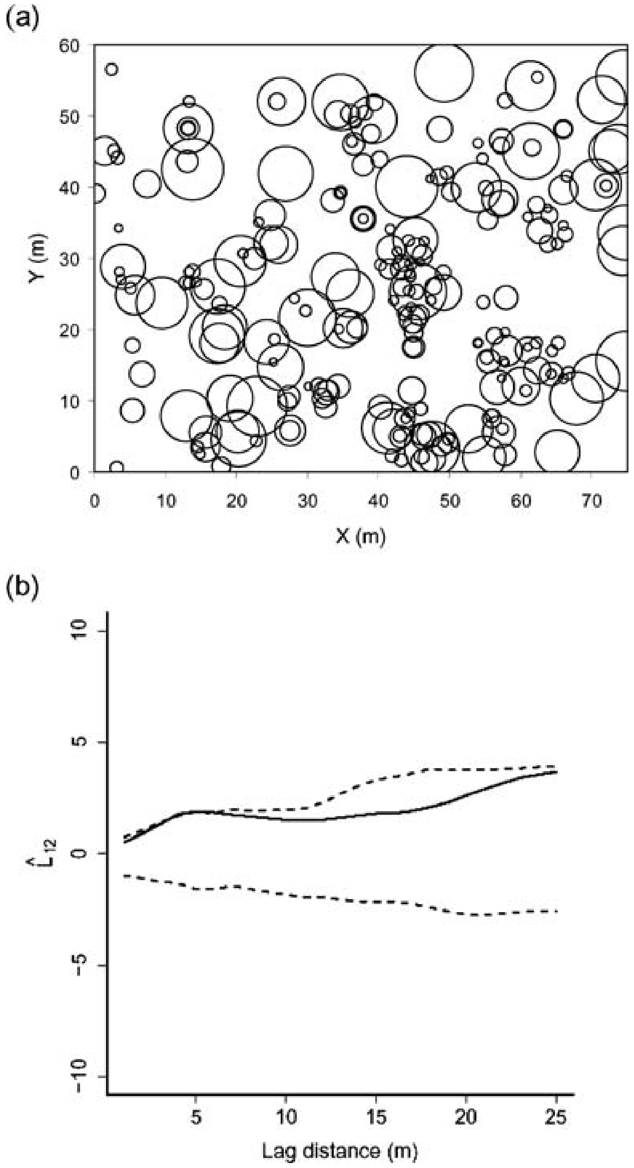

Figure 1 Point pattern of *Cryptocarya turbinata* trees in secondary forest large plot (V8). a) Stem map where size of circle is proportional to stem diameter, and concentric circles indicate multiple-stemmed trees; and, b) the $L_{12}(d)$ transform of bivariate Ripley's K for small vs. large trees shown with simulated confidence intervals, indicating slightly positive association at $d = 3$ to 6-m lag. $L_{12}(d) = \sqrt{\frac{K_{12}(d)}{\pi}} - d$.

in late-successional plots. Just as there were few cases of small trees positively associated with large trees, juvenile density of these species was positively associated with conspecific adults (within subplots or at greater spatial lags) in only a few cases. While the data are limited they do not support the prediction that positive association of seedlings and saplings with conspecific adults is stronger for shade-tolerant species in secondary than in primary forest (Table 3). Density of seedlings and saplings of shade-establishing *Cryptocarya turbinata* in the secondary plot showed a negative association with conspecific adults at lag 2 (10 m), with the small and large trees (each clustered and positively associated with each other) clumped in the upslope portion of the main plot, and regeneration concentrated in the downslope half (Figure 2). While this pattern could be explained by gravity dispersal it was not seen in any other case.

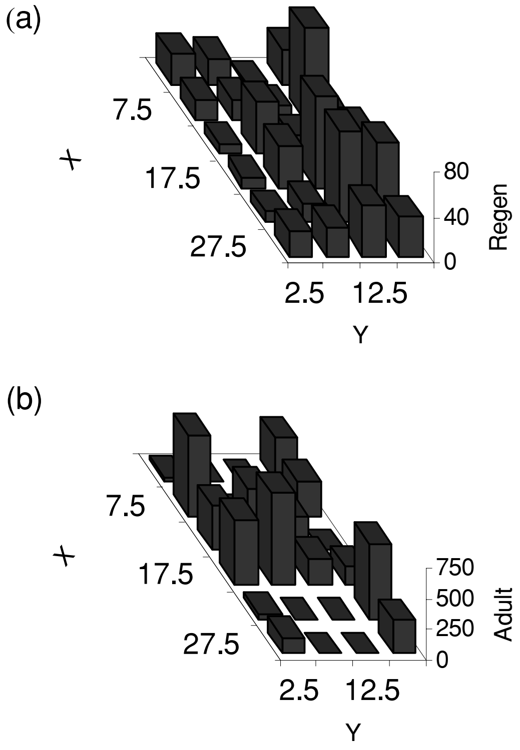

Figure 2 Spatial pattern of *Cryptocarya turbinata* in 5 × 5-m subplots of 30 × 20-m main plot V8 (early successional) viewed from upslope right side. Density (counts) of seedlings and saplings (< 5 cm dbh) (a) and adult abundance (sum of basal area in cm^2) (b).

For gap-associated and pioneer species, density of seedlings and saplings tended to be negatively associated with total basal area of all trees at lag 2 or positively associated with the light variables in both late-successional and secondary forest. The gap-establishing *Pleiogynium timoriense* was negatively associated with conspecific adults in the late-successional site, and positively in the secondary forest.

Notably, only two of the spatial linear models showed residual spatial dependence (Table 3), indicating that the positive autocorrelation observed for density of seedlings and saplings in 9/15 cases was almost always explained by the predictor variables. Shade-tolerant *S. clusiifolium* showed error dependence which could arise from boundary and scale mismatches, or an omitted exogenous variable. A spatial autoregressive error model was estimated and the autocorrelated error parameter, λ, was significant (Table 3). While the same two predictors,

Table 4. The number of tree species in each main plot buffered by 15 m on all sides compared to the number of species found as seedlings and saplings in the main plot that did not occur in the larger (60 × 50 m) area. Per cent of total regeneration (density of seedlings and saplings) in the main plot given in parentheses.

Type of species	Late E23	Late U2	Early V8
Tree species main plot plus buffer (60 × 50 m)	22	25	24
Regeneration only species in main plot:	7 (9.3%)	12 (2.2%)	14 (4.6%)
Introduced	0	1 (0.1%)	2 (0.2%)
Shade tolerant and shade-establishing	3 (7.3%)	7 (2.0%)	9 (4.0%)
Pioneer and gap-establishing	4 (2.0%)	4 (0.4%)	3 (0.5%)

Other Regeneration and conspecific adult abundance, were significant in the OLS model (not shown), their P-values were an order of magnitude smaller in the autoregressive model, giving stronger support for the third prediction in this case.

The pioneer *R. taitensis* showed residual spatial dependence in a late-successional plot due to a missing spatially-lagged dependent variable (density of conspecific juveniles in adjacent subplots). Although there is no expected causal relationship, this could result from spillover effects, e.g. an independent variable such as light that affects not only the subplot in which it is measured, but also nearby ones. A spatial autoregressive lag model was estimated by maximum likelihood; the autocorrelation parameter, ρ, was significant (Table 3) and this model showed no residual spatial autocorrelation. A significant negative coefficient was estimated for All Trees, seemingly contradictory to the small but significant negative relationship with a light variable; this could result from the questionable light measurements.

Active dispersal

A conservative estimate of the minimum number of species actively dispersed into the plots was based on those species found in the main plot as regeneration, but not found within 15 m of the main plot as adults (Table 4). Allowing that introduced trees may be planted by people, there were still 30 cases (23 native species in one or more of three plots) of regenerating species likely to have been actively dispersed. These 7–12 species per plot represent 32–50% of the respective plots' overstorey species richness (Table 4).

DISCUSSION

Shade-tolerant and shade-establishing species were randomly distributed at many scales in late-successional plots (although there was some clustering, usually at about 10–20 m). This is in contrast with the first prediction and with other studies of late-successional forest in which at least half of the many species considered showed clumped distributions at similar scales (Aiba *et al.* 2004, Condit *et al.* 2000, Debski *et al.* 2000, Okuda *et al.* 1997, Webb & Fa'aumu 1999). What could account for this difference? Perhaps these populations are not as dispersal-limited, and/or environmental conditions are not as patchy as in other rain forests. Less dispersal limitation could result from uniformity of dispersal syndromes among species combined with a limited but effective set of extant dispersers. It could also be related to the low density of species and high density of individuals per species. Previous studies examined many rare species. When comparing patterns of the recruitment (seedlings and saplings) and mature life stages, these species showed positive spatial association as juveniles but were random as trees in half the cases, suggesting some density-dependent mortality. Although only one shade-establishing species (*Cryptocarya turbinata*) was found in all sites, as anticipated this species was more clustered in secondary than in late-successional forest.

Seedlings and saplings of gap-establishing and pioneer species showed positive spatial association in late-successional forest but tended to be randomly distributed as trees in secondary forest. This was consistent with the second prediction.

For only one of the shade-establishing and none of the shade-tolerant species was juvenile density negatively related to abundance of conspecific adults at the scales measured (up to 10 m), and in fact they were positively related in some cases, consistent with the third prediction. This is concordant with the previously cited studies that found very few cases of reduced sapling density near adults.

Seedling and sapling density of gap-establishing and pioneer species was negatively related to total tree abundance or positively related to light at a scale of 10 m (lag 2), suggesting that they were associated with gaps in late-successional forest (perhaps resulting from the recent hurricane), consistent with the fourth prediction. However, shade-establishing (*Cryptocarya turbinata, Arytera brackenridgei*) and gap-establishing (*Pleiogynium timoriense*) species that dominated the secondary forest plot all showed clustering (adults) and strong positive spatial association (regeneration) at several scales. This pattern could result from environmental heterogeneity in the secondary forest (contrary to the fourth prediction), or dispersal limitations.

Previous studies suggest dispersal limitations for both pioneer and primary forest species in secondary forest following shifting cultivation (Laurence 2004) or logging (Toriola *et al.* 1998). This is consistent with the nucleation model of succession (reviewed in Hooper *et al.* 2004) and may be caused by lack of effective dispersal by vertebrate dispersers that prefer primary forest. The trees analysed are all vertebrate-dispersed (Table 2), and avian frugivores, especially those that disperse large seeds, are much more abundant in late-successional than in secondary forest in the study area (Steadman & Freifeld 1998). Fruit bats also prefer primary forest (Banack 1998). Dispersal limitation may be operating in secondary forest in Tonga in spite of the fine grain of land-use patterns (the field size or agricultural allotment, the ‘api uta, is 3.4 ha). Studies of seed dispersal by frugivores in Tonga suggest that, while smaller seeds are consumed and pass through pigeons (< 20 mm diameter) and bats (< 4 mm), and are therefore potentially dispersed some distance from the parent tree, large seeds are regurgitated or spat out (McConkey & Drake 2006, McConkey *et al.* 2004). These large seeds are mainly dispersed near the parent tree, but also experience higher survival and lower predation there (Meehan *et al.* 2005).

The fifth prediction was supported. Species estimated to have been actively dispersed represented almost half of tree species richness even at the small spatial extent examined, and active dispersal appears to be especially important to late-successional species in secondary forest (but would also be easier to detect there with this method). The estimated proportion of juveniles that were actively dispersed was small (< 10% of the total density) and much lower than has been found in species-rich rain forests (60%; Webb & Peart 1999).

The application of spatially explicit regression techniques revealed significant spatial associations between species juveniles and conspecific adults, total tree cover, and the light environment. In almost all cases the dependent variables showed spatial dependence but the model residuals did not, suggesting that the spatial patterns observed in seedlings and saplings resulted from the spatial patterns in the explanatory variables, or so-called induced spatial dependence (Fortin & Dale 2005, Legendre 1993). This highlights the importance of extending the spatial context of factors that influence regeneration to include those beyond the individual subplot by using spatially lagged predictors as in this study, or by using a more mechanistic model (Uriarte *et al.* 2005). Moreover, in some cases this spatial association takes a positive form, while in others it is negative, suggesting a form of process heterogeneity, e.g. multiple recruitment syndromes (Uriarte *et al.* 2005), that should be examined in future research. In cases where model residuals showed spatial dependence we used recently developed model specification strategies (Anselin & Rey 1991, Anselin *et al.* 1996, 2004) that allowed us to distinguish between lag and error dependence, and estimate the appropriate autoregressive model, an approach we have not seen used much in ecology.

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