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RESEARCH ARTICLE

Spatial distribution and regeneration strategies of the main forest species on Robinson Crusoe Island

Distribución espacial y estrategias de regeneración de las principales especies forestales de la Isla Robinson Crusoe

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ABSTRACT

We describe the structure of the endemic Robinson Crusoe Island forest. We analyse the regeneration strategies of the trees: *Myrceugenia fernandeziana*, *Fagara mayu*, and *Drimys confertifolia*. Inventories were taken on nearly intact montane forest remnants with emphasis on spatial patterns by using Ripley's K (t) function. We hypothesized that i) ornithochorous and barochorous species should show a clumped regeneration, as a consequence of seed rain; ii) nurse effect, if present, should also contribute to a clustered pattern; iii) clustering should disappear at more developed life-stages due to self-thinning; iv) if gaps influence tree mortality and regeneration, these will present grouped patterns. *Myrceugenia fernandeziana* was the most abundant tree species, followed by *F. mayu* and *D. confertifolia*. The diameter distribution of *M. fernandeziana* suggested a continuous regeneration. The diameter distribution of *F. mayu* was typical of species that require disturbances to regenerate, whereas the diametric pattern of *D. confertifolia* was intermediate compared with the previous species. *M. fernandeziana* demonstrated *a* spatially clumped regeneration given its dispersal mode (hypothesis i), but did not show association with the large tree individuals, discarding a possible nurse effect (hypothesis ii). The large specimens of *M.fernandeziana* were randomly distributed, likely due to self-thinning (hypothesis iii). Mortality of *M. fernandeziana* trees did not seem to be a consequence of local disturbances, rejecting hypothesis iv). *Fagara mayu* distributed randomly showing in cases some aggregation. *Drimys confertifolia* presented a clustered pattern. Regeneration of *F. mayu* and *D. confertifolia* occurred mainly in gaps, but also under canopy for the latter species. *D. confertifolia* tended to regenerate near larger trees of the same species (hypothesis ii). *M. fernandeziana* seems to exhibit shade tolerance, although it showed plasticity to use different regeneration environments. *F. mayu* showed characteristics of a shade intolerant species, possibly requiring gaps, or larger disturbances to regenerate. *D. confertifolia* seems to be a shade semi-tolerant species, requiring areas with low canopy cover to establish.

Key words: forest regeneration, Juan Fernández Islands, Myrtisylva, Ripley's K-function, spatial point pattern analysis.

RESUMEN

Se describe la estructura del bosque endémico de la Isla Robinson Crusoe. Se analizan las estrategias de regeneración de los árboles: *Myrceugenia fernandeziana*, *Fagara mayu*, y *Drimys confertifolia*. Se inventariaron remanentes de bosque montano, con énfasis en los patrones espaciales usando la función K(t) de Ripley. Se hipotetiza que: i) especies ornitócoras y barócoras debieran mostrar regeneración agrupada, a consecuencia de la lluvia de semillas; ii) si existe efecto nodriza, existirá también un patrón agregado de regeneración; iii) en estados de desarrollo avanzado la agregación se atenuará, a consecuencia del autorraleo; iv) si las aperturas de dosel influencian la regeneración y mortalidad, estas presentarán patrones agrupados. *M. fernandeziana* fue la especie arbórea más abundante, seguida por *F. mayu* y *D. confertifolia*. La distribución diamétrica de *M. fernandeziana* sugirió una regeneración continua. *F. mayu* exhibió una distribución típica de especies con regeneración esporádica. La distribución diamétrica de *D. confertifolia* fue intermedia respecto a las otras especies. La regeneración de *M. fernandeziana* fue espacialmente agrupada, dado su modo de dispersión (hipótesis i), pero no mostró asociación con individuos adultos, descartándose un posible efecto nodriza (hipótesis ii). Los individuos adultos de *M. fernandeziana* se distribuyeron aleatoriamente probablemente debido a autorraleo (hipótesis iii). La mortalidad de adultos de *M. fernandeziana* no pareció responder a alteraciones locales, descartándose la hipótesis iv. *F. mayu* se distribuyó aleatoriamente exhibiendo, en casos, leve agregación. *D. confertifolia* presentó un patrón agrupado. La regeneración de *F. mayu* y *D. confertifolia* ocurrió principalmente en claros, aunque esta última especie se presentó también bajo dosel. *D. confertifolia* tiende a regenerar cercana a ejemplares adultos de la propia especie (hipótesis ii). *M. fernandeziana* mostró tolerancia a la sombra, aunque es muy plástica, ocupando diferentes ambientes de regeneración. *F. mayu* mostró características de intolerante a la sombra; posiblemente requiera claros, o disturbios mayores para regenerar. *D. confertifolia* parece ser semitolerante a la sombra requiriendo claros, o áreas con menor cobertura para establecerse.

Palabras clave: análisis espacial, archipiélago Juan Fernández, K (t) de Ripley, Myrtisylva, regeneración forestal.

INTRODUCTION

The Robinson Crusoe Island (RCI), part of the Juan Fernández Archipelago, is a recognised centre of plant endemism (61.1 %; Danton & Perrier 2006), that presents a precarious flora conservation status (Dirnböck et al. 2003). The tree species of the RCI forest are all endemic. They exhibit a wide range of dispersal strategies (Skottsberg 1928, Danton 2006) and rely on many different species-specific disturbance regimes (Castro et al. 1995, Cereceda et al. 1996). Few studies have considered either the structure of the natural forest, or auto-ecological aspects of the main tree species of the island (Bannister et al. 2006, Cuevas & Vargas 2006, Vargas et al. 2006). An understanding of the original structure and dynamics of the forests has fundamental importance when designing a management plan to contribute to their restoration and conservation (Donoso 1993). We studied nearly intact, forest remnants on RCI, which means that these data can serve as a reference for future conservation and restoration attempts.

The appearance of the vegetation in the community is an aspect regularly considered to describe a forest (i.e., physiognomy, Mueller-Dombois & Ellenberg 1974). By analyzing the physiognomy and structure of a forest, it is possible to make conclusions about the ecological site conditions and the autoecological behaviour of the species (Donoso 1993).

Disturbance is considered to be a major factor driving plant dynamics, creating environmental heterogeneity for species coexistence (Pickett & White 1985). Alternative mechanisms for coexistence are life-history differentiation (Veblen 1992), resource partitioning and different regeneration niches for the species in competition (Grubb 1977). An approach for understanding regeneration dynamics is through spatial distribution patterns of trees (Donoso 1993).

Different stages and processes of plant life cycles may influence the distribution pattern of individuals. For instance, differences on seed/fruit dispersal modes (Willson 1992, Bustamante 1995), seedling germination (Harper 1977), seedling survival (Janzen 1970) or a nurse effect of large trees upon regeneration can affect the spatial pattern of species (Fuentes et al. 1986). This could also be determined by self-thinning and competition at more advanced life stages, especially when the initial recruitment was clustered (Closset-Koop et al. 2007).

We analyse the structure of the forest in RCI, focusing on the main tree species: *Myrceugenia fernandeziana* (Hook. et Arn.) Johow, *Fagara mayu* (Bertero ex Colla) Engler and *Drimys confertifolia* Phil. We studied the spatial distribution of trees and regeneration, considering also standing dead individuals, in order to show that different species life histories, in addition to the disturbance regime that they face, result in different regeneration strategies, making possible species coexistence. We hypothesize the following: i) ornithochorous and barochorous species should have clumped seed rain, and thus, a clumped regeneration, following antecedents of grouped propagule dispersal by gravity or by directed bird dispersal (Bustamante 1995, Cuevas 2000, Willson 1992). ii) Nurse effect, if present, should also contribute to a clustered pattern (Oliver & Larson 1990, Fuentes et al. 1986). iii) Clustering should disappear with the self-thinning that is common on many species at older life stages, resulting in a random pattern (Fangliang et al. 1997). iv) Tree mortality and tree regeneration, if is triggered by gaps, should also show a clustered pattern due to the restricted area of these disturbances (Salas et al. 2006). Our four hypotheses are not mutually exclusive.

In addition to hypotheses testing, we aim i) to describe the structure of the endemic forest on RCI, and ii) to provide an explanation about the regeneration strategies of the main tree species.

METHODS

Study sites and main tree species

The Juan Fernández Archipelago comprises three islands located between 680 and 860 km west of Chile. The Robinson Crusoe Island is the closest one to the continent (47.9 km^2, 33°37’ S, 78°51’ W). The archipelago was designated National Park in 1935, and UNESCO World Biosphere Reserve in 1977. San Juan Bautista, on RCI, is the only town permanently inhabited of the archipelago (Fig. 1). The climate is Mediterranean with oceanic influence. Average annual temperature and precipitation are 15.2 °C and 957 mm, respectively (Hajek & Espinosa 1987).

The forests on RCI are closely related to the Valdivian rainforests of southern Chile, and exhibit common characteristics with the Cleistocalyx communities of the subtropical islands in the New Zealand region, as well as with the Hawaiian Metrosideros-forest (Skottsberg 1953, Mueller-Dombois & Fosberg 1998). Skottsberg (1953) and Greimler et al. (2002) identified several vegetation units on the island, including two forest assemblages: ‘endemic upper mountain forest’ and ‘endemic lower mountain forest’. Danton (2006) proposed a specific name for these forest communities, ‘Myrtisylva (-ae)’, based on their unique characteristics, and the dominance of the endemic myrtle tree, *M. fernandeziana*.

With no human influence before 1574, disturbances like fires, selective cuttings, and introduction of exotic animals and plants have affected severely the RCI, since human occupation (Woodward 1969, Dirnböck et al. 2003). Natural abiotic disturbances as erosion, landslides, rock falls, torrential rains (Castro et al. 1995), strong winds (Cereceda et al. 1996), earthquakes, volcanic eruptions and even tsunamis (Skottsberg 1920-1956, p. 403) have also shaped the landscape of the island.

We selected the study sites considering absence or negligible biotic, non-native disturbances impeding natural forest regeneration, in particular herbivory by rabbits, rats, domestic cattle and wild goats; the presence of exotic species in the undergrowth (mainly *Aristotelia chilensis* (Mol.) Stunz and/or *Rubus ulmifolius* Schott.), and previous anthropogenic alterations. Plazoleta el Yunque (PLY), Quebrada de Damajuana (QDA) and Quebrada de Villagra (QVI) sites were selected (Fig. 1). These areas were located on middle elevation sectors, and form part of the endemic lower and upper mountain forests (Greimler et al. 2002).

From January to February (2003), we studied the three most abundant endemic trees in the RCI forests (Cuevas 2002): (i) *Myrceugenia fernandeziana* (Myrtaceae) that reaches 28 m height, and 1.1 m of diameter at breast height (DBH). Its fruit is a red round berry of 7-8 mm in diameter that contains 2-3 seeds of 5 mm length (Rodríguez et al. 1983), which

Site	Latitud S	Longitud W	Altitude (masl)	Slope(%)	Aspect	Location
PLY	33°39' 32.4"	78°50'40.4"	348	15	25°NE	Middle slope
QDA	33°39'47.1"	78°50'6"	500	35	20°N	Upper slope
QVI	33°38'9.1	78°51'46.4"	355	41	186°S	Middle slope

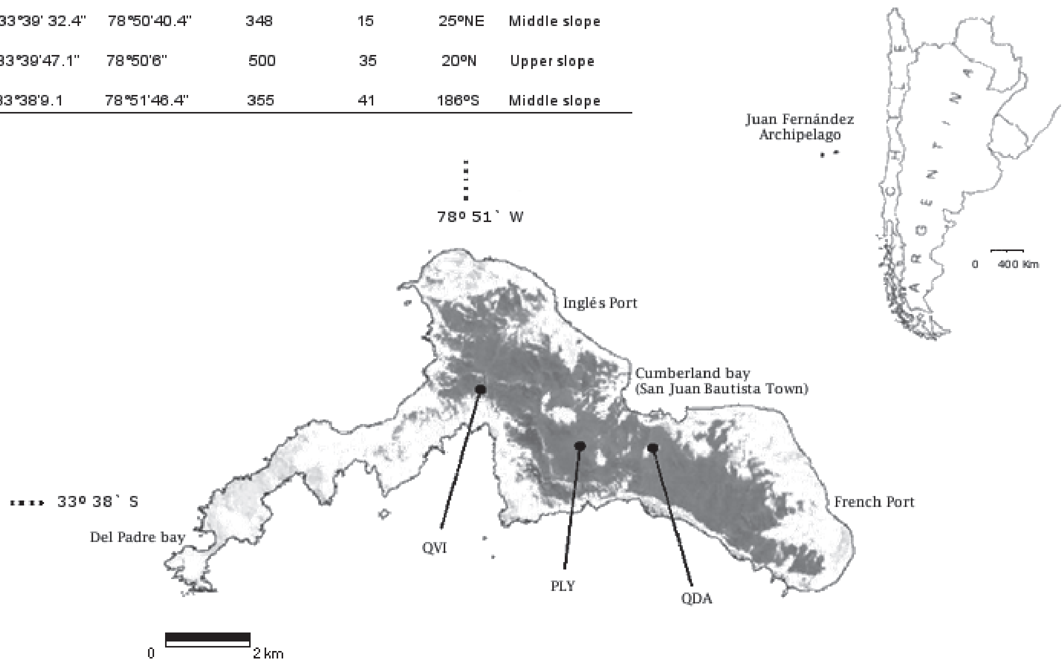

Fig. 1: Robinson Crusoe Island and study site characteristics. The shading indicates the vegetation cover. Study sites: PLY = Plazoleta del Yunque, QDA = Quebrada de Damajuana, QVI = Quebrada de Villagra (based on maps prepared by Greimler et al. 2002 and Universidad Mayor 2004).

Isla Robinson Crusoe y características de los sitios de estudio. La zona sombreada indica la cobertura vegetacional. Sitios de estudio: PLY = Plazoleta del Yunque, QDA = Quebrada de Damajuana, QVI = Quebrada de Villagra (basado en mapas preparados por Greimler et al. 2002 y Universidad Mayor 2004).

may be dispersed by birds or gravity (Skottsberg 1953). (ii) *Fagara mayu* (Rutaceae), the biggest tree on RCI, reaches more than 30 m height and 200 cm DBH. Its fruit is a hard capsule of ca 6-7 mm in diameter, which contains a seed of 5 mm, dispersed by gravity. It grows up to 600 masl. (Rodríguez et al. 1983). (iii) *Drimys confertifolia* (Winteraceae) grows between 200 and 900 masl. It can reach 15 m height and 50 cm DBH (Skottsberg 1953). Its fruit is a round berry (0.8-1 cm diameter) that contains 14-20 angular seeds of 2.5-3 mm, dispersed by birds or gravity (Rodríguez et al. 1983, Skottsberg 1953).

Forest structural aspects

A 2000 m^2 sample plot (40 m x 50 m) was established at each study site (Fig. 1). In each plot, we registered all trees > 5 cm DBH, considering: species, sociological position (sensu Donoso 1993), DBH, total height, and crown radii projection lengths. Heights were measured with a Suunto® hypsometer. Tree individuals < 5 cm DBH were considered regeneration and classified as sexual (i.e., single seedling or sapling) or vegetative renewal (i.e., clustered, originated from a thicker root or stem base). The coverage of strata was estimated using the average crown radius, assuming circular areas (Donoso 1993).

There is scant age data for RCI trees. Johow (1896) referred to the slow growth of *M. fernandeziana*, pointing out that the annual rings would be about 3 mm wide. Honeyman et al. (2005), using a small sample of cores, found a direct relationship between DBH and age ($r = 0.86$, $P = 0.000$, $N = 9$ for *M. fernandeziana*; $r^2 = 0.98$, $P = 0.008$, $N = 4$ for *F. mayu*; and $r^2 = 0.92$, $P = 0.009$, $N = 5$ for *D. confertifolia*). Sample sizes were necessarily low due to the endangered status of the archipelago flora, and its protection in a National Park (Honeyman et al. 2005). In spite of these restrictions, our interpretation of diameter structures assumed a good correlation with age, taking into account that stand size structures, combined with spatial information, can provide good insights into forest regeneration processes and disturbance histories (Veblen 1992, Salas et al. 2006).

The diameter distributions were tested against three common models in forest dynamics: a negative exponential model ($F = a^* e^{-b^*DBH}$), which applies to a population with constant recruitment and constant mortality rates. A power function model ($F = a^* DBH^{-b}$), which assumes a stable recruitment, but allows a decreasing mortality rate (Hett & Loucks 1976). And a normal distribution model, that applies to a population with episodic recruitment (equation 1) typical for species that need disturbances to regenerate (Veblen 1992, Donoso 1993). The Statistica 6.0 software was used to fit the models through the Levenberg-Marquardt algorithm.

$$(F = 1/(\sigma\sqrt{2\pi}) * e^{-0.5*[(DBH-\mu)/\sigma]2} \qquad [1]$$

F is the frequency in trees per hectare, DBH is the diameter class measured at breast height (in cm), e is the base of the natural logarithms, π is the mathematical constant, a and b are constant values > 0; σ and μ are the parametric standard deviation and mean, respectively.

Tree spatial distribution

We divided the 2000 m^2 plot in 80 squares (5 x 5 m) to facilitate the register of individuals. Every seedling, sapling and tree was recorded to the nearest centimetre using an X, Y coordinate system. We studied the forest spatial arrangement using Ripley's K(t) function (Ripley 1977). This method calculates the distance between all pair of points (plants), and permit to analyse, at different spatial scales, the association within a class of points (e.g., species), and between separate point categories (e.g., between species 1 and 2) (Moeur 1993, Salas et al. 2006). An univariate analysis (null hypothesis of randomness) was conducted, calculating the function L(t), a transformation of Ripley's K(t) function that allows easier interpretations (Salas et al. 2006):

$$L(t) = \sqrt{(K(t)/\pi)} - t \qquad [2]$$

If the tree distribution is random (Poisson distribution), then $K(t) \approx \pi t^2$ and $L(t) = 0$ (Duncan 1991). If the L(t) value < 0, it indicates an uniform or regular horizontal distribution, and if the L(t) value > 0 it indicates that the distribution is clustered or aggregated (Duncan 1991).

We considered the spatial distributions of each tree species independently (*M. fernandeziana, D. confertifolia* and *F. mayu*). For all spatial analysis, groups with less than 8 individuals were not considered (Salas et al. 2006). Due to the major abundance of *M. fernandeziana*, its spatial distribution could be analysed for different sizes (regeneration < 5 cm; small ≥ 5 ≤ 10 cm; intermediate > 10 ≤ 30 cm; and large individuals > 30 cm DBH), and for standing dead individuals.

To further analyse the species regeneration, we carried out a bivariate spatial relationship analysis. We compared the distribution pattern of the large individuals (i.e., tree species independently, > 30 cm DBH), with the regeneration individuals of *M. fernandeziana* and *D. confertifolia* (< 5 cm DBH). Due to sample size restrictions, *F. mayu* regeneration was not analysed. We used the $L_{12}(t)$ function, which is a transformation of the $K_{12}(t)$ function (Salas et al. 2006) to test the spatial independence hypothesis (Duncan 1991). If the $L_{12}(t)$ function value equals zero, the groups are spatially independent; a value > 0 indicates attraction between individuals, and a value < 0 indicates repulsion (Salas et al. 2006). We used Duncan's (1990) spatial distribution programmes for the estimation of K(t). Significant differences were determined between the observed and expected values for a random (univariate) and an independent (bivariate) distribution, generating 99 Monte Carlo simulations to establish the upper and lower confidence envelopes at 99 % (Duncan 1991). The t distances attained a maximum of 20 m (half of the shortest plot side).

Regeneration in gaps

We considered as gaps all openings larger than 25 m , where there was no tree coverage and no direct impediment to solar radiation reaching the forest floor (Veblen 1992). Gap percentage at the landscape level was determined by using three 100 m long transects starting in the centre of each plot with a defined cardinal direction (i.e., adjacent transects were perpendicular between them). Along these transects, the distance below tree coverage was quantified and the occurrence of gaps along the transects recorded. In each study site, we selected one gap visually similar in size and shape to the average gaps observed within the study area (i.e., a 'representative' gap). Inside the expanded gap we recorded the regeneration of trees by direct counting, registering also the main potential successors (i.e., trees > 5 cm DBH, Rebertus & Veblen 1993).

RESULTS

Structural aspects of the Myrtisylva

The montane forest of RCI exhibited a *M. fernandeziana* dominant stratum (16.3 ± 3.5 m height; mean values from all sites ± standard deviation), with emergent individuals of *F. mayu* (24.6 ± 0.9 m). In the intermediate stratum (8.2 ± 2.2 m), *M. fernandeziana* and *D. confertifolia* individuals were found. On occasions, the latter species occupied the codominant stratum (12.3 ± 2.3 m). *M. fernandeziana* also grew in the suppressed stratum (5.2 ± 0.1 m), accompanied in low numbers by *Rhaphithamnus venustus*. *Boehmeria excelsa* and *Coprosma pyrifolia* individuals were also found, mostly in the dominant or codominant strata, but these were rare. *Coprosma oliveri* was occasionally observed, present at very low densities in the intermediate stratum of the upper forest.

The most important species in the Myrtisylva forest was *M. fernandeziana* (Table 1), which contributed most basal area (> 65 %), and stocking density (90 %). *F. mayu* was less frequent but represented > 18 % of the stand basal area (Table 1, Fig. 2). *D. confertifolia* presented between 20 and 60 individuals ha^{-1}, contributing 0.6-8.8 % to the basal area. Less important was *R. venustus*. *Coprosma oliveri*, *C. pyrifolia*, and *B. excelsa* occurrences were rare (Table 1).

TABLE 1

Descriptive variables of the forest tree species on Robinson Crusoe Island (± standard deviation).

Variables descriptivas de las especies arbóreas en los bosques de la Isla Robinson Crusoe (± desviación estándar)

Species/site	Frequency (trees ha^{-1})	Mean quadratic diameter (cm)	Mean height (m)	Basal area (m^2 ha^{-1})	Standing dead individuals (trees ha^{-1})	Canopy cover (%)	Potential successors in gaps (trees ha^{-1})
PLY site							
M. fernandeziana	800	26.1 ± 2.8	13.4 ± 2.5	34.48 ± 2.8	45	173	0
F. mayu	70	57.5 ± 1.9	20.0 ± 0.8	18.18 ± 1.7	5	51	44
D. confertifolia	25	12.6 ± 1.9	8.6 ± 4.1	0.31 ± 0.1	0	4	0
R. venustus	5	6.5	4.5	0.02	0	0.3	0
Total	900	27.4 ± 2.7	12.01 ± 2.6	53.01 ± 2.7	50	228	44
QDA site							
M. fernandeziana	1050	23.6 ± 2.4	11.7 ± 2.8	45.79 ± 4.2	40	144	382
F. mayu	40	60.9 ± 31.2	19.7 ± 7.0	11.66 ± 1.5	10	24	0
D. confertifolia	20	27.4 ± 12.9	10.5 ± 5.6	1.18 ± 0.2	5	0.6	0
R. venustus	35	12.0 ± 3.1	6.1 ± 2.0	0.40 ± 0.1	5	1.5	0
C. oliveri	5	12.0	5.0	0.04	0	0.4	0
Juania australis	0	0	0	0	0	0	64
Total	1150	25.6 ± 2.4	11.8 ± 4.1	59.07 ± 4.2	60	171	446
QVI site							
M. fernandeziana	1155	18.6 ± 2.5	12.9 ± 1.5	31.45 ± 4.2	100	89	361
F. mayu	30	65.7 ± 25.3	14.6 ± 1.1	8.76 ± 1.4	5	14	0
D. confertifolia	60	29.8 ± 1.5	11.4 ± 1.2	4.20 ± 0.6	5	6	0
R. venustus	45	16.3 ± 3.7	7.3 ± 1.5	0.94 ± 0.4	0	2	0
C. pyrifolia	5	30.0	11.0	0.35	0	0.5	0
B. excelsa	5	30.0	11.0	0.35	0	0.8	0
Total	1300	21.5 ± 3.3	10.3 ± 1.73	47.48 ± 4.1	110	112	361

The diameter distributions of the cumulated and single Myrtisylva species followed a negative power curve at PLY (inverse J) (Fig. 2). The diameter trend of *F. mayu* and *D. confertifolia* revealed in all stands an absence of individuals in certain diameter classes. In QDA, the negative exponential model was the best fit for the whole stand and *M. fernandeziana* trees, while *D. confertifolia* fit better the power function, although not significantly (Fig. 2). *Fagara mayu* showed a normal distribution with a reduced fit (r = 0.36). The best models in QVI were the exponential for the whole stand and *M. fernandeziana* individuals; the normal one for *F. mayu,* and the power function for *D. confertifolia*, which was significant (Fig. 2).

M. fernandeziana dominated all sociological strata (Table 2). The only exception was the emergent stratum in PLY, where *F. mayu* prevailed. The relative importance of *F. mayu* increased in the upper sociological positions (dominant, emergent). The QVI site did not present emergents and had less stratification.

Gaps were formed mainly as result of small scale disturbances (tree falls), representing almost one quarter of the forest area in PLY and QDA, but only 8 % in QVI (Table 3).

Tree spatial distribution

The regeneration of *M. fernandeziana* (< 5 cm DBH) showed a clustered distribution (Fig. 3). The small individuals of this species (5-10 cm DBH) presented an inconsistent trend among sectors, tending to aggregation only in PLY. The intermediate individuals of *M. fernandeziana* (> 10-30 cm DBH) distributed

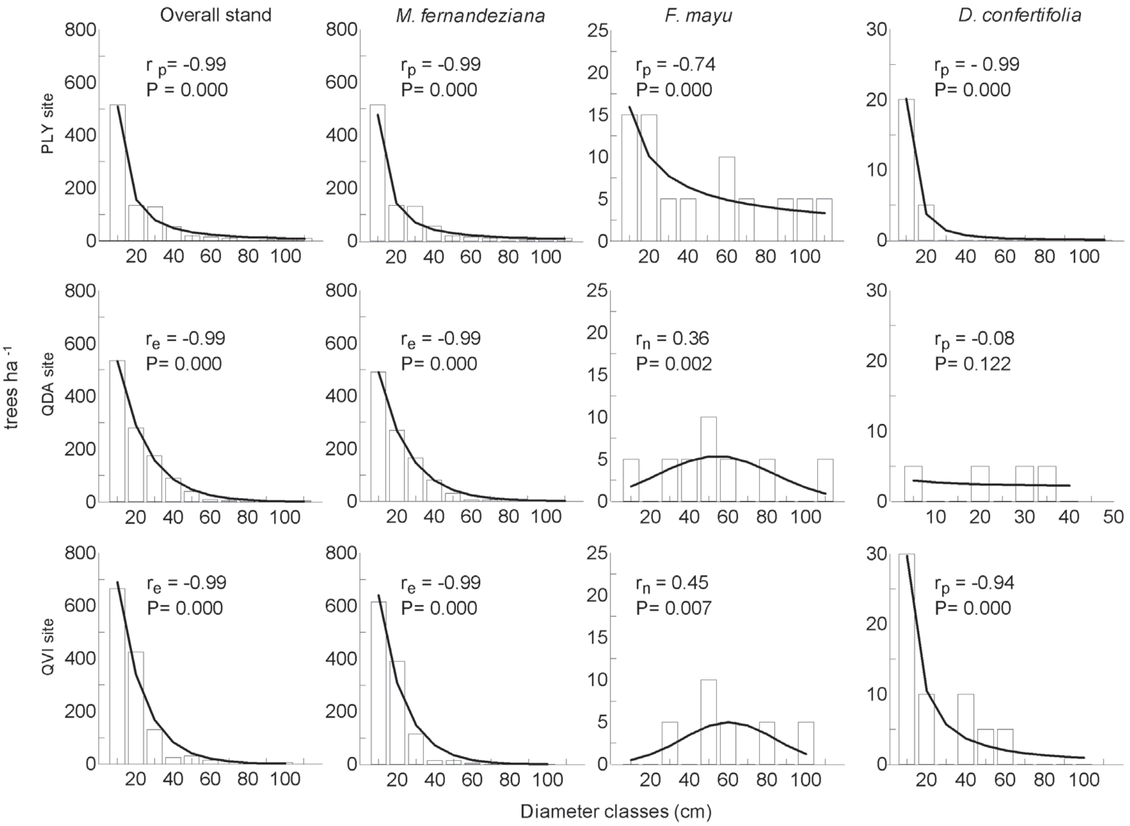

Fig. 2: Diameter distributions of the tree species studied at three locations on Robinson Crusoe Island. The correlation coefficient (r) and the associated probability value (P) for the best fit models are shown (tested models: exponential$_{(e)}$, normal$_{(n)}$, power$_{(p)}$). See Fig. 1 for information about the sites.

Distribución diamétrica de las especies arbóreas estudiadas en los tres sitios de la isla Robinson Crusoe. Se muestra el coeficiente de correlación (r) y la probabilidad asociada (P) para los modelos de mejor ajuste (modelos probados: exponencial$_{(e)}$, normal$_{(n)}$, potencia$_{(p)}$). Ver Fig. 1 para información sobre los sitios.

randomly up to 4 m, tending to aggregate at longer distances in PLY. The larger *M. fernandeziana* specimens (> 30 cm DBH) distributed randomly; only in QVI they were clustered over 5 m. The mortality pattern of *M. fernandeziana* was generally random, although it showed a slight aggregation at short distances in the PLY and QVI sites (Fig. 3). *Fagara mayu* distributed mostly random, showing some aggregation at short distances in QDA and QVI sites (Fig. 4). *D. confertifolia* horizontal distribution presented an aggregated pattern, especially in QDA (Fig. 4).

The spatial association between large individuals (> 30 cm DBH) and the regeneration of *M. fernandeziana* (< 5 cm DBH) was mostly independent in PLY and QDA sectors. In QVI, these groups repelled between 4 and 12 m, the opposite occurred in PLY at larger distances (Fig. 5).

TABLE 2

Frequencies (%) of the principal tree species on each study site according to sociological position.

Frecuencias (%) de las principales especies arbóreas en cada sitio de estudio de acuerdo a posición sociológica.

Species	*M. fernandeziana*			*F. mayu*			*D. confertifolia*			*R. venustus*		
Sociological position/site	PLY	QDA	QVI	PLY	QDA	QVI	PLY	QDA	QVI	PLY	QDA	QVI
Dead trees	90.0	66.6	90.9	10.0	16.6	4.5	0	8.3	4.5	0	8.3	0
Suppressed	97.8	94.8	80.0	0	0	0	0	2.5	20.0	2.2	2.5	0
Intermediate	88.2	92.4	89.2	3.9	1.3	0	7.8	0	6.2	0	6.3	4.6
Codominant	92.1	98.2	92.6	5.3	0	0	2.6	1.8	0.9	0	0	5.6
Dominant	89.3	91.4	81.8	10.7	5.7	9.1	0	2.9	7.3	0	0	0
Emergent	14.3	57.1	0	85.7	42.9	0	0	0	0	0	0	0

TABLE 3

Abundance and origin of the forest regeneration on Robinson Crusoe Island (< 5 cm DBH ha^{-1}).

Abundancia y origen de la regeneración forestal en la isla Robinson Crusoe (< 5 cm DAP ha^{-1}).

Site	PLY		QDA		QVI	
Species/Origin	Seed	Vegetative	Seed	Vegetative	Seed	Vegetative
Under canopy						
M. fernandeziana	4625	430	4934	96	380	5
F. mayu	0	0	0	10	15	0
D. confertifolia	35	5	20	70	17	8
R. venustus	5	0	25	0	20	0
Total	4665	435	4979	176	432	13
Total %	91.4	8.5	96.6	3.4	97.0	3.0
In gaps						
M. fernandeziana	2070	176	892	0	2169	0
F. mayu	1321	88	0	0	0	0
D. confertifolia	1453	748	0	0	0	0
Juania australis	0	0	64	0	0	0
Total	4844	1012	956	0	2169	0
Total %	82.7	17.3	100	0	100	0
Site	PLY		QDA		QVI	
Gap proportion in forest (%)	25.0		27.5		8.0	
Size representative gap (m)	227		157		83	

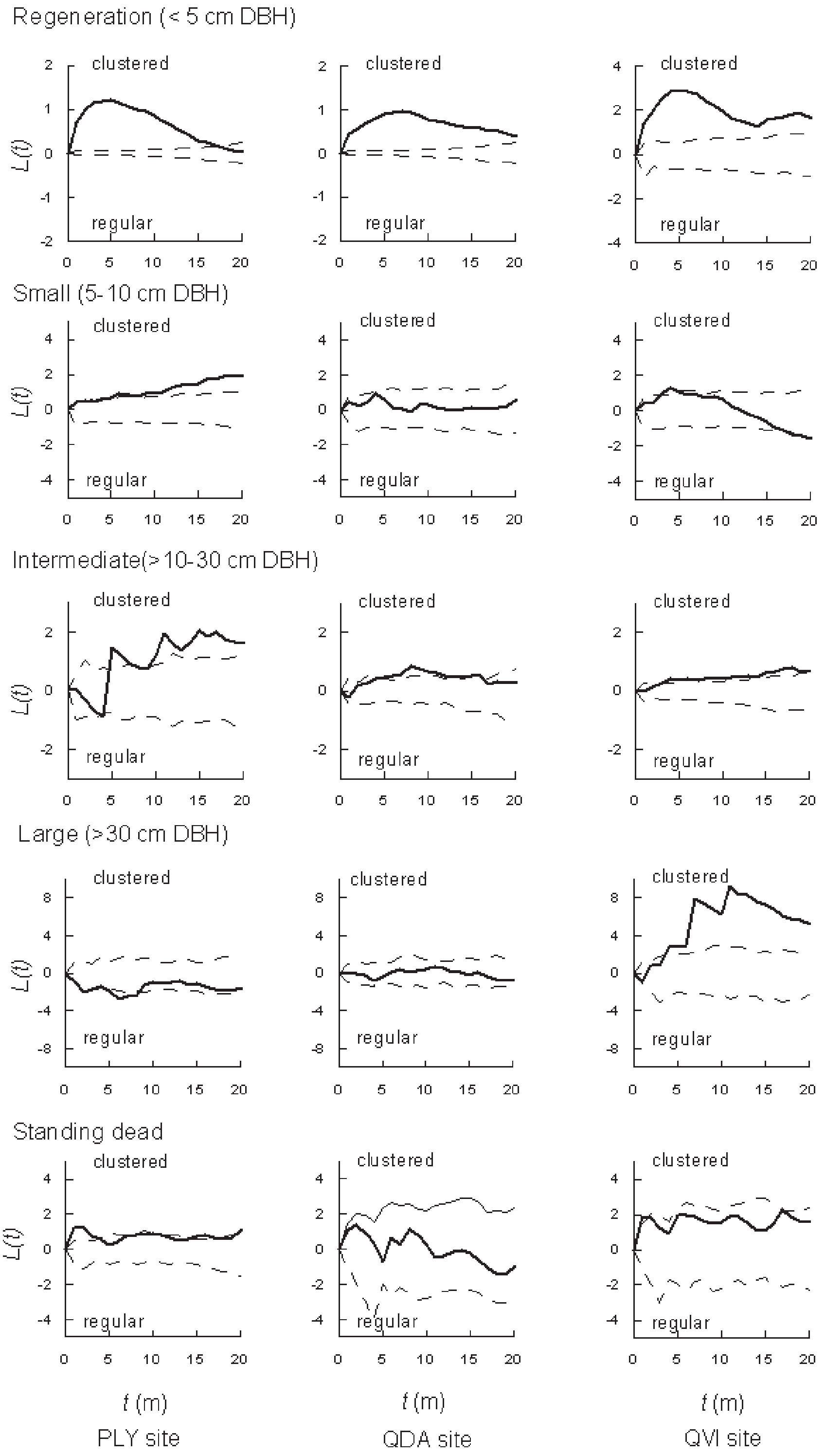

Fig. 3: Spatial distribution (function L(t)) of *Myrceugenia fernandeziana* trees of different diameter categories. The dashed lines represent the confidence envelopes for a random distribution (α = 99 %). See Fig. 1 for information about the sites.

Patrón espacial (función L(t)) de individuos de *Myrceugenia fernandeziana* para diferentes clases diamétricas. Las líneas segmentadas representan las envolturas de confianza para una distribución al azar (α = 99 %). Ver Fig. 1 para información sobre los sitios.

Large individuals of *M. fernandeziana* were, in general, not related with the regeneration of *D. confertifolia*, although slightly in QDA at large distances (Fig. 5). Large trees of *D. confertifolia* were spatially related with the regeneration of *M. fernandeziana* in PLY, but repelled it in QDA and QVI beyond 8 m. The pattern of *D. confertifolia* with respect to its own regeneration showed always a positive relationship between 3-7 m.

The large trees of *F. mayu* showed a slight repulsion towards the regeneration of *M. fernandeziana* between 6-8 m in QVI (Fig. 5). A similar pattern presented the regeneration of *D. confertifolia* at 8-12 m in QDA.

Tree regeneration

The composition of the tree regeneration below canopy was similar in all sites (Table 3). *Myrceugenia fernandeziana* was the most common species, followed by *D. confertifolia* and *R. venustus*. *Fagara mayu* regenerated below canopy only in QDA and QVI. There was no recruitment of *B. excelsa* and *Coprosma* spp. The QVI site presented in average 11 times less regeneration than the other study sectors (Table 3).

Below canopy, the regeneration of *M. fernandeziana* was higher than in gaps at PLY and QDA. *Fagara mayu* regeneration was absent below canopy in PLY, even though in gaps, exceeded 1000 individuals ha^{-1}. *Fagara mayu* did not show regeneration in the gaps of the other sites, and recruited scarcely below canopy (10 to 15 plants ha^{-1}).

Drimys confertifolia presented low recruitment below coverage in PLY, inferior to that observed in gaps. In the other study sites, *D. confertifolia* showed an intermediate regeneration below canopy (90-25 individuals ha^{-1}), with no recruitment in gaps.

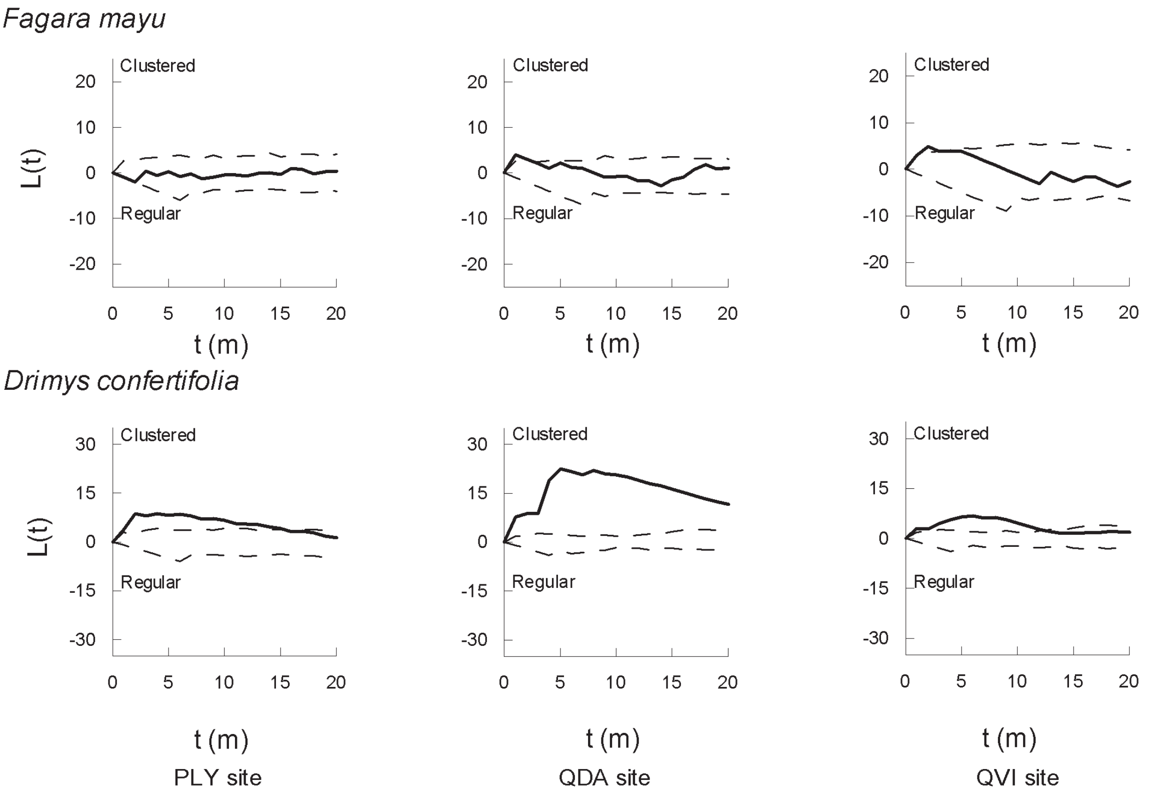

Fig. 4: Spatial pattern (function L(t)) for all individuals of *Fagara mayu* and *Drimys confertifolia*. The dashed lines represent the confidence envelopes for a random distribution (α = 0.99). See Fig. 1 for information about the sites.

Patrón espacial (función L(t)) para todos los individuos de *Fagara mayu* and *Drimys confertifolia*. Las líneas segmentadas representan las envolturas de confianza para una distribución al azar (α = 0.99). Ver Fig. 1 para información sobre los sitios.

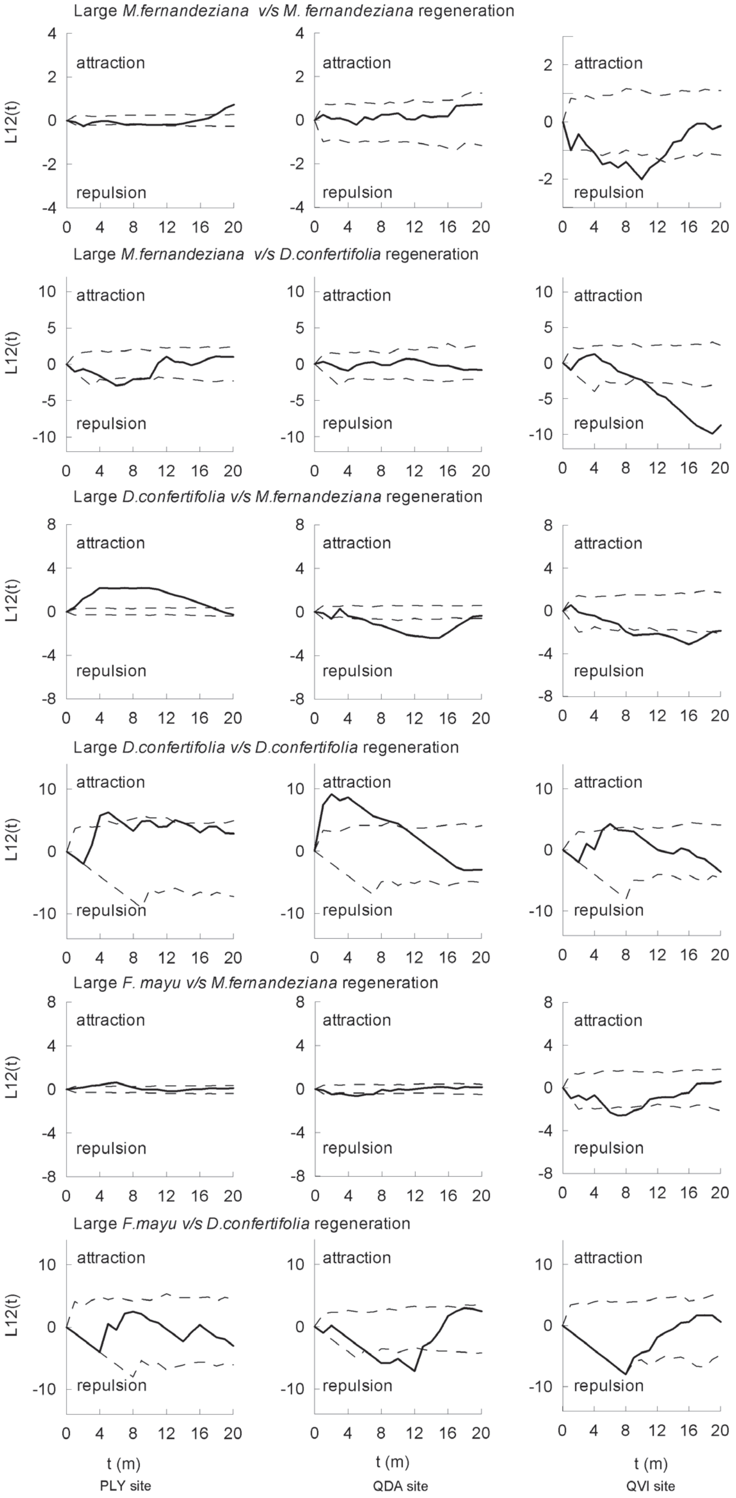

Fig. 5: Association between regeneration (< 5 cm DBH) and large individuals (> 30 cm DBH) of several tree species. The dashed lines represent the confidence envelopes (α = 99 %) for an independent distribution. See Fig. 1 for information about the sites.

Asociación entre la regeneración (< 5 cm DAP) y los individuos grandes (> 30 cm DAP) de varias especies arbóreas. Las líneas segmentadas representan los intervalos de confianza (α = 99 %) para una distribución independiente. Ver Fig. 1 para información sobre los sitios.

Regeneration developed principally from seeds below canopy, particularly that of *M. fernandeziana* (Table 3). *F. mayu* showed 40 % of vegetative plants. Most regeneration of *D. confertifolia* originated asexually below canopy (54 %). *R. venustus* regenerated exclusively from seeds. In gaps, *M. fernandeziana*, *F. mayu* and *D. confertifolia* tended to regenerate sexually (Table 3).

Within the studied gaps, the main potential successors in QDA and QVI belonged to *M. fernandeziana*. *F. mayu* was the only potential replacement species in the PLY gap (Table 1). *D. confertifolia* did not feature as potential successor.

DISCUSSION

Structural aspects of the Myrtisylva

Our findings agree with previous reports that give the following sequence of tree heights and diameters: *F. mayu* > *M. fernandeziana* > *D. confertifolia* (Johow 1896, Skottsberg 1953, Rodríguez et al. 1983). Specimens of *M. fernandeziana* growing > 110 cm DBH have not been reported earlier. Similar stand features were obtained by Cuevas (2001, 2002), based on the analysis of 17 forest areas on RCI. Tree species richness is poorer than that of analogous Pacific island forests such as Lord Howe and Norfolk Islands (Mueller-Dombois & Fosberg 1998) or conifer-broadleaved forests, lowland conifer, and warm-temperate *Nothofagus* forests of New Zealand (Wardle J. 1984, Wardle P. 1991). However, the forest physiognomy does not seem to differ greatly from them (Mueller-Dombois & Fosberg 1998). The gap proportions are in the range of warm temperate forests (Yamamoto 1992). Gaps on RCI forest were formed by the individual trees falling, sometimes causing a small-scale domino-effect, but not as stand-level mortality like the synchronous forest dieback reported for subtropical *Metrosideros*-forests of Hawaii (Hart 2010) or temperate *Nothofagus* forests of New Zealand (Wardle J. 1984).

Myrceugenia fernandeziana diameters always fitted the negative function model, either the exponential or the power functions. Both models usually fit on uneven aged forests that present continuous regeneration (Veblen 1992, Donoso 1993). Although *F. mayu* adjusted to the power function in PLY, generally the distribution can be considered discontinuous given the lack of some diameter classes. The best adjustment to the normal model in QDA and QVI is consistent with a sporadic regeneration strategy that may be triggered by fine scale gaps or larger disturbances such as landslides and blowdowns, which are common on RCI (Castro et al. 1995). The diametric distribution of *D. confertifolia*, fitted significantly the power model in two sites. The recurrent lack of diametric classes suggests that *D. confertifolia* also presents discontinuous recruitment, possibly requiring the occurrence of small gaps.

Tree spatial distribution

The clustered distribution exhibited by the smallest individuals of *M. fernandeziana* may be the result of the species dispersion strategy (hypothesis i). Vargas et al. (2006) stated that *M. fernandeziana* berries are dispersed by either endozoochory or barochory. The only native frugivore on the RCI is the Austral Thrush (*Turdus falcklandii magellanicus*), and given the abundance of fleshy-fruited species, there is probably an excess of food supply for these birds (Skottsberg 1928). *M. fernandeziana* seeds usually germinate inside the fruits (Ricci 1998), and it is unknown whether they can survive the digestive tract of the thrush. Consequently, barochore dispersal of fruits is a probable explanation for the clustering of small *M. fernandeziana* individuals at distances of about 5 m (hypotesis i). We cannot rule out that this pattern could also be the result of distribution of sites suitable for its development. The spatial association between the regeneration of *M. fernadeziana* and the large trees of the same species was generally independent. The regeneration of *M. fernandeziana* showed in several cases a spatial repulsion against the large trees beyond 8 m. Thus, our data does not support a possible nurse effect on the regeneration of *M. fernandeziana* (hypothesis ii). The clustering of *M. fernandeziana* disappeared progressively with increasing diameters, with the exception of the QVI site. This is consistent with results from other forest communities such as the Malaysian rainforest, where a self-thinning effect has been reported (Fangliang et al. 1997) (hypothesis iii). The standing dead individuals of *M. fernandeziana* did not show a considerable deviation from randomness, thus we discard the premise of localized mortality under canopy for this species (hypothesis iv).

Fagara mayu generally showed a random spatial pattern. At two study sites, the individuals of this species clustered slightly at short distances. Barochore dispersion may explain this pattern, given the fruit characters not eaten by birds (Bannister et al. 2006) (hypothesis i). This aggregated pattern of *F. mayu* could also be explained by local disturbances as gaps (Salas et al. 2006), but we cannot support this premise based only on the spatial data of the species (hypothesis iv).

Considering the fruit characters of *D. confertifolia*, its spatial grouped pattern might be indicative of zoochory. *Drimys confertifolia* seeds would be strong enough to survive to the thrush's digestive tract (Skottsberg 1928). Nevertheless, it is easy to find numerous fruits laying on the forest litter (personal observations), indicating that birds do not consume all fruits. *Drimys confertifolia* presents germination difficulties without seed stratification (Cuevas & Figueroa 2007). Accordingly, birds could improve dispersal, and probably germination chances through endozoocory (hypothesis i). The vegetative reproduction was recurrent for *D. confertifolia,* and may also contribute to the clump generation (Oliver & Larson 1990). *Drimys confertifolia* regeneration was spatially and positively related with the large trees of the same species, which suggests an intra-species nurse effect (hypothesis ii). The clumped pattern of *D. confertifolia* could also be explained by the limited area of sites suitable for its recruitment, like canopy gaps (hypothesis iv). In continental Chile, *Drimys winteri* seems to present a similar behaviour in primary forests, where the species requires space for its development, but present dispersal limitations that links its recruitment with mother trees (Donoso et al. 1984, Lusk 1996).

Tree regeneration strategies

M. fernandeziana regeneration was considerably higher below canopy than in gaps, with one exception at the QVI site. Thus, *M. fernandeziana* seems to show a plastic behaviour, from tolerant to shade to shade intolerant. The shade tolerance is consistent with the continuous regeneration suggested by the diameter structure of the species, which reflected common features of multilayered, uneven aged forests (Donoso 1993). The good germination of this species, at least under laboratory conditions (Ricci 1998), and its regeneration plasticity might explain its higher abundance in the Myrtisylva. In continental Chile, *Myrceugenia planipes* possess a high degree of shade tolerance, although it may colonise open fields (Donoso 2006a), and it exhibits an inverted J-shaped diameter distribution (Donoso et al. 1985). *Myrceugenia exsucca* (Donoso 2006b) and *M. ovata* (Donoso 2006c) show similar characteristics, and the latter species establishes also in gaps (Armesto & Fuentes 1988). Then, the regenerative behaviour of *M. fernandeziana* looks similar with its continental relatives.

There was no regeneration of *F. mayu* below canopy in PLY, whereas in gaps it exceeded 1000 individuals ha^{-1}. *F. mayu* did not regenerate in the gaps present at the other sites (smaller than the PLY gap), but there was scant recruitment of this species below the canopy. These antecedents, in addition to *F. mayu*'s diameter distribution, are characteristics of species with sporadic regeneration (Veblen 1992, Donoso 1993). The lack of individuals in some diameter classes is likely due to the absence of canopy openings during a certain period. Seed cycles and restrictions in dispersal and germination may also impose additional regeneration discontinuities. Seeds require acid scarification to germinate (Ricci 1998), and they are not dispersed by birds (Bannister et al. 2006). The relative importance of *F. mayu* increased towards the upper sociological strata (dominant, emergent). This indicates the species' shade intolerant nature. The superficial root system (Rodríguez et al. 1983, Bannister et al. 2006) and shade intolerance are also typical characteristics of pioneer species (Oliver & Larson 1990). The species' dependence on open areas might be responsible in part for its minor abundance relative to *M. fernandeziana*, where *Myceugenia* does not need to "wait" for the occurrence of gaps in order to recruit. Studies of other *Fagara* species worldwide (i.e., *F. ailanthoides* in Japan) have revealed a direct relationship between gaps and its occurrence, with *F. ailanthoides* considered to be a pioneer species requiring large disturbances to regenerate (Tanouchi & Yamamoto 1995).

D. confertifolia regeneration in PLY was considerably lower below the canopy than in gaps. In QDA and QVI, *D. confertifolia* exhibited a reduced self-replacement under canopy, with no regeneration in gaps. The species presented a semi-continuous diameter distribution. *Drimys confertifolia* individuals were observed growing in areas where the canopy coverage was lower (semi-shade). Like *M. fernandeziana*, the species would also benefit from the protection granted by other higher plants at early stages (Cuevas & Vargas 2006). In continental Chile, *Drimys winteri* var. *chilensis* and var. *punctata* (Donoso et al. 2006) exhibit pioneer behaviour in open forests (Corvalán et al. 1987), requiring semi-shade to establish (Lusk 1995). The *punctata* variety regenerates below the canopy and responds rapidly to gap formation (Rebertus & Veblen 1993). Thus, *D.winteri* and *D. confertifolia* match, both exhibiting a dual mode of regeneration, in semi-shade and in gaps, which is indicative of a semi-shade tolerant species.

Concluding remarks

We studied the spatial patterns of the main endemic trees of RCI. We related their spatial patterns with their regeneration strategies considering: seed dispersal, nurse effect, self-thinning and localized disturbances. Barochory and endozoochory reflected particularly in the clumped pattern of *M. fernandeziana* and *D. confertifolia*. Intra-specific nurse effect was suggested in the case of *D. confertifolia*. Self-thinning was suggested for *M. fernandeziana*. Localized disturbances like gaps appear to determine the occurrence of *F. mayu*, and may influence positively the recruitment of *D. confertifolia* and *M. fernandeziana*.

This information acquires interest considering the conservation problems affecting the Myrtisylva of RCI. Currently the action of alien invasive species (principally *R. ulmifolius* and *A. chilensis*) leads actively a process of novel forest formations (Dirnböck et al. 2003). Structural parameters of original forest remnants should be used as a reference to guide recovery activities. Detailed ecological studies considering light, soil, micro-site characters and the influence of invasive species over the natural regeneration of this forest seem urgent to further develop effective conservation measures.

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