Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population

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Summary

1. Seed dispersal is considered critical for shaping the spatial structure of plant populations, though little empirical effort has been made to interpret this effect in terms of the scale at which plant species are distributed and cope with environmental heterogeneity. We assessed the spatial role of seed dispersal in *Tristerix corymbosus*, a mistletoe dispersed exclusively in the temperate forests of Patagonia by the endemic marsupial *Dromiciops gliroides*.

2. We examined how fruit resource tracking and seed dispersal by the marsupial affects mistletoe recruitment, employing a spatially explicit approach aimed at breaking down the spatial structure of the mistletoe and marsupial populations at different scales.

3. In a single fruiting season, we evaluated the abundance of mistletoe fruits, adult plants, dispersed seeds and recruits (seedlings and saplings), as well as the abundance of marsupials, along a 1500-m linear transect.

4. Both mistletoe and marsupial abundances were distributed hierarchically in space, with large patches containing smaller ones. Marsupial patchiness matched that of mistletoe fruits, at least at a broad scale within the transect. Marsupial abundance also varied at a large-scale, being conditioned by habitat features and decreasing progressively along the transect. Mistletoe seed rain accounted for the patchiness of adult plants and fruits, and for the large-scale pattern of marsupial activity. The spatial pattern of mistletoe recruitment closely matched seed rain.

5. *Synthesis.* Seed dispersal by marsupials shaped the scale of mistletoe recruitment in two ways. First, marsupials created a spatial match between mistletoe adults and recruits as a result of fruit resource tracking. Second, they generated patchiness in mistletoe offspring at a larger scale than in adults. Dispersal process performed as a strong demographic filter capable of changing the mistletoe spatial structure from adults to recruits, despite a low frequency of far-from-adult dispersal events. Similar effects of scale shaping by seed dispersers may be generalized among plants in which there is a sharp spatial match between fruits and frugivores, and whose dispersed seeds have a higher probability of recruiting than undispersed ones.

Key-words: *Dromiciops gliroides*, fruit resource tracking, principal coordinates analysis of neighbour matrices, recruitment, spatial patchiness, southern Argentina, *Tristerix corymbosus*

Introduction

Seed dispersal spatially links adult plants and their offspring. The physical dimension and the directionality of the movement of seeds far from their parent plants are expected to determine the spatial structure of plant populations (Nathan & Müller-

Landau 2000; Wang & Smith 2002). Seed dispersal may affect the distribution of recruitment within populations (Schupp & Fuentes 1995; García *et al.* 2005), the total area occupied by a plant population or metapopulation (Freckleton & Watkinson 2002; Purves & Dushoff 2005), and the geographical range of a species (Nathan 2006). From a functional perspective, seed dispersal may constrain the range of environmental heterogeneity encountered by a plant species along its life cycle (Snyder & Chesson 2003; Gómez *et al.* 2004). Integrating spatial and functional effects, seed dispersal may be viewed as

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the process that shapes the spatial scale at which plant species function, that is, the spatial extent over which plant population processes operate and over which plant species cope with heterogeneity. Despite this integrative potential, the concept of seed dispersal as a major moulder of a plants' spatial scale has seldom been applied (but see Kollmann 2000; Fragoso *et al.* 2003).

A preliminary step in understanding the effects of seed dispersal with regard to scale is to describe seed deposition patterns in terms of patchiness, that is, spatial aggregation, as seed patch size is a primary constraint of the spatial extent of recruitment (Fragoso 1997; García *et al.* 2005). Seed patchiness is assumed to be strong and deterministic in animal-dispersed plants, as it derives from two complementary mechanisms. First, seeds are frequently dispersed together through sharing a dispersal bout', such as the unitary dropping of a frugivorous bird or the unitary catch of a scatter-hoarding rodent (Jordano 2000; Schupp *et al.* 2002). Second, many seeds are deposited cumulatively at specific locations which are collectively and/ or repeatedly used by animals during and after foraging for fruits and/or seeds (Schupp *et al.* 2002). Many animals tracking fruits and seeds spend considerable time in the canopy of fruiting plants or nearby, thereby generating high-density clumps of dispersed seeds beneath or around adult plants (Peres & Baider 1997; Jordano & Schupp 2000; Russo & Augspurger 2004). Additionally, some dispersers may generate seed clumps in locations far away from adult plants, but spatially associated with perching structures, resting sites, heterospecific fruiting canopies and latrine areas (Fragoso *et al.* 2003; García *et al.* 2007; Jordano *et al.* 2007). Since fruiting plants and the structures used by seed dispersers may themselves exhibit a patchy structure (e.g. trees within forest stands across the landscape; García & Ortiz-Pulido 2004), seed patchiness may occur in a hierarchical fashion, with small patches nested within larger patches (i.e. hierarchically-nested or multi-scaled spatial patchiness; Kotliar & Wiens 1990).

Despite the above-mentioned findings, it remains unclear how the patchiness in animal-generated seed rain influences the spatial scale of recruitment (Fragoso 1997; Aukema 2004). One approach to this question has been to explore the occurrence of a positive spatial feedback between adults and their offspring, that is, a spatial matching between fruiting adults and recruitment resulting from disproportionate dispersal close to adults, coupled with disproportionate establishment in high-density seed clumps (Aukema & Martínez del Río 2002; Carlo & Aukema 2005). It may, in fact, be seed dispersers that govern this feedback by determining the relative importance of seed clumping near to, and far from, adults. For example, lowly mobile vertebrates, such as territorial birds or small rodents, disperse the majority of seeds of certain plants under the canopies of adult individuals, determining that the spatial extent occupied by recruits would seldom exceed that of adults (Wenny 2000; García & Houle 2005). However, other highly mobile frugivores, such as tapirs and monkeys, disperse a significant proportion of seeds of some plants to sites far from adults, potentially enlarging the population extent from adults to recruits (Fragoso 1997; Russo & Augspurger 2004).

Nevertheless, a complete understanding of how seed dispersal by animals affects the spatial scale of plant populations needs to go beyond checking the adult-to-recruit spatial feedback. We need mechanistic approaches that link plant recruitment patterns to the activity of animals when tracking spatially-heterogeneous fruit resources (Carlo & Morales 2008). We also need spatially explicit approaches (Overton 1996; Aukema 2004; Russo & Augspurger 2004) to dissect and correlate the spatial variability of both plant and seed disperser populations along gradients of scale.

Fleshy-fruited, parasitic mistletoes and the frugivorous vertebrates that disperse their seeds are ideal systems for testing hypotheses regarding the spatial consequences of seed dispersal (e.g. Overton 1994, 1996; Aukema & Martínez del Río 2002; Carlo & Aukema 2005). Mistletoes are plants for which there is a strong likelihood of spatial concordance between the activity of seed dispersers and recruitment, because undispersed seeds do not germinate or become established (Reid 1991; Ladley & Kelly 1996; Watson 2001), and seed dispersal is spatially directed to host plants, which represent the only microsite for recruitment (Reid 1991; Aukema & Martínez del Río 2002). In addition, the spatial structure of mistletoe populations is frequently contagious at different scales, as it results from aggregated dispersal within host plants and within neighbourhoods of hosts (Aukema 2004; Carlo & Aukema 2005). Taking into account these features, we evaluated the role of seed dispersal in shaping the spatial scale at which a mistletoe population functions. We studied the mistletoe *Tristerix corymbosus* and its obligate seed disperser, the endemic marsupial *Dromiciops gliroides*, in a temperate forest of Patagonia. Using a spatially explicit, multi-scaled approach, we aimed to address the following questions: (i) How similar are the patterns of spatial aggregation of the abundance of mistletoe adults, fruits, dispersed seeds and recruits, and those of frugivorous marsupials, at different scales? (ii) Do frugivorous marsupials track mistletoe fruits at different spatial scales? (iii) If so, does the scale-dependent spatial structure of mistletoe recruitment relate to the patterns of seed dispersal generated by the marsupial when tracking fruits?

Methods

STUDY SYSTEM

Tristerix corymbosus (L.) Kuijt ('quintral', Loranthaceae) is a shrubby mistletoe distributed along the Pacific rim of South America from 32° to 42° (Kuijt 1988). It parasitizes more than 30 different woody species in the temperate forests of Patagonia, but its main hosts are understorey trees and shrubs, such as *Aristotelia chilensis*, *Azara microphylla* and *Maytenus boaria*. This mistletoe flowers from March (austral fall) to November (austral spring), and is pollinated by the hummingbird *Sephanoides sephaniodes* (Aizen 2003). During the austral summer (December to March), flowers mature into 1×0.6 cm green pseudoberries, each containing a 'naked' seed, 0.7 cm long, surrounded by a sweet, viscous and sticky pulp (Amico & Aizen 2000). Reproductive individuals may bear hundreds of berries (average crop size per individual plant is 780 fruits; Rodríguez-Cabal *et al.* 2007). Fruits senesce on the plant after 2–3

weeks if they are not removed. Senescent fruits are not removed because they have a wrinkled pericarp and a bitter pulp. Ripe fruits are consumed in low proportions by the bird *Phrygilus patagonicus*, which is a pre-dispersal seed predator, and anecdotally, by some frugivorous birds species (Amico & Aizen 2005). The almost exclusive legitimate seed disperser of this mistletoe in the temperate forests is the arboreal marsupial *Dromiciops gliroides* Philippi (monito del monte', Microbiotheridae, Amico & Aizen 2000). The marsupial behaves as a specialized frugivore during the mistletoe fruiting season, consuming massive amounts of mistletoe fruits during the austral summer. It defecates the soft mistletoe seeds undamaged, triggering the germination of the seeds (Amico & Aizen 2000). Almost all dispersed seeds germinate, independently of the substrate in which they are deposited, but only seeds germinating on host plants are able to establish as seedlings (Amico 2000).

STUDY SITE

The present study took place in the Reserva Municipal Llao-Llao, a protected forest area 25 km west of San Carlos de Bariloche, Argentina (41°8′ S, 71°19′ W). The native forest vegetation in the area belongs to the South American Temperate Forest of the Subantarctic biogeographical region (Mermoz & Martín 1986). The predominant tree species are the evergreen southern beech *Nothofagus dombeyi*, and the cedar *Austrocedrus chilensis*. Average tree cover in the reserve is *c.* 72% (Amico *et al.* 2008). The understorey is dominated by the bamboo *Chusquea culeou* and the shrub *Aristotelia chilensis* (*c.* 31% and 27% of understorey cover, respectively). The two forest layers are well differentiated, with tree canopy reaching up to 40 m in height and understorey reaching up to 7 m in height.

SAMPLING OF MISTLETOES

We conducted field work between mid January and early April 2005. This temporal window covered almost a whole season of interaction between the mistletoe and the marsupial, because the marsupial hibernates during winter and the mistletoe's main fruiting season is late summer (Aizen 2003).

We sampled the abundance of mistletoes in a linear transect of 1500×20 m (established in January 2005), which crosses the reserve following a straight trail. The transect was subdivided into 75 contiguous 20×20 m plots. Differences in altitude of the plots along the transect were < 100 m. Each 20×20 m plot was divided into eight subplots (5×10 m) that covered the whole area (four at each side of the trail). For sampling, we chose four non-adjacent subplots in each plot, sequentially alternating the left and right sides of the trail. In these subplots, we visually estimated the canopy cover (percentage) of each tree species (woody plants ≥ 10 m tall) and understorey species (woody plants ≤ 10 m tall, including tree saplings), as well as the total cover of tree canopy and understorey.

We assessed the abundance of established mistletoes in January 2005, by counting the number of individuals in each sampling subplot. For each individual, we recorded the host species and the presence of flowers and fruits, and visually estimated the crown diameter. Flowering frequency for plants with crown diameters ≤ 0.2 m was 0.17, whereas for plants with diameters > 0.2 m it was 0.82 ($N = 329$ plants). Thus, we considered an adult to be a flowering or fruiting mistletoe of any size, or any individual of diameter larger than 0.2 m. The abundance of mistletoe adults per plot was calculated as the cumulative number of adult plants in all four subplots. We counted the number of mistletoe adults per individual host plant, to calculate the intensity of infection (average number of mistletoe per host plant). We also counted the number of host plants parasitized by the mistletoe and the total number of individuals of the potential host species, to calculate the infection rate (proportion of individuals parasitized by the mistletoe) for different host species. We visually estimated the crop size of all mistletoes in mid January, by means of a Fruiting Abundance Index (FAI; Saracco *et al.* 2004) considering five values: 0 = without fruits; 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10 000. We calculated the cumulative abundance of mistletoe fruits per plot as the sum of individual FAIs from all four subplots.

We estimated the abundance of dispersed mistletoe seeds and recruits in the second week of March 2005, by selecting, for logistical reasons (see *Sampling of marsupials*), the two central subplots in each plot. We visually established five cylindrical volumes of 1-m diameter and 3-m height from the ground, randomly located and perpendicular to the ground in each subplot. The basal area of the cylinders represented 8% of the area of the subplot. We counted all seeds and seedlings present within each cylinder. Marsupial-dispersed seeds are easily distinguishable, as they occur in marsupial faeces forming characteristic necklaces' of peeled seeds glued to the bark of woody plants, and develop a typical holdfast (i.e. haustorial connection) after rapid germination (Amico & Aizen 2000). We considered both seedlings (established from seeds dispersed in the previous year and distinguishable by the presence of a first pair of leaves) and juveniles of crown diameters of < 0.2 m as mistletoe recruits. The abundances of dispersed seeds and mistletoe recruits were calculated on a per plot basis by averaging abundance values from the ten cylinders in the two subplots.

SAMPLING OF MARSUPIALS

We sampled the presence and abundance of the marsupial by live-trapping methods. We placed one Tomahawk-style trap in each of the two central subplots in each plot along the transect ($N = 150$ traps). We chose systematic sampling of the two central subplots of each plot, instead of random subplot sampling, to facilitate fast trap retrieval and subsequent delivery of animals trapped in surveys. Each trap was fixed on a branch of the shrub closest to the centre of the subplot, and placed 1–2 m above the ground. Traps were baited daily at dawn (with fresh apple and banana), over three sampling events between late January and early March in 2005; each event lasting three to four nights and separated in time by 6–7 days. We checked the traps daily before dusk. All trapped marsupials were marked with an individual code, based on ear perforations, and then released at the point of capture. We also noted the presence of faeces containing mistletoe seeds in all traps visited by marsupials. Recaptures were noted in subsequent trapping periods. The difference in the position of capture between successive recaptures was used to calculate the minimum distance travelled by individual marsupials. We summed the number of captures per plot across all surveys. This sum may include records corresponding to the same individual in the same location but collected in different surveys. Nevertheless, we considered the sum of captures to be an accurate parameter for evaluating spatial distribution because it is the best estimate of the probability of occurrence of the species in a given sampling location. We thus considered the sum of captures to represent the abundance of marsupials in the transect area. Previous work has also shown the usefulness of marsupial abundance as a surrogate for marsupial frugivore activity (Rodríguez-Cabal *et al.* 2007).

Data analysis

We sought to examine the multi-scaled spatial structure of both mistletoe and marsupial abundances by evaluating their spatial patchiness at different scales (i.e. by examining the number and the shape of the patches along the transect) as well as by breaking down their spatial variability at different scales. We considered that the mistletoe and/or marsupial abundances presented a hierarchically nested patchiness when these variables presented aggregated spatial structures along a hierarchy, or gradient, of scales, with larger patches containing smaller ones (Borcard & Legendre 2002). In analytical terms, the hierarchical patchiness corresponds to the well defined allocation of the spatial variance of these variables at several scales along the gradient (Borcard & Legendre 2002).

Before analyses, definitions of the spatial framework and the gradient of scales covered by the study are needed. Our sampling framework was a 1500 m linear transect with 75 equidistant sampling points, in which all sampled biological variables were spatially referenced to the one-dimensional geographic coordinate of the centroid of the plot (i.e. the distance along the transect; the first plot referring to 0, the second plot to 20 m, ... , and the last plot to 1480 m). We considered that the unidimensional structure of the framework was not a handicap in detecting patchiness in the ecological objects of interest (mistletoes and marsupials). We assumed that the processes underpinning the patterns of patchiness were isotropic, and that the spatial resolution of the sampling scheme (it covers a large extent, 1500 m, with a fine grain, 20 m, that is, the length of the distance between plot centroids) was strong enough to detect patchy distributions in all the ecological variables of interest. The gradient of scales under study ranged from the spatial dimension represented by the transect grain (20 m, the distance between plot centroids) to that represented by the transect extent (1500 m). For logistical reasons, our design was unable to cover the variability operating at the fine scale defined by the extent of the individual host plant (only the presence of mistletoe adults and fruits was referenced to individual host plants). Nonetheless, this limitation was not considered a handicap to a rigorous checking of our main hypotheses, since we would still deal with a large gradient of scales previously demonstrated to account for a large portion of spatial variability in mistletoes (Aukema 2004; Carlo & Aukema 2005).

We first addressed the existence of a spatial structure at the largest scale potentially represented by the sampling design, that is, the whole sampling extent, by checking the presence of significant linear trends in the mistletoe and marsupial abundances along the transect. Significant linear trends are indicative of progressive, lineal increases or decreases of abundance of mistletoes and marsupials along the transect and, at the same time, of patches of abundance that are even larger in size than the whole sampling extent (Legendre & Legendre 1998; Borcard *et al.* 2004). Linear trends were checked by means of simple regressions fitting the log-transformed abundances of mistletoes and marsupials to the spatial coordinate of each plot. The representation of the predicted values of these linear trend models along the transect (i.e. the regression lines) were used to interpret gradient-like spatial structures of the abundances of mistletoes and marsupials. The coefficients of determination (R^2) of the linear trend models were considered to represent the percentage of spatial variance of the abundances of mistletoes and marsupials accounted for by these gradient-like structures.

Having detected linear structures, we were interested in identifying the spatial structure of mistletoe and marsupial abundances across a gradient of scales arbitrarily defined *within* the sampling scheme. For this, we first detrended the abundances of mistletoes and marsupials from any significant linear trend, and calculated the residuals of the regression fit of these response variables to the plot coordinate. We then used these detrended abundances in a principal coordinates of neighbour matrices analysis (PCNM; Borcard & Legendre 2002). The PCNM analysis is a tool for identifying relationships between ecological descriptors (e.g. abundance) and environmental factors (e.g. resource availability) at multiple spatial scales by, first, identifying significant spatial structures in the ecological descriptors along the gradient of these scales and, second, relating the form of these scale-specific spatial structures to environmental factors (Borcard *et al.* 2004, see also application in Ramette & Tiedje 2007). We preferred PCNM to other multi-scaled methods, such as bivariate point-pattern statistics (e.g. Watson *et al.* 2007), because our study was designed to sample quantitative values of different variables (e.g. the abundance of mistletoe adults) in a group of georeferenced observation points, and because we were interested in simultaneously checking the scale-dependent response of a given ecological descriptor to more than one ecological conditions (see next Section). The PCNM is based on four main steps (Fig. 1):

Step 1: Creating a set of spatial variables, called Principal Coordinates Vectors (PCNM vectors) that represent all spatial scales that the sampling scheme (in our case, a linear transect of equidistant points) could perceive. These PCNM vectors are positive eigenvectors obtained from applying an ordination procedure to the truncated matrix of Euclidean distances between all sampling points. For our linear transect, the PCNM vectors are a series of 50 sine waves with progressively decreasing periods. When plotted against the distance along the transect, they represent templates of periodic patches at different scales, from the broadest patches of *c.* 750 m diameter (PCNM 1) to the finest patches of *c.* 65 m diameter (PCNM 50). Vectors were generated using SpaceMaker 2 software (Borcard & Legendre 2004).

Step 2: Using the PCNM vectors to detect the predictable and scale-dependent spatial variability in any biological variable within the sampling scheme. For this, all PCNM vectors are used as explanatory variables in a multiple regression model for each response variable of interest (in our case, the abundances of mistletoes and marsupials; detrended after linear
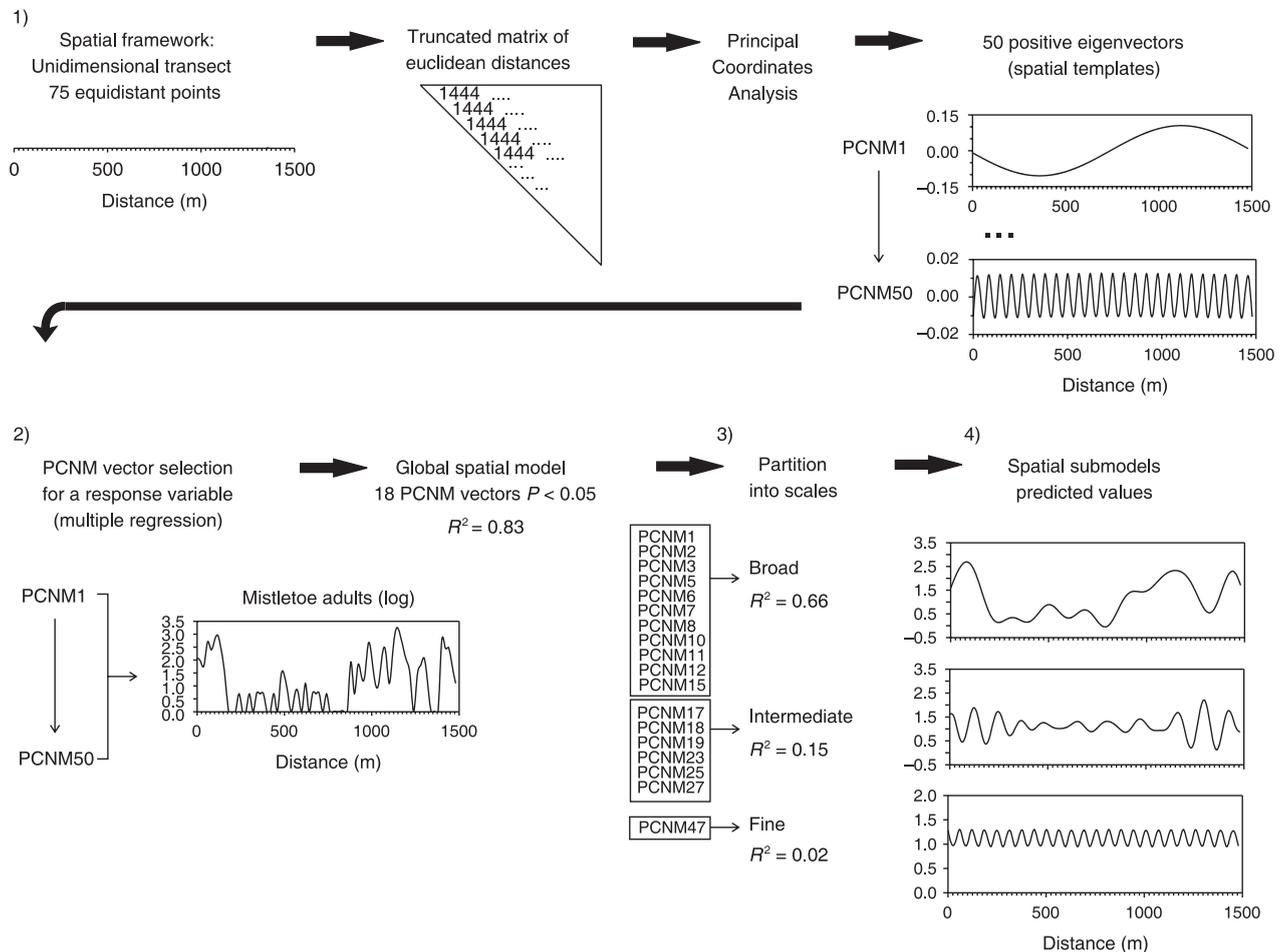
Fig. 1. Representation of the four steps (1–4, see also main text) of the PCNM procedure considering the sampling scheme of the unidimensional linear transect with 75 equidistant points, and the log-transformed abundance of adults of *Tristerix corymbosus*, as response variable.

fit, or log-transformed if not strictly normal). The PCNM vectors that show significant partial regression fits are considered as the templates that account for any significant spatial variance in the response variable. These significant PCNM vectors are therefore selected to build a global spatial model, whose coefficient of determination (R^2) indicates the percentage of spatial variance accounted for along the complete gradient of scales of analysis (i.e. the predictable spatial variability of the response variable within the spatial framework).

Step 3: Arbitrarily partitioning the global spatial model for a given response variable (i.e. the abundances of mistletoes and marsupials) into several additive submodels, which account for the spatial variability at different spatial scales within the extent of the sampling scheme. Here, significant PCNM vectors were assigned to three groups representing three equitable sections of the gradient of scales of analysis: *broad* scale (including significant vectors among the first 16 PCNM vectors, which represented progressively smaller patches from *c.* 750 to 180 m diameter); *intermediate* scale

(significant vectors from PCNM 17 to 34, which represented patches from *c.* 170 to 80 m diameter); and *fine* scale (significant vectors from PCNM 35 to PCNM 50, which represented patches from *c.* 75 to 65 m diameter). These spatial submodels were also multiple regression fits that considered the selected PCNM vectors as explanatory variables, while also providing additive coefficients of determination reflecting the percentage of spatial variability in the response variable accounted for by each portion of the gradient of scales.

Step 4: Calculating the predicted values of a given response variable (i.e. the abundances of mistletoes and marsupials) corresponding to each spatial submodel, for all points in the sampling scheme (i.e. all equidistant points in the transect). These predicted values may be considered as surrogates of the variability of the response variable at a given, specific, spatial scale. When plotted against the distance along the transect, these predicted PCNM values may be used to interpret the shape of patches, in terms of both magnitude (height of the peak) and spatial dimension (extent on the *x*-axis) of the response variable at different spatial scales.

We evaluated the scale-dependent role of seed dispersal by marsupials in creating the spatial structure of the mistletoe by developing four mechanistic hypotheses, which were sequentially checked at different spatial scales. Each hypothesis related a group of explanatory variables to one of the following response variables: the abundance of mistletoe adults, the abundance of marsupials, the abundance of mistletoe seeds dispersed and the abundance of mistletoe recruits. We verified the hypotheses by using causal modelling and path analysis (Legendre & Legendre 1998), which allowed the various direct and indirect causal relationships between a group of predictor variables (e.g. habitat features, resource availability) and a target variable (mistletoe and marsupial abundances) to be explored simultaneously. This method also permitted consideration of colinearity among explanatory variables, as it provided path coefficients representing the individual effect of a given variable and took into account the potential effect of the remaining ones. We formally stated a set of *a priori* causal links between the explanatory variables and the response variables, developing the following hypotheses (see also Fig. 4 in *Results* section):

1. Effect of resources on the abundance of mistletoe adults. We evaluated whether the abundance of established mistletoes was related to the long-term availability of resources, that is, light and host plants (Hoffman *et al.* 1986). For this, we built a path model that considered the forest canopy cover (an inverse measure of light availability in the understorey) and the cover of host species as explanatory variables, the potential link between them, and the abundance of mistletoe adults as response variable.

2. Fruit tracking by marsupials. The abundance of marsupials may be positively affected by mistletoe fruit availability (fruit resource tracking), but also by habitat structural features, such as the availability of forest (Rodríguez-Cabal *et al.* 2007) and of bamboo (a resource for den location and nest building; Jiménez & Rageot 1979). We thus related forest canopy cover, bamboo cover and mistletoe fruit abundance to the abundance of marsupials. We also considered the links between canopy cover and bamboo cover, and between forest cover and mistletoe fruit abundance.

3. Effect of fruit tracking on seed dispersal. We sought to explain the spatial patterns of seed dispersal as a function of the fruit-resource tracking by the marsupials. We built a path model considering the abundances of mistletoe fruits and marsupials as explanatory variables, the link between them and the abundance of dispersed mistletoe seeds as the response variable. We considered the variation in seed dispersal accounted for by the abundance of fruits to represent the effect of the marsupial when tracking mistletoe fruits. Similarly, the variation accounted for by the marsupial abundance alone represented the effect of the marsupial activity independent of fruit tracking.

4. Spatial feedback between mistletoe adults and recruits. We aimed to explain the patterns of recruitment as a function of the spatial structure of mistletoe adults and of seed dispersal. The path model considered the abundances of mistletoe adults and dispersed seeds as explanatory variables, the link between them and the abundance of mistletoe recruits as the response variable. We assumed that a positive effect of adult abundance on recruitment represented the positive spatial feedback caused by the marsupial when tracking mistletoe fruits, whereas a positive effect of the abundance of dispersed seeds alone represented the role of seed dispersal independent of fruit tracking activity.

Each hypothesis was checked at different spatial scales, by repeatedly running a given path model with the values of the response variable predicted by the different spatial submodels (i.e. the linear trend model and the PCNM submodels, see Borcard *et al.* 2004). We assumed that these predicted values represented the variability in a response variable at a given spatial scale, with a degree of fit indicated by the coefficient of determination of the corresponding spatial submodel. We performed Path analyses of a given hypothesis only with the values of the response variable predicted by those spatial submodels with coefficient of determination (R^2) ≥ 0.05 and degree of significance (P) < 0.1. Explanatory variables were used with their actual values in all path models, but were transformed (arc sin square root, for covers; log x + 1, for abundances) before analyses.

Path analyses provided standardized path coefficients for all causal links, estimated from multiple linear regression procedures. They also provided coefficients of determination (R^2) that indicated the proportion of variance of a given response variable accounted for by the causal cascade. As path models worked with the values of response variables predicted from different spatial submodels, we calculated the proportion of spatial variance of the raw response variable explained by the path model by multiplying the coefficient of determination of the path model by that of the corresponding spatial submodel. Path analyses were performed with Piste software (written by Alain Vadour and Philippe Casgrain, University of Montreal).

Results

SAMPLING OF MISTLETOES AND MARSUPIALS

Adult mistletoe plants occurred unequally on the three host species, with low numbers of mistletoes per infected host plant and low infection rates (Table 1). The host plants occurred in 97.3% of sampling plots, with an average host plant cover of 37.8% (± 3.2 SE). Of all plots with host plants, 71.2% also contained mistletoe adults and 50.7% contained mistletoe recruits. Most mistletoe adults (72.2%) bore ripe fruits, with an average individual crop of 422.5 (± 37.7 SE) fruits. Representation of the densities of dispersed seeds and recruits against the density of adults per sampling plot exhibited low dispersal and recruitment in plots with low adult density, but variable magnitudes of dispersal and recruitment in plots with high adult density (Fig. 2). Seedlings represented 31.37% of counted recruits (N = 392).

Table 1. Occurrence of *Tristerix corymbosus* on different host plant species. The percentage of occurrence of mistletoe adults on infected host plants ($N = 329$ mistletoes), the mean ($\pm$ SE) and maximum (between parenthesis) number of mistletoe adults per infected host plant (intensity of infection), and the percentage of individuals of each species infected by the mistletoe (infection rate; number of individuals between parenthesis) are shown

	Aristotelia chilensis	*Azara microphylla*	*Maytenus boaria*
Percentage of occurrence	76.30	20.62	3.08
Intensity of infection	1.44 ± 0.06 (5)	1.28 ± 0.05 (4)	1.14 ± 0.14 (2)
Infection rate	17.57 (993)	11.91 (446)	11.23 (62)
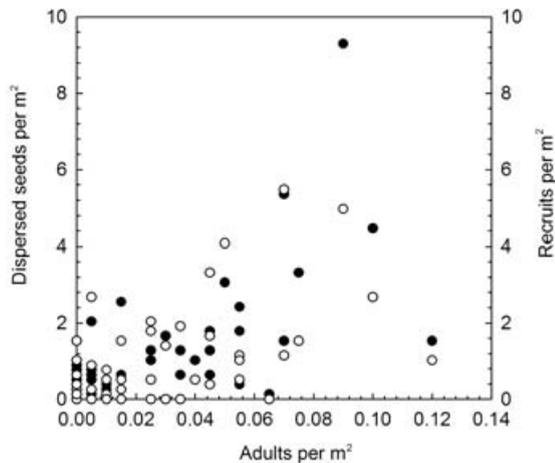
Fig. 2. Densities of dispersed seeds (filled circles) and recruits (open circles) of *Tristerix corymbosus* as a function of the density of adults. Each point represents a sampling plot.

Seedling and juvenile abundances were positively correlated (Mantel Partial Correlation Coefficient: $r = 0.649$, $P = 0.001$, $N = 75$).

The total number of marsupial records amounted to 119, of which 70 corresponded to captures of different individuals, 24 to recaptures, and 25 to marsupials visiting inactivated traps, but identified by the presence of faeces with mistletoe seeds. Less than 10% of registered movements, estimated from recapture data, exceeded 50 m ($N = 24$, maximum travelling distance 200 m). In 92% of cases, marsupials defecated 1–18 mistletoe seeds (5.37 ± 0.37 SE seeds on average) within the trap.

SPATIAL STRUCTURE OF MISTLETOE AND MARSUPIAL ABUNDANCES AT DIFFERENT SPATIAL SCALES

Linear trend models evidenced differences in the large-scale spatial structure among the abundances of different life stages of the mistletoe, and between the abundances of mistletoes and marsupials. The abundances of mistletoe adults and fruits slightly increased along the transect, but these linear trends were not significant (Fig. 3a,b). Conversely, the abundance of marsupials decreased progressively along the transect, as suggested by a negative and significant linear trend (Fig. 3a,b). This gradient-like structure accounted for more than 20% of the spatial variance of marsupial abundance in our spatial framework. The abundances of dispersed mistletoe seeds and recruits also decreased progressively along the transect, with negative and significant linear trends that accounted for ca. 5% of their spatial variance (Fig. 3a,b).

The number of PCNM spatial predictors (from the 50 vectors generated by the PCNM analysis in the 75-plot linear transect) that accounted significantly for spatial variation ranged from 19 (in the case of the abundance of mistletoe adults) to 6 (in the case of the abundance of marsupials, see Table S1 in Supporting Information). Most significant PCNM vectors were incorporated into the submodels at broad and intermediate scales. PCNM vectors accounted for 80% of the predictable spatial variance in the abundance of mistletoe adults and fruits, 70% in the abundances of dispersed mistletoe seeds and recruits, and 36% in the abundance of marsupials. The broad-scale submodels always explained a larger percentage of variance than intermediate- and fine-scale submodels, the latter never accounting for more than 6% of spatial variance (Fig. 3c; Table S1).

The representation of the predicted values for the abundances of mistletoes and marsupials within the transect at the broad and the intermediate scales suggested strong patchiness at both these spatial scales (Fig. 3c). The spatial patterns of mistletoe fruit abundance mirrored those of adult abundance at both the broad and the intermediate scales, as did the predicted distributions of recruits relative to those of dispersed seeds. Broad scale patterns of adult mistletoe and fruit abundances suggested the existence of three main patches along the transect with similar magnitude (height of the peak on the axis of predicted value) but different extents (a first narrow one at *c.* 0–250 m, a second wide one at 850–1300 m, and a third narrow one at 1350–1500 m). This pattern of broad-scale patchiness of adults and fruits was also found in the abundances of dispersed seeds and recruits, at least in the relative position of the patches along the transect. However, in the case of the abundance of dispersed mistletoe seeds and, notably, the abundance of mistletoe recruits, the magnitude of the three main broad-scale patches decreased strongly towards the end of the transect, with a high-peak, narrow patch at *c.* 0–250 m, but relatively much lower peak patches at 850–1300 m, and, especially, at 1350–1500 m (Fig. 3c). Such a decreasing trend was also indicative of a gradient-like structure in the abundances of dispersed mistletoe seeds and recruits.
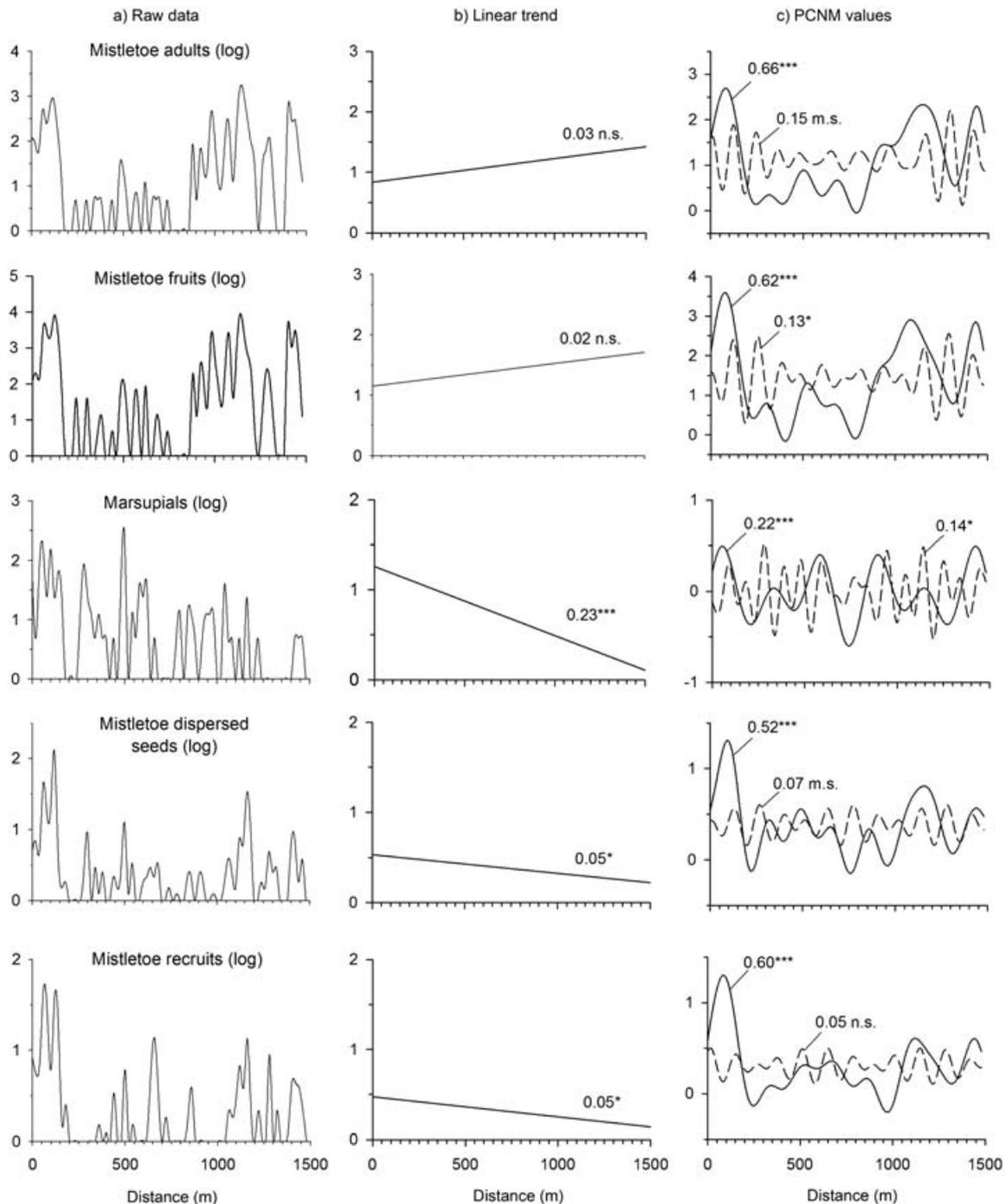
Fig. 3. Representation of (a) the log-transformed (and smoothing spline fitted) abundance of adults, fruits, dispersed seeds and recruits of *Tristerix corymbosus*, and the abundance of *Dromiciops gliroides*; (b) the values predicted by the linear trend models (fit to the one-dimensional coordinate) of these variables; and (c) the values predicted by the PCNM-based spatial submodels at different spatial scales (broad, continuous line; intermediate, dashed line) of these variables, along the 1500 m sampling transect. For each model in (b) and (c), the respective values of the coefficient of determination (R^2) and the level of significance (n.s.: $P > 0.01$; m.s.: $0.01 \geq P > 0.05$; *$P \leq 0.05$; ***$P \leq 0.001$) are also shown.

SCALE-DEPENDENT RELATIONSHIPS BETWEEN MISTLETOES AND MARSUPIALS

Effect of resources on the abundance of mistletoe adults

Forest canopy and host plant covers affected the abundance of mistletoe adults at different spatial scales (Fig. 4a). At the broad scale defined by the PCNM, the path model on the predicted values of mistletoe adult abundance detected a weak, but positive and significant effect of host plant cover. At the intermediate scale, the path model also revealed a positive and significant effect of host plant cover, but a negative and significant effect of forest canopy cover on the predicted values of mistletoe adult abundance.
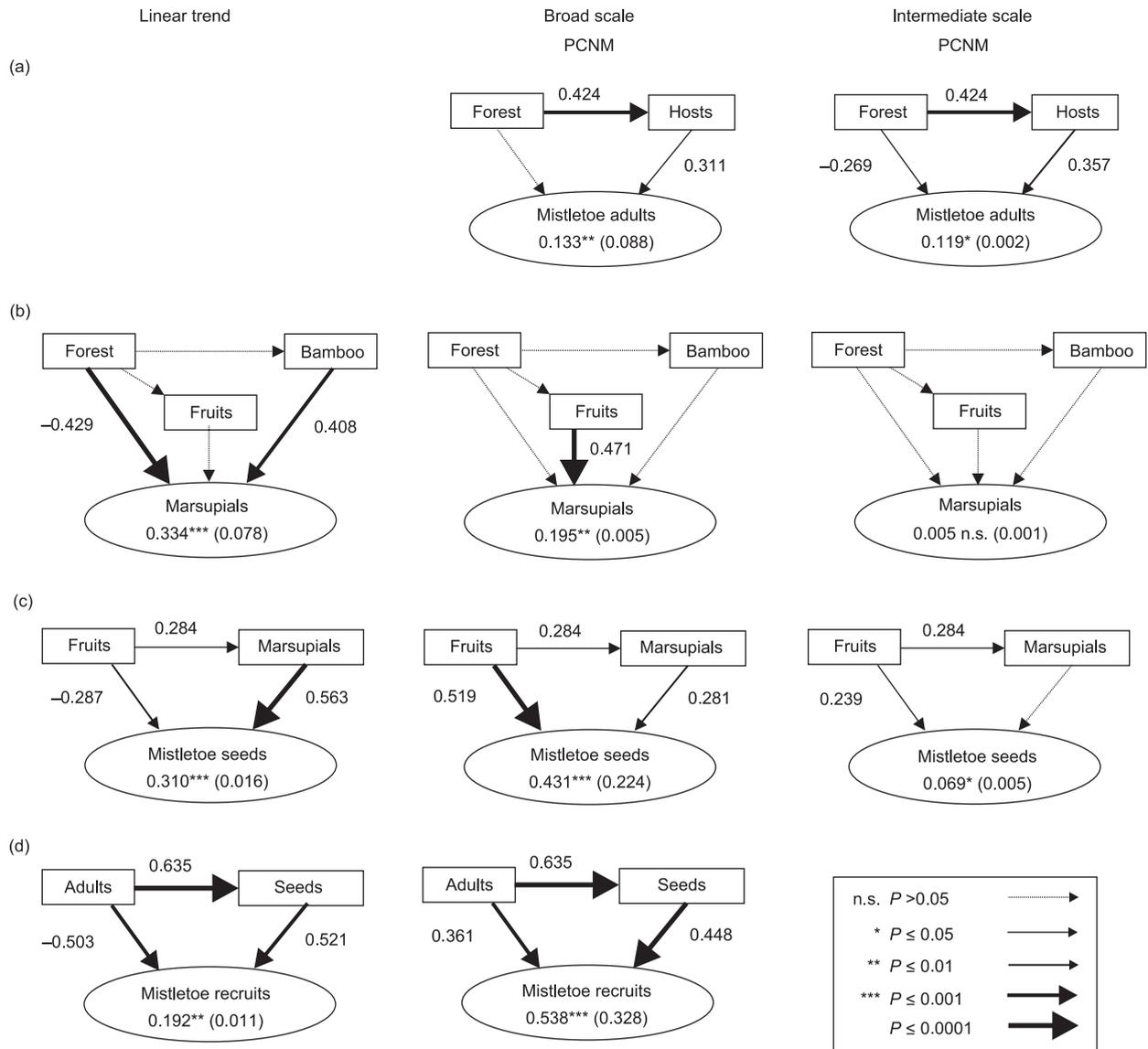
Fig 4. Path models for four different hypotheses (a–d, see also main text) evaluating the effect of seed dispersal by *Dromiciops gliroides* in the spatial structure of *Tristerix corymbosus.* Each hypothesis was evaluated at different spatial scales by using the predicted values of different spatial submodels (linear trend, PCNM broad and intermediate) of each response variable (ellipse). Each model shows the sign and the value of the standardized path coefficients for statistically significant causal links. The coefficient of determination (R^2), and the level of significance of the path model at each spatial scale, are shown for each response variable. Between parenthesis are the values of the proportion of spatial variance of each raw response variable explained by the path model.

Fruit tracking by marsupials

The path models suggested that different ecological factors explained the spatial patchiness of marsupial abundance at different scales. The gradient-like spatial structure of the abundance of marsupials was largely a response to the combined, but opposite, effects of forest and bamboo covers, but was independent of fruit abundance (Fig. 4b). Conversely, the patchiness depicted by the broad-scale PCNM submodel was only related to mistletoe fruit abundance, indicating stronger aggregation of marsupials in large rich-fruit patches within the transect and habitat features having no effect.

Effect of fruit tracking on seed dispersal

The abundances of fruits and marsupials together explained *c.* 30% of the large-scale patchiness in the abundance of dispersed mistletoe seeds (Fig. 4c) predicted by the linear trend model, with a positive correlation to the abundance of marsupials, and, to a lesser extent, a negative correlation to the abundance of fruits. Thus, the progressive decrease of seed dispersal along the transect was affected by the spatial patterns of marsupial abundance generated by other factors than fruit tracking. The causal models evidenced positive effects of fruit availability and, to a lesser extent, of marsupial abundance on the abundance of seeds predicted by PCNM

submodels. This suggested that broad- and intermediate-scale patchiness of seed dispersal mostly resulted from seed deposition by marsupials when searching for fruits.

Spatial feedback between mistletoe adults and recruits

The negative linear trend of mistletoe recruit abundance along the transect was explained by the combined, but opposite, causal effects of the abundances of mistletoe adults and dispersed seeds (Fig. 4d). This indicated that, at the largest scale, recruitment was less likely to occur in areas devoid of marsupials but still densely populated by mistletoe adults. At the broad scale defined by the PCNM, both adult and dispersed seed abundances accounted for more than 30% of the spatial variance in the predicted abundance of mistletoe recruits. The broad-scale path model suggested that patches of mistletoe recruits mostly occurred in areas of high abundance of adults, but also in areas of high seed density, independently of the presence of adults.

Discussion

Our study suggests that seed dispersal by the marsupial *D. gliroides* plays a crucial role in shaping the spatial structure of the populations of the mistletoe *T. corymbosus*. As a consequence of the spatial tracking of mistletoe fruits by the marsupial, many seeds were dispersed in the immediate surroundings of the fruiting plants. Seedling recruitment was also highly predictable in space, and concordant with the seed rain template generated by the marsupial. Thus, seed dispersal provoked a positive spatial feedback between the mistletoe fruiting adults and the newly established recruits. This spatial feedback was, however, scale-dependent and incomplete. This is because where the marsupial was scarce, recruitment was lower than expected from adult and fruit abundances, and where the marsupial was abundant, a small fraction of seeds was deposited far from adults. More importantly, the large-scale patterns of marsupial activity, determined by habitat features, provoked a spatial fingerprint on mistletoe seed rain and recruitment, which ultimately showed a gradient-like structure along the transect. Seed dispersal by the marsupial shaped the spatial scale of the mistletoe population by maintaining a spatial feedback between adults and recruits, but also by generating spatial patchiness in offspring at a larger scale than in adults.

Previous studies have suggested a significant role for seed dispersal by animals in determining the strong patchiness in seed rain or seedling populations, with an expected effect on the degree of clumpiness of adults (e.g. Peres & Baider 1997; Aukema 2004; Russo & Auspurger 2004). For example, Fragoso (1997) linked the large-scale spatial structure in the palm *Maximiliana maripa* to the patterns of seed dispersal by tapirs, whose long-distance movements and seed defecation in latrines generated clumps of recruits far from adult palms. Similarly, Aukema (2004) explained the patchiness of the mistletoe *Phoradendron californicum* as a consequence of the spatial structure of seed dispersal by birds. Our study goes

further than previous ones, in the sense that it integrates the comparative spatial information of the different stages of a plant population (i.e. adults, dispersed seeds and recruits), and provides a mechanistic and spatially-explicit baseline for explaining the role of seed dispersal in terms of scale. Nevertheless, the biological interpretation of the data presented here must consider that our causal models worked exclusively with the spatial variability in mistletoe and marsupial abundances previously explained by the linear trend and PCNM sub-models. Thus, their predictive power on the actual values of these response variables was somewhat diluted. In fact, the low values of the multiplicative coefficients of determination in many of these causal models suggest a high degree of stochasticity in the spatial distributions of mistletoe and marsupials along the sampling transect, combined with the potential effect of unmeasured ecological factors (Borcard *et al.* 2004). In any case, our multi-scaled approach was still a valuable and robust tool for evaluating how different ecological factors may explain the spatial patchiness in mistletoe and marsupial abundances at different spatial scales.

THE SPATIAL STRUCTURE OF MISTLETOE AND MARSUPIAL POPULATIONS

The abundances of the marsupial and the different life stages of the mistletoe were all structured in space showing large patches that they themselves contained smaller ones. That is, they were distributed in space following a hierarchically-nested pattern of patchiness (as shown for other mistletoes, e.g. Aukema 2004). The distribution of the spatial variability across scales, and the shape of the patches were, however, different between the mistletoe and the marsupial.

Most of the predictable spatial patchiness in the abundance of mistletoe adults and fruits occurred at a broad scale within the transect. Some significant clumpiness at finer scales was also evident in mistletoe adults and fruits. Although we have not explicitly analysed the scale represented by the extent of the individual host plants, we would argue that, unlike other mistletoes parasitizing large trees or cacti (e.g. Martínez del Río *et al.* 1996; Overton 1996; López de Buen *et al.* 2002), the clumping of many individuals on the same host plant probably accounted for a small fraction of the fine-scale spatial variability in *T. corymbosus*. In fact, almost 75% of host individuals were parasitized by only one mistletoe, and < 10% of infected individuals hosted more than two mistletoes. Thus, the finest level of aggregation observed in our study probably resulted from the aggregation of parasitized individual hosts in neighbouring areas (see also Carlo & Aukema 2005).

Previous studies have found that the spatial structure of mistletoe populations may result from long-term responses to large-scale environmental gradients related to the availability of host plants and light in the immediate surroundings of the host plant (Hoffman *et al.* 1986; Norton & Reid 1997; López de Buen *et al.* 2002; Aukema 2004). In our study, the spatial structure of the *T. corymbosus* population may be partially attributable to the spatial coupling between mistletoes and their resources (i.e. host plants and light), as suggested by

the fraction of the spatial variability of adult abundance accounted for by the abundance of host plants and tree canopy openness at the broad and the intermediate scales. Nevertheless, our data also show that the mistletoe was unable to colonize the entire potential spatial universe generated by the host plants. In fact, the availability of host plants was high throughout almost the entire transect, but many host individuals were devoid of mistletoes. Therefore, we suggest that the hierarchical patchiness of the mistletoe may be chiefly linked to the long-term spatial effect of seed dispersal (as suggested for other vertebrate-dispersed mistletoes, e.g. Hoffmann *et al.* 1986; López de Buen *et al.* 2002; Aukema 2004; but see Overton 1996).

In contrast to mistletoe adults and fruits, the abundance of marsupials showed a progressive decrease along the transect. This gradient-like structure was indicative of large population patch sizes which surpassed the dimension of mistletoe fruiting patches and even the extent of the transect. Significant clumpiness was also observed for the marsupial at several scales distinguished within the transect. More importantly, as suggested by path models, different environmental factors affected marsupial abundance at different spatial scales. In fact, the decrease of marsupial abundance along the transect was mostly caused by the variations in forest cover and bamboo availability, whereas the broad-scale patchiness within the transect matched the abundance of mistletoe fruits. Thus, our data suggest a scale-dependent fruit-resource tracking by the marsupial, as previously evidenced for other vertebrate frugivores (García & Ortiz-Pulido 2004; Saracco *et al.* 2004).

CONSEQUENCES OF SEED DISPERSAL IN TERMS OF SPATIAL SCALE

Mistletoe seed rain (i.e. the spatial pattern of seed dispersal) was spatially contagious at different scales (see also Overton 1996; Aukema 2004, for bird-dispersed mistletoes). Our sampling was unable to detect fine levels of clumpiness, such as those caused by the simultaneous deposition of small groups of seeds when regurgitated or defecated together (Reid 1991; Ladley & Kelly 1996), or by the predominant seed deposition in already infected hosts (Overton 1996; Aukema & Martínez del Río 2002). Nevertheless, our results revealed strong patchiness at a broad spatial scale, mainly derived from the activity of the marsupials when searching for, and feeding on, fruits on or near to mistletoe adults. The activity of the marsupials not associated with fruit tracking also contributed to shaping the mistletoe seed rain, by eventually dispersing seeds to locations with no mistletoe adults, and, more importantly, by preventing seed deposition in those locations where there were no marsupials, despite a high abundance of fruits (Fig. 2). As a whole, the mistletoe seed rain was the spatial combination of a pattern of progressive decrease along the transect with a multi-scaled patchiness within the transect. The first large-scale, gradient-like spatial structure was similar to that of marsupial abundance, whereas the second spatial structure was similar to those of mistletoe adults and fruits.

The observed spatial pattern of mistletoe recruitment mirrored the seed rain, especially at the broad spatial scale. Our study lacks of an explicit treatment of the phase between seed dispersal and establishment, as we do not have data about the microhabitat of deposition and the long-term fate of dispersed seeds and seedlings. Previous work at the same site has shown that *c.* 77% of seeds dispersed by the marsupials are deposited on branches or trunks of host plants, and less than 10% of defecated seeds fall to the ground (Amico 2000; Rodríguez-Cabal 2003). Establishment success is *c.* 30% for seeds on host plants, postdispersal losses of germinating seeds being mostly caused by fungal attack, light-resource limitation and host mortality (Amico 2000; Rodríguez-Cabal 2003; see also Yan & Reid 1995; Norton & Reid 1997). These quantitative losses may explain why, in our study, most adult mistletoes exist as single plants on a host even with a seed disperser that spends most of its time in areas of high mistletoe density and does not travel far. In any case, our spatial data suggest that none of these post-dispersal facts were sufficiently strong and heterogeneous to erase the pattern of long-term establishment imposed by the seed rain template, since mistletoe seedling abundance was a good spatial proxy for juvenile abundance. Thus, the spatial matching between seeds and recruits (seed-seedling concordance, García *et al.* 2005) and the lack of infection in most host plants present in the study site suggest that the mistletoe recruitment was limited more by seed availability than by the availability of microsites suitable for establishment.

Irrespective of the consideration of the post-dispersal processes, this study suggests that the spatial pattern of recruitment mirrored the broad-scale patchiness of mistletoe adults, and it was also structured at a larger scale, with a gradient-like distribution. This enlargement of the functional spatial scale from adults to recruits was attributable to some establishment from seeds dispersed far from adults, and, especially, to the reduced establishment in those locations occupied by adult mistletoes but seldom visited by marsupials. In other words, despite the low frequency of far-from-adult dispersal events, the process of seed dispersal by the marsupial was able to shape the spatial scale of the mistletoe simply by acting as a survival factor (as only seeds handled by the marsupial have the potential to become established) that filtered the initial template of propagules attached to mistletoe fruiting adults (see also Lavorel *et al.* 1999). In conclusion, this study highlights the fact that the spatial scale of a plant population may be strongly constrained by the performance of the seed dispersal process as a spatially heterogeneous demographic sieve in the multi-staged regeneration cycle of the plant.

BEYOND THE *TRISTERIX CORYMBOSUS-DROMICIOPS GLIROIDES* CASE STUDY

Dromiciops gliroides moulded the spatial scale of *T. corymbosus* recruitment by generating patchiness at a scale larger than that occupied by mistletoe adults, but more strongly, by creating a positive spatial feedback between mistletoe adults

and their offspring. We would argue that these mechanisms may also operate in mistletoes dispersed by birds. However, avian dispersers may differ from marsupials in the frequency of far-from-adult events of seed dispersal, and in the spatial structure of their populations (patch size relative to that of mistletoe adults). Given the ability of birds to move seeds over large distances and to show population spatial structures characterised by larger patchiness, we would expect a stronger ability of birds to enlarge the spatial scale of mistletoes from adults to recruits, even when generating mistletoe aggregated distributions at the landscape scale (Lavorel *et al.* 1999; Aukema & Martínez del Río 2002; Ward & Paton 2007). Additionally, we consider that our findings may also be generalized to other plant-frugivore systems in which there is sharp spatial matching between fruit resources and frugivorous seed dispersers and, consequently, large aggregations of dispersed seeds occur near fruiting adults (e.g. Schupp *et al.* 2002; Russo & Augspurger 2004). More importantly, we would expect a stronger impact of seed dispersers in shaping the spatial scale in plants, other than mistletoes, in which dispersed seeds clearly have a much higher probability to recruit than undispersed seeds. Plants whose germination is strongly enhanced by the passage through the disperser's digestive tract (Traveset 1998), and plants whose seeds are directed by dispersers to favourable microsites (Wenny 2001) would fit well into this category. Therefore, we would call for a wider consideration of seed dispersal as a demographic template that determines the spatial extent a plant species is able to occupy and the range of environmental heterogeneity a plant is able to perceive.

Acknowledgements

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Supporting Information

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

Table S1. PCNM analysis for detecting the spatial variability of biological variables at different scales. Summary of multiple regressions fitting the detrended abundances of different life cycle stages of *Tristerix corymbosus* and the detrended abundance of *Dromiciops gliroides* to PCNM vectors at different (broad, intermediate and fine) scales. The significant PCNM vectors for each submodel are also shown

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