

Spatial structure of *Aspidosperma polyneuron* in two semi-deciduous forests in Southeast Brazil

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Abstract. Description of the spatial structure of vegetation is the first step in generating hypotheses regarding underlying processes. It is also important to take into account variation in spatial structure between different localities to be able to distinguish between life history traits and the influence of environment on population processes. Correlogram analysis was used to examine spatial recruitment and mortality patterns of *Aspidosperma polyneuron*, an emergent tree species, at Reserva Municipal de Santa Genebra (SG), a forest fragment in southeast Brazil. The spatial structure of individuals was compared with two areas with similar physiognomy, one in the same forest and another at Mata do Ribeirão Cachoeira (RC), a semi-deciduous forest located ca. 14 km away. Seedling, sapling and adult mortality occurred in clumps, while seedling recruitment occurred mostly in one region of the area. The spatial pattern varied among the three study areas, and the differences were higher between fragments than within SG. The adults showed a negative correlation in space with saplings and seedlings in one of the SG areas, which could be a consequence of intraspecific competition, or the influence of density or distance dependent natural enemies. However, this pattern was not observed in the other areas. The results suggest that the mechanisms governing the spatial population dynamics of *A. polyneuron* vary among nearby and similar localities.

Keywords: *Apocynaceae*; Correlogram; Emergent tree; Population dynamics; Spatial variation.

Nomenclature: Carvalho (1994); Lorenzi (1992).

Abbreviations: bd = Basal diameter; RC = Mata do Ribeirão Cachoeira; SG = Reserva Municipal de Santa Genebra.

Introduction

The spatial distribution of individuals of tree species may be studied at different scales, from biogeographic to the arrangement of individuals within a community. At the largest scales, all species show a clumped pattern resulting from the spatial heterogeneity of suitable environmental conditions (Lieberman & Lieberman 1994). But within a community, the spatial pattern of individuals may be, at various scales, random, uniform or may show different degrees of aggregation. The study of this pattern can give insights in population dynamics and intra or interspecific competition (Forget et al. 1999).

Within a community the most frequent spatial arrangement found in tropical tree species is a decrease in clumping from the smaller to the larger size classes (Henriques & Souza 1989; Oliveira-Filho et al. 1996; He et al. 1997; Martens et al. 1997; Barot et al. 1999; Condit et al. 2000). The clumping of individuals may be a consequence of limited dispersion, vegetative reproduction or environmental heterogeneity (Phillips & MacMahon 1981; Hutchings 1997). Density or distance dependent mechanisms, such as influence of natural enemies (Janzen 1970; Connell 1971), competition between seedlings or between seedlings and adults (Howe & Smallwood 1982; Clark & Clark 1984) can cause a seedling distribution discordant with the distribution of dispersed seeds, resulting in a spatial segregation between juveniles and adults. This spatial segregation could also be caused by shifting in the environmental requirements through ontogeny (Clark & Clark 1992; Dalling et al. 2001). Therefore, different processes may result in the same pattern, and the spatial distribution of individuals may be caused by the interaction of different mechanisms (He et al. 1997; Grau 2000).

The description of spatial structure is the first step in working out hypotheses about the underlying processes, which should then be tested in further studies (Barot et

al. 1999; Jeltsch et al. 1999). Therefore, the analysis of the spatial pattern of mortality and recruitment can give insights into the factors that influence these processes. The spatial structure, however, may vary within a population, or among populations of the same species (e.g. Skarpe 1991; Lieberman & Lieberman 1994; Forget et al. 1999; Wiegand et al. 2000). Thus, in order to distinguish between life history traits and the influence of environment on population processes, it is important to take into account variation in spatial structure (Lieberman & Lieberman 1994). The purposes of the present study were to investigate: (1) the spatial pattern of dead and recruited individuals of *Aspidosperma polyneuron* in a semi-deciduous forest fragment and (2) the spatial variation of the population structure at small scales, comparing samples within the same forest fragment, and between two forest fragments of similar size and vegetation physiognomy, and subjected to the same climatic conditions. We expected to find a pattern consistent across nearby and similar areas.

Methods

Study site

This study was carried out at Reserva Municipal de Santa Genebra (SG) and at Mata do Ribeirão Cachoeira (RC; Table 1), both located in the municipality of Campinas, São Paulo state, southeast Brazil. The predominant vegetation type is seasonal semi-deciduous forest (Velooso 1992) and the climate is CWA in the Köppen classification in both areas. Mean annual temperature in the region is 20.6 °C and annual rainfall is ca. 1380 mm, most of which falls during the October-March summer wet season.

Until the late 1970s SG was used as a nursery for coffee seedlings and as a source of roundwood and firewood (Morellato & Leitão-Filho 1995). In 1981 the area was designated a conservation unit. At present, SG is the largest forest fragment in the region and is isolated from other forest fragments by agricultural and urban areas.

RC is a forest fragment located ca. 14 km from SG. There are, however, some differences between the two areas. The RC is surrounded by country cottages, pastures, *Eucalyptus* plantations and other small forest patches, which probably contribute to the superior conservation status of this area. The altitude and topography in this fragment are also different from those at SG (Anon. 1993; Table 1), and there is a stream cutting through the area. Despite these differences, the similarities in fragment size, vegetation physiognomy and climatic conditions provide the best available comparison of spatial variation in demographic characteristics of *A. polyneuron* under similar environmental conditions.

Study species

Aspidosperma polyneuron (Apocynaceae) is an emergent (20-30 m) evergreen tree. It occurs from 10° N (Venezuela) to 25° 50' S (Brazil), from 80 m to 1000 m a.s.l. and under mean annual rainfall from 1100 - 2500 mm (Carvalho 1994). The flowering cycle is supra annual (September to November) and abundant seed production occurs at 2 - 4 yr intervals (Lorenzi 1992). Fruits mature between July and October (Grombone-Guaratini & Rodrigues 2002), releasing wind dispersed winged seeds. Seeds have no dormancy, losing their viability after six months when stored in the laboratory (Carvalho 1994). The species is shade-tolerant, judged by the high density of seedlings and saplings in the shaded understorey. Bernacci & Leitão-Filho (1996) and Martins & Rodrigues (2002) classified this species as late secondary. It is a long-lived tree with relatively high wood density (0.79 g.cm⁻³; Lorenzi 1992) and has been intensively harvested in some areas because of its high commercial value.

A. polyneuron is the second most abundant tree species > 5 cm DBH at SG (Santos et al. unpubl.) and is often found in floristic and quantitative inventories in semi-deciduous forests in São Paulo State, with generally high importance values, because of the high density and large DBH of individuals (Maltez 1997). According to Velooso (1992), this species characterizes the semi-deciduous forest of São Paulo and Paraná States.

Census methods

From October 1994 to July 1995 (hereafter 1995 sample) we counted the number of *A. polyneuron* individuals with DBH > 5 cm in a 100 m × 50 m (0.5 ha) area subdivided into 5 m × 5 m plots (hereafter SG1), at SG. We also counted the number and measured the basal diameter (bd) of individuals < 5 cm DBH in the same area. Individuals with cotyledons or cotyledon scars were not sampled. The area was recensused from August to December 1999 (hereafter 1999).

To investigate variation in the spatial pattern of individuals among areas, we sampled two other 100 m × 50 m areas subdivided into 5 m × 5 m plots in 1999. One

Table 1. Characteristics of the study forest fragments, Reserva Municipal de Santa Genebra (SG) and Mata do Ribeirão Cachoeira (RC).

Forest fragment	SG	RC
Location	22° 49' S, 47° 06' W	22° 50' S, 46° 55' W
Fragment size	251.8 ha	233.7 ha
Altitude (m a.s.l.)	580 - 610	630 - 763
Topography	Relatively flat	Slopes from 10° - > 45°

of them was located at SG, 200 m from SG1 (hereafter SG2), and another at RC (hereafter RC1). Both areas had a canopy height and openness similar to SG1. At RC the chosen area had a gentle slope and was situated ca. 500 m from the stream. The criterion for choosing the areas was to reduce, as much as possible, the environmental heterogeneity, but the density of *A. polyneuron* was not used as a criterion.

Data analysis

The individuals were grouped in the following size classes: (1) seedlings: individuals without cotyledons or cotyledon scars and < 1 cm bd; (2) saplings: individuals ≥ 1 cm bd and < 5 cm DBH; (3) adults: individuals ≥ 5 cm DBH. The annual mortality rate (m_a ; Primack et al. 1985) of each size class and the recruitment rate (i) in the seedling size class were calculated using the following exponential models:

$$m_a = 1 - (1 - M/N_t)^{1/\Delta t} \quad (1)$$

$$i = \ln((N_t + I)/N_t) / \Delta t \quad (2)$$

where Δt is the time elapsed between samples, M is the number of individuals dead in Δt , N_t is the number of individuals at the beginning of the period and I is the number of recruits, i.e. individuals that reached the seedlings size class during Δt .

The spatial pattern of each size class was analysed using Moran's I (Moran 1950) spatial autocorrelation coefficient. Moran's I is calculated for different distance classes and varies between -1 and $+1$. There is autocorrelation, either negative or positive, when it is possible to predict the value that a variable takes at a given location from the values that the same variable takes at other sampling points of known positions (Legendre & Fortin 1989). The null hypothesis that the coefficient at each distance class is not significantly different from zero, indicating randomness, can be tested. The spatial correlogram, which is a graph of I values as a function of the distance classes, can then be plotted. However, the correlogram is considered globally significant only if at least one of the I values is significant at the $\alpha' = \alpha/n$ significance level, where α is the chosen overall significance level (0.05 in this study) and n is the number of distance classes considered (Bonferroni criterion; Oden 1984). We calculated the correlograms for the density of individuals that died in each size class between 1995 and 1999 in SG1, for the density of individuals that reached the seedling size class in the same period and for seedling, sapling and adult density in SG1, SG2 and RC1 in 1999. The coordinates of each 5 m \times 5 m plot centre were used in the analyses and we chose 21 distance classes of 5.0 m width. The 21st class, however, had only

16 pairs of plots and is not shown. All other distance classes have more than 103 pairs of plots. The autocorrelation analyses were performed using the R package v.4 (Casgrain & Legendre 2001).

To examine if there was correlation between the abundance of individuals of different size classes we calculated Spearman rank correlation coefficients (Ludwig & Reynolds 1988) considering two plot sizes: 5 m \times 5 m ($n = 200$ plots) and 10 m \times 10 m ($n = 50$). The Spearman Rank coefficient provides a useful summary of monotonic dependence, whether linear or not, although it does not describe some spatial features of data (Rossi et al. 1992). We used a modified t -test developed by Dutilleul (1993) for correlation coefficients to correct for spatial autocorrelation in the data, which causes inflated rates of type I error (Legendre et al. 2002). These tests were performed using the Program Mod_t_test (Legendre 2000). In addition, we used a sequential Bonferroni test (Rice 1989) to control the type-I error rate for the six correlations within each area (three size classes and two plot sizes).

Results

Mortality and recruitment spatial pattern

The number of seedlings and adults declined between 1995 and 1999 in SG1 while the density of saplings increased (Table 2). The seedling, sapling and adult annual mortality rates were, respectively, 6.1%, 4.0% and 3.2%. The seedlings recruitment rate was 2.9%.yr⁻¹. The seedlings and saplings that died between 1995 and 1999 were clumped, with clumps of ca. 15 m separated by ca. 85-90 m (Figs. 1 and 2). The correlogram for the density of dead adults showed an alternation of positive and negative coefficients, some of them not significant (Fig. 2), suggesting the occurrence of irregularly spaced clumps (Fig. 1). Individuals recruited in the seedling size class between 1995 and 1999 ($n = 114$; Fig. 3) were positively autocorrelated at short distance classes and negatively autocorrelated at larger distance classes, indicating that this process occurred in only one region of the sampled area (Fig. 1). These individuals had a positive and significant correlation with saplings already present in 1995 in plots of 25 m² (Table 3).

Spatial structure variation among areas

The number of individuals in each size class differed among the three areas, and the total density in SG2 was ca. three to four times lower than in SG1 and RC1 (Table 2). The spatial pattern of seedlings, saplings and adults also varied among study areas (Figs. 1 and 4). In

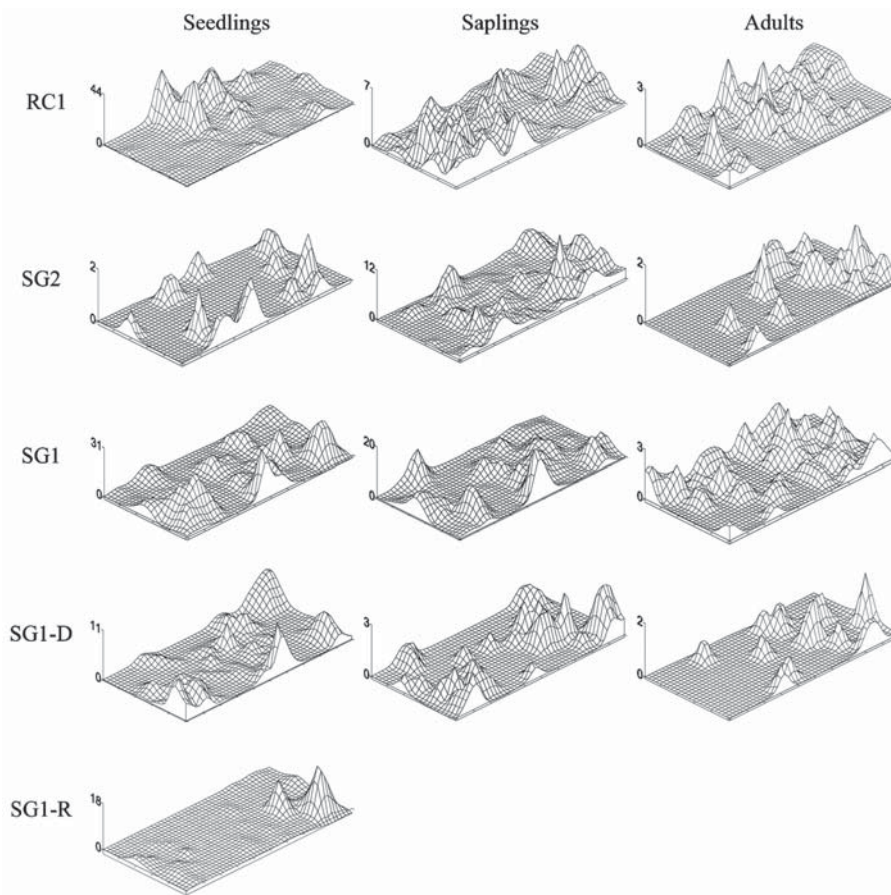


Fig. 1. Surface maps of the number of *Aspidosperma polyneuron* seedlings, saplings and adults in three 100 m × 50 m areas subdivided into 25 m² plots. RC1 = sampled area at Mata do Ribeirão Cachoeira; SG1 and SG2 = sampled areas at Reserva Municipal de Santa Genebra; D = dead; R = recruited individuals between 1995 and 1999.

SG1, seedlings were clumped, with clumps of 5 - 10 m, ca. 40 - 45 m apart. In SG2 seedlings had positive autocorrelation at 5 m and at 60-65 m and negative marginally significant ($P = 0.054$) autocorrelation at 35-40 m, indicating the occurrence of smaller and more scattered clumps than those found in SG1. Seedlings in RC1 were concentrated in only one region of the 0.5 ha area. Here, saplings were positively autocorrelated up to 20 m, and negatively autocorrelated at larger distances (Fig. 4) and it was not possible to clearly define a clump size (Fig. 1). Correlograms for adult density in SG2 and RC1 were not globally significant, indicating randomness, while in SG1 adults were distributed in clumps of 20-25 m.

Table 2. Number of *Aspidosperma polyneuron* individuals sampled in each area in 1999 and in SG1 in 1995.

	SG1		SG2	RC1
	1995	1999	1999	1999
Seedlings	827	670	21	692
Saplings	328	379	255	245
Adults	92	75	20	55
Total	1247	1124	296	922

A positive and significant correlation between seedlings and saplings abundance was observed for SG1 and SG2 in 1999, but not RC1 (Table 4). Adults had negative correlation with seedlings and saplings for both plot sizes in SG1, but not in SG2 or RC1 (Table 4).

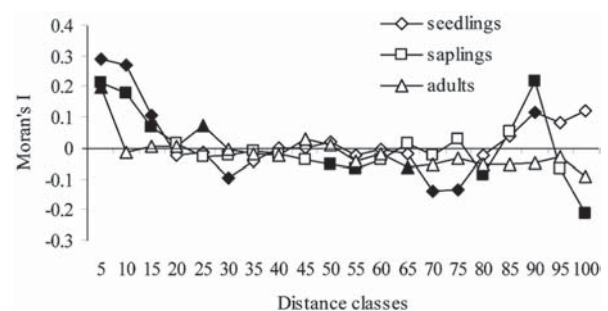


Fig. 2. Spatial correlogram of the density of seedlings, saplings and adults of *Aspidosperma polyneuron* that died between 1995 and 1999 in SG1. The abscissa corresponds to the upper limit (m) of each distance class. Black points indicate significant Moran's I values at the $\alpha = 5\%$ level (for globally significant correlograms), and white points are non-significant values.

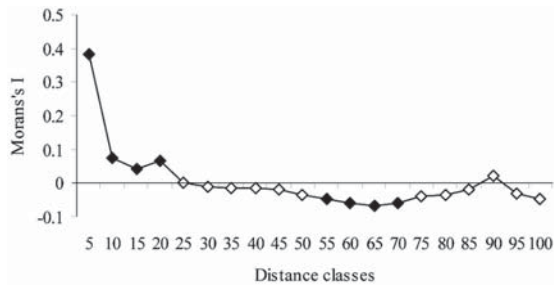


Fig. 3. partial correlogram of the density of individuals that reached the seedling size class between 1995 and 1999 (recruits) in SG1. The abscissa corresponds to the upper limit (m) of each distance class. Black points indicate significant Moran's I values at the $\alpha = 5\%$ level, and white points are non-significant values.

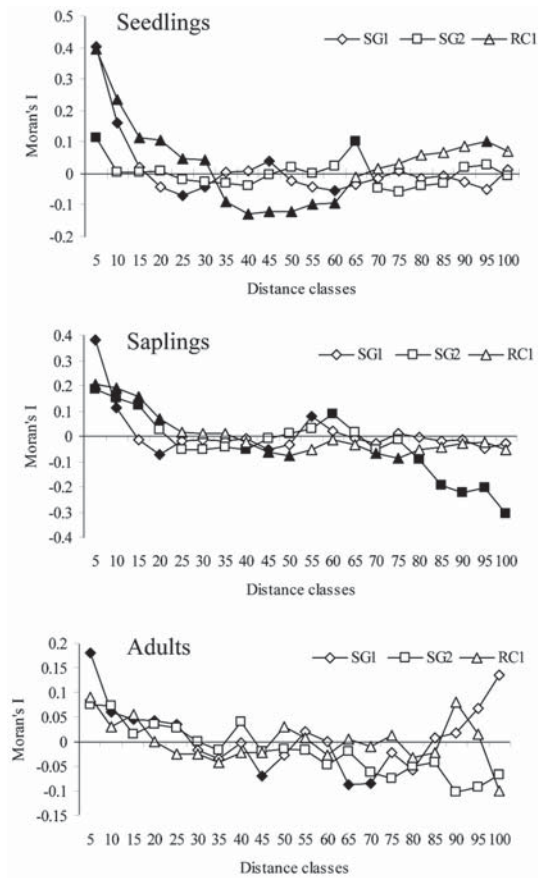


Fig. 4. Spatial correlogram for seedling, sapling and adult density of *Aspidosperma polyneuron* in SG1, SG2 and RC1 in 1999. The abscissa corresponds to the upper limit (m) of each distance class. Black points indicate significant Moran's I values at the $\alpha = 5\%$ level (for globally significant correlograms), and white points are non-significant values.

Table 3. Spearman rank coefficients between individuals that reached the seedling size class between 1995 and 1999 (recruits) and seedlings, saplings and adults alive in 1995 in SG1. P values (Dutilleul's modified t -test) are presented next to each coefficient in parentheses; * = significant at the table-wide 0.05 level (sequential Bonferroni correction).

Plot size (m ²)	Recruits × Seedlings	Recruits × Saplings	Recruits × Adults
25	0.208 (0.027)	0.241* (0.008)	-0.191 (0.033)
100	0.170 (0.353)	0.340 (0.047)	0.124 (0.576)

Table 4. Spearman rank coefficients between size classes in each plot size in SG1, SG2 and RC1 in 1999. P values (Dutilleul's modified t -test) are presented below each coefficient in parentheses; * = significant at the table-wide 0.05 level (sequential Bonferroni correction).

Plot size (m ²)	Seedlings × Saplings			Seedlings × Adults			Saplings × Adults		
	SG1	SG2	RC1	SG1	SG2	RC1	SG1	SG2	RC1
25	0.565* (0.000)	0.303* (0.000)	0.179 (0.092)	-0.325* (0.000)	-0.099 (0.166)	-0.082 (0.308)	-0.208* (0.008)	0.052 (0.509)	0.043 (0.581)
100	0.799* (0.000)	0.453* (0.003)	0.067 (0.725)	-0.450* (0.004)	-0.069 (0.606)	0.116 (0.459)	-0.392* (0.008)	0.210 (0.196)	-0.1861 (0.251)

Discussion

The mortality rate found for *Aspidosperma polyneuron* adults in SG1 was higher than that found for emergent (Clark & Clark 1996) and congeneric (Condit et al. 1995; Felfili 1995) tree species in other tropical forests. This high mortality rate can be related to the isolation and small size of SG (Laurance et al. 1998). Even with these high demographic rates, the 4-yr period of this assessment is relatively short compared to the life cycle of *A. polyneuron*. This provides one possible explanation for the spatial pattern not changing between 1995 and 1999, except for a slight decrease in the seedling clump size, from 10 - 15 m in 1995 (data not shown) to 5 - 10 m in 1999.

The spatial pattern of seedlings, saplings and adults that died between 1995 and 1999 were somewhat different from the spatial pattern of individuals in these size classes in 1995, suggesting that mortality rate was not evenly distributed in space. Furthermore, recruited seedlings were positively autocorrelated at larger scales than seedlings alive in 1995. These results suggest that the spatial pattern might change at a larger time scale.

The observed spatial segregation between seedlings and adults could occur if there were a higher germination and/or growth in abiotic conditions not found below the crown, such as a higher light intensity or temperature. Although the positive correlation between individuals that reached the seedling size class between 1995 and 1999 with saplings already present in 1995 was weak, it indicates a tendency for establishment of different cohorts in the same spots, and suggests that the environmental conditions suitable for the establishment and development of these size classes are stable, at least in the time scale of this study. However, an analysis of the canopy height in SG1 (Santos et al. unpubl.) showed that in the plots where most of the seedling recruitment occurred the canopy was ca. 5 - 10 m tall in 1995 and 1999, as in 70% of the 0.5 ha area. Therefore, the environmental conditions suitable for the establishment of seedlings do not seem to be related to canopy gaps.

A negative correlation between seedling and adult abundances could also suggest the influence of natural enemies (Janzen 1970; Connell 1971) on the initial development stages of *A. polyneuron* in SG1, or below-ground competition. Intense competition for nutrients and light between seedlings of *Aspidosperma carapanauba* and adult trees was documented by Lewis & Tanner (2000) in the Brazilian Amazon.

The low density of seedlings and adults in SG2 could explain the lack of correlation between them in this area. However, although in RC1 the number of individuals was similar to SG1 we detected no spatial

segregation between seedlings and adults. None of the hypotheses which explained this pattern in SG1 could be discarded because the same process does not appear to be occurring in the other study areas. Some factors, such as the density of natural enemies, soil fertility or the distribution of light intensity in the understorey, could vary among these sites, contributing to the observed differences in spatial pattern.

In RC1, seedlings tended to be concentrated in one region of the area and not distributed in scattered clumps, as was the case in SG1 and SG2. Indeed, 67% of seedlings in RC1 are concentrated in a 30 m × 40 m area (24% of the total). The gentle slope in RC1, and related edaphic factors (e.g. drainage), could explain this result. Differences in tree species spatial patterns related to topography were also found in other tropical forests (Lieberman & Lieberman 1994; Condit et al. 2000).

Our results indicate that the spatial structure of *A. polyneuron* individuals vary at small scales among nearby and apparently similar areas. The differences were higher between forest fragments than within the same forest fragment, as expected, even though the difference in *A. polyneuron* density was larger between areas at SG. Nevertheless, this should be considered only as a first approximation, because we do not have replicates to test this assertion.

While much controversy exists about how broadly applicable the Janzen and Connell model is, it is interesting to ask whether these processes are important in all areas where a species occurs. In this study, if their model applies in SG1, these processes appear not to be important in nearby and similar areas. Therefore, the identification of the spatial variation in these population structures is the first step in the search for the mechanisms governing *A. polyneuron* dynamics and assessing their relative importance in different places.

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