

Extending point pattern analysis for objects of finite size and irregular shape

THORSTEN WIEGAND, W. DANIEL KISSLING*, PABLO A. CIPRIOTTI†
and MARTÍN R. AGUIAR †

Department of Ecological Modelling, UFZ Centre for Environmental Research, PO Box 500136, 04301 Leipzig, Germany, and †Cátedra de Ecología–IFEVA, Facultad de Agronomía, Universidad de Buenos Aires CONICET, San Martín 4453, Buenos Aires C1417DSQ, Argentina

Summary

1 We use a grid- and simulation-based approach to extend point pattern analysis to deal with plants of finite size and irregular shape, and compare the results of our approach with that of the conventional point approximation. The plants are approximated by using an underlying grid and may occupy several adjacent grid cells depending on their size and shape. Null models correspond to that of point pattern analysis but need to be modified to account for the finite size and irregular shape of plants.

2 We use a mapped area of a grass-shrub steppe in semi-arid Patagonia, Argentina, to show that the shrub community is essentially randomly structured, but that shrubs facilitate grasses in their immediate neighbourhood.

3 The occurrence of this random spatial structure provides important new information on the biology of shrub populations. In general, previous data from semi-arid and arid ecosystems have shown that adult shrubs tend to show over-dispersed patterns, whereas juveniles are clumped.

4 We find that the point approximation may produce misleading results (i) if plant size varies greatly, (ii) if the scale of interest is of the same order of magnitude as the size of the plants, and (iii) if the plants of a given pattern are constrained through competition for space by the presence of other plants. The point approximation worked well in all other cases, but usually depicted weaker significant effects than when the size and shape of plants were taken into account.

5 Our approach to quantifying small-scale spatial patterns in plant communities has broad applications, including the study of facilitation and competition. Ecologists will be able to use the software available to take advantage of these methods.

Key-words: community structure, facilitation, grid-based implementation, neighbourhood effects, null models, pair-correlation function, point pattern analysis, Ripley's *K*-function, spatial pattern, second-order spatial statistics

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Introduction

An important aim of ecology is to reach an understanding of processes underlying observed patterns (Levin 1992), such as the distribution of plants in space.

Because most plants cannot move from one environment to another they do not respond to some spatial average of the properties of the overall community but rather to their immediate neighbourhood (the so-called 'plant's-eye view', Turkington & Harper 1979). Although spatial pattern might therefore be expected to contain information about the underlying processes, identical spatial patterns may be generated by several substantially different processes (e.g. Levin 1992; Barot *et al.* 1999; Wiegand *et al.* 2003). One approach for inferring underlying processes from spatial patterns is to contrast

Correspondence: Thorsten Wiegand (tel. +49 341235 2479; fax +49 341235 3500; e-mail thorsten.wiegand@ufz.de).
*Present address: Community and Macroecology Group, Department of Ecology, Institute of Zoology, Johannes Gutenberg-Universität Mainz, D-55099 Mainz, Germany.

measured patterns with null models derived from specific assumptions about the underlying processes (Schurr *et al.* 2004; Wiegand & Moloney 2004). A useful framework for doing this is provided by point pattern analysis, a set of tools for analysing the spatial distribution of discrete points, e.g. individual trees mapped to Cartesian coordinates within a study area (Ripley 1981; Stoyan & Stoyan 1994; Diggle 2003). Methods using second-order statistics, such as Ripley's K function or the pair-correlation function $g(r)$ (Ripley 1976, 1981; Stoyan & Stoyan 1994), have proved particularly useful, especially in plant ecology (e.g. Goreaud & Pélissier 2003; Wiegand & Moloney 2004; Perry *et al.*, in press).

One of the limitations of point pattern analysis in plant ecology, however, is that the plants are idealized as points. The point approximation is valid where the size of the plants is small in comparison with the spatial scales investigated, but may obscure the real spatial relationships at smaller scales (e.g. Simberloff 1979; Prentice & Werger 1985), the relationship in which ecologists are mostly interested when interactions among plants are studied (Purves & Law 2002).

We extend a grid-based approach to point pattern analysis (Wiegand & Moloney 2004) to deal with objects of finite size and irregular shape. The basic idea is to represent plants in a study area by means of a categorical raster map with a cell size smaller than the size of the plants. A plant is represented by one or several adjacent grid cells, depending on its size and shape, in a map representing categories such as bare ground, cover of species 1, cover of species 2, and so on (Fig. 1). Although this approach corresponds with conventional point pattern analysis, the explicit consideration of real world structures (i.e. objects of finite size and irregular shape) prevents an analytical treatment. Our extension is therefore a simulation-based approach for testing specific 'ad hoc' hypotheses about the spatial dependencies of objects in a particular system.

A vegetation map of a study plot in the grass-shrub steppe in semi-arid Patagonia, Argentina, is used to illustrate our approach and to contrast it with one that approximates plants as points. We ask whether, and at which spatial scales, the patterns of shrubs show signi-

ficant non-random inter- and intraspecific relations (i.e. competition or facilitation) as frequently found in semi-arid plant communities (Aguilar & Sala 1999). Secondly, we ask whether the spatial pattern of grass tussocks shows evidence of facilitation by shrubs as hypothesized by Soriano *et al.* (1994). To promote a broader application of our approach the software Programita that implements the methods presented here is provided on request by the first author.

Point pattern analysis, grid-based estimators and categorical raster maps

Ripley's K function (Ripley 1976, 1981) and the pair-correlation function g (Stoyan & Stoyan 1994; Stoyan & Penttinen 2000), both of which are based on the distribution of distances between pairs of points, are commonly used to characterize spatial point patterns. The K -function can be interpreted as the expected number of additional points found within a distance r of an arbitrarily chosen point. This number, viewed as a function of radius and divided by overall point density, is based on all distances between points in the pattern. To stabilize the variance, a square root transformation of $K(r)$, $L(r) = (K(r)/\pi)^{0.5} - r$, is usually used. The pair-correlation function $g(r)$ is also derived from the K -function [$g(r) = (2\pi r)^{-1} dK(r)/dr$], and $K(r)$ and $g(r)$ are related to the cumulative distribution function and probability density function of distances between pairs of points (Stoyan & Penttinen 2000; Diggle 2003). Values of $g(r) > 1$ indicate that interpoint distances around r are more frequent, and values of $g(r) < 1$ that they are less frequent, than they would be under complete spatial randomness (CSR). For better interpretation, a transformation $O(r) = \lambda g(r)$ allows straightforward interpretation of local neighbourhood density, and is therefore sometimes used instead of the pair-correlation function $g(r)$ (e.g. Galiano 1982; Condit *et al.* 2000; Wiegand & Moloney 2004). The analogous bivariate extensions of all spatial statistics (here $K_{12}(r)$, $L_{12}(r)$, $g_{12}(r)$ and $O_{12}(r)$) follow as natural generalizations, so that $\lambda_2 K_{12}(r)$ is the expected number of type 2 points within distance r of an arbitrary type 1 point (where λ_2

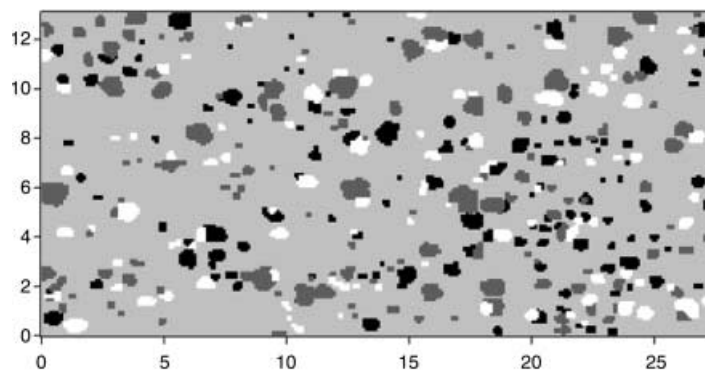


Fig. 1 Categorical map of the 27.4 × 13 m study plot in the semi-arid grass-shrub steppe showing individuals of the dominant shrub species *Adesmia campestris* (black), *Mulinum spinosum* (dark grey), and *Senecio filaginoides* (white). Each cell is 10 × 10 cm. Note that shrubs of several different species tend to grow in close proximity and to touch each other.

is the intensity of type 2 points in the study area). Further details can be found in standard textbooks (e.g. Ripley 1981; Stoyan & Stoyan 1994; Bailey & Gatrell 1995; Diggle 2003).

Wiegand & Moloney (2004) proposed simple grid-based estimators of the bivariate functions K_{12} , L_{12} and $g_{12}(r)$ (see equations A1, A2 and A3 in Appendix S1 in Supplementary Material), which can be easily extended to allow analysis of categorical raster maps such as Fig. 1. The size of the smallest plants, or other criteria for a minimal required resolution, is used to define an appropriate size for the cells.

To calculate the second-order statistics of categorical maps with the estimators given in the appendix (equations A2 and A3), a point pattern is formally constructed from the map. A given cell obtains one type 1 point if it is covered by one of the categories assigned to pattern 1 (e.g. all shrub species) and one type 2 point if it is covered by one of the categories assigned to pattern 2 (e.g. all grass species), but is classed as empty if it is not covered by either pattern 1 or 2 but is located within the study area, and is assigned to the 'mask' if the cell is outside the study area (see below 'Masking (space limitation)'). A more detailed description of the grid-based estimators used in this study is provided in the appendix.

Null models for plants with finite size and real shape

We use our approach to test null hypotheses concerning whether plants of a given species are randomly distributed, without overlaps, over the study area, whether the spatial patterns of two species are independent, or whether plants of species 2 experience competition (or facilitation) from plants of species 1. Although conceptually analogous to the most simple null models in point pattern analysis (described as CSR, independence and antecedent condition in Wiegand & Moloney 2004; see also below), consideration of the finite size and irregular shape of plants requires specification of more biological detail.

OVERLAP BETWEEN PLANTS

An important difference between the approaches is that plants considered as points cannot overlap (unless they occupy exactly the same location), but randomization of the position of plants of finite size requires rules to determine whether they are allowed to overlap. Because a category (and not a number of points) is assigned to each cell, overlap of two plants of the same pattern is not allowed, and, to avoid several small plants occupying the same grid cell, the size of the grid cell may need to be reduced. Depending on the null hypothesis, however, we may (or may not) allow plants of two different patterns to overlap, and this will affect data collection and mapping, as well as the application of null models.

RANDOMIZATION OF THE POSITION OF PLANTS

The null models CSR (complete spatial randomness) and antecedent condition (i.e. pattern 1 fixed, pattern 2 random) require randomization of the position of the plants (Wiegand & Moloney 2004). Randomization of points simply involves assignment of random coordinates, whereas the shape of a plant occupying several cells needs to be preserved. This can be achieved by rotating and mirroring the plant by 0, 90, 180 or 270 degrees (each of the eight variants being equally probable) and randomly shifting it as a whole.

Repeated trials are performed for each individual plant: if, after being randomly mirrored, rotated and shifted, a plant overlaps with an already distributed plant of the same pattern (or the other pattern if appropriate), falls partly outside an irregularly shaped study area, or does not conform with the selected method of edge correction (see below), this trial is rejected. The procedure is repeated until a location is found for all plants.

EDGE CORRECTION

The finite size of the plants requires edge correction as randomly displaced plants may fall partly outside the arbitrarily selected study rectangle. In the null model, this would reduce the proportion, λ , of occupied cells and produce a (positive) bias towards aggregation. We included three methods in the software Programita to mitigate this effect. First, randomized plants are not allowed to fall partly outside the study rectangle. This produces a negative bias towards regularity as fewer plants of the null model are distributed close to the border. The second method avoids this problem by treating the rectangular study plot encompassing the study region as a torus, i.e. the part of a plant outside the rectangle is made to appear at the corresponding opposite border. However, breaking relatively large plants into two smaller plants produces a slight positive bias. A third method uses the torus correction, but calculates the second-order statistics only inside an inner rectangle excluding cells close to the border (guard area). For a guard area wider than the diameter of the largest plants, the biases of the first and the second method disappear, but this may reduce the size of the study rectangle and thus the size of the sample of plants considerably. Therefore, the guard area selected needs to be wider than the diameter of most plants, but still small enough to yield a large enough sample of plants.

NULL MODEL 1 (CSR): RANDOMIZING PLANT POSITION FOR UNIVARIATE PATTERNS

The most simple and most widely used null model for univariate point patterns is complete spatial randomness (CSR), where any point of the pattern has an equal probability of occurring at any position in the study area, and the position of a point is independent of the

position of any other point (i.e. there is no interaction). Plants of finite size and irregular shape are, in analogy to CSR, distributed randomly as described above. This null model operates as a dividing hypothesis to detect further regularity or aggregation in univariate patterns.

NULL MODEL 2 (TOROIDAL SHIFT): INDEPENDENCE OF BIVARIATE PATTERNS

The null model testing for independence of two point patterns assumes that independent stochastic processes created the component patterns. Departure from independence indicates that the two patterns display attraction or repulsion, regardless of the univariate pattern of either group by itself. Preserving the separate second-order structures of observed patterns, whilst breaking their interdependence, can be achieved by simulations that involve random shifts of the whole of one component pattern relative to the other (Dixon 2002; Diggle 2003; Goreaud & Pélissier 2003). The same idea applies for plants of finite size and irregular shape: pattern 1 remains fixed whereas pattern 2 is randomly shifted as a whole across the study area, using a torus (toroidal shift). Note that this null model uses the torus method to treat plants that fall partly outside the study rectangle and that it requires that objects of different patterns are allowed to overlap. The latter may introduce a bias towards repulsion at small scales if the objects are known not to overlap. As an alternative, a univariate null model could be introduced to describe the second-order structure of pattern 2 and, if appropriate, an overlap of plants could be prohibited.

NULL MODEL 3 (ANTECEDENT CONDITION): RANDOMIZING ONLY ONE PATTERN OF A BIVARIATE PATTERN

The investigation of some processes, such as facilitation or competition, is more concerned with showing that plants of one pattern are not randomly distributed in the neighbourhood of the plants of the other pattern. The appropriate bivariate null model for this question keeps the plants of pattern 1 fixed and distributes the plants of pattern 2 randomly over the parts of the study area not occupied by plants of pattern 1 (this is called the antecedent condition in Wiegand & Moloney 2004). Note that the null models 'antecedent condition' and 'independence' are not the same because 'antecedent condition' does not preserve the observed second-order structure of pattern 2, and thus makes a specific assumption on the second-order structures of pattern 2. If plants of pattern 2 show large-scale variations in their intensity, one may distribute them in accordance with a heterogeneous Poisson null model (Wiegand & Moloney 2004).

MASKING (SPACE LIMITATION)

Competition for space is an important ingredient of null models for plants of finite size. We may encounter

situations where plants of the focal species cannot inhabit some areas, e.g. those already occupied by other species. Our approach facilitates an elegant extension of null models 1 (CSR) and 3 (antecedent condition) to consider these restrictions by assigning all non-accessible cells to a third pattern (called 'mask') and excluding them from the study region.

Masking is especially important for null model 3 (antecedent condition). Not considering the plants of the third pattern will reduce the intensity of pattern 2, which then appears to be aggregated with respect to pattern 1. For univariate analysis (i.e. null model 1, CSR) this effect is only important if larger continuous areas are non-accessible (see examples in Wiegand & Moloney 2004).

CONFIDENCE LIMITS OF THE NULL MODEL

We use Monte Carlo simulations of the stochastic process underlying the specific null model for construction of confidence limits. Each simulation generates a $g(r)$, $g_{12}(r)$, $L(r)$ or $L_{12}(r)$ function. We calculate approximate $n/(n+1) \times 100\%$ confidence limits from the highest and lowest values of these functions taken from n simulations of the null model (Bailey & Gatrell 1995), i.e. $n = 99$ simulations corresponds to 99% confidence limits. Thus if, for instance, $g_{12}(r)$ has some part outside that limit, it is judged to be a significant departure from the null model.

Analysis of shrubs in the semi-arid Patagonian steppe, Argentina

We illustrate our approach by analysing a categorical vegetation map of a study plot in the grass-shrub steppe in semi-arid Patagonia, Argentina. We focus on the spatial pattern of dominant shrub species because they are plants with finite size and irregular shape. In all analyses we contrast the respective spatial patterns with Monte Carlo simulations of appropriate null models. Additionally, we compare our approach with point pattern analysis, where each plant is idealized as a point, corresponding to the centre of the area it occupies.

STUDY SITE

The study site is located near Rio Mayo, Chubut, Argentina (45°41' S, 70°16' W), in the *Stipa speciosa*, *Stipa humilis*, *Adesmia campestris*, *Berberis heterophylla* and *Poa lanuginosa* community (Golluscio *et al.* 1982). The vegetation is codominated by tussock grasses and shrubs that have a basal cover of 32% and 8–12%, respectively, the rest being mostly dead material and bare ground (Golluscio *et al.* 1982; Sala *et al.* 1989). The mean annual rainfall for a 37-year period is 154 ± 44 mm (mean \pm SD), most of which occurs during fall and winter (March through August), and the mean annual temperature is 8.4 °C, with a mean monthly temperature ranging from 2 to 14 °C, in July and January, respectively (Fernández *et al.* 1991; Jobbágy *et al.* 1995). Soils have

an upper sandy layer 45–60 cm deep and a low calcareous stony layer (Paruelo *et al.* 1988).

THE GRASS-SHRUB STEPPE

The shrub community is composed of three dominant shrub species having more than 1% cover (*Mulinum spinosum*, *Senecio filaginoides* and *Adesmia campestris*) and three non-dominant shrub species having less than 1% cover (*Verbena tridens*, *Acantholippia eriphioides* and *Berberis heterophylla*). We only focused on the three dominant shrub species because the sample sizes of the non-dominants were too small for our purpose. These shrubs differ both in architecture and phenology. The shape of *M. spinosum* and *S. filaginoides* is approximately hemispherical, while *A. campestris* is similar to an inverted cone, its branches diverging from a central area at the base of the plant. *Adesmia campestris* is a deciduous species, bearing leaves from September to February. *Mulinum spinosum* keeps dead and spiny leaves, corresponding to five or more growth periods, and branches are devoid of them only at their base. *Senecio filaginoides* is an evergreen shrub that keeps its green and leafy appearance throughout the year (Soriano *et al.* 1994). Shrubs in general do not overlap, but they may grow close to each other (Fig. 1).

The dominant grass species (> 1% cover) are *Poa ligularis*, a palatable tussock grass, and the unpalatable tussock grasses *Stipa speciosa* and *Stipa humilis*. Other species in our study plot are non-dominant grasses such as *Bromus pictus*, *Bromus setifolius*, *Hordeum comosum* and *Stipa ibari* and sedges (*Carex* spp.). Tussock grasses are approximately 30 cm in height with linear, plicate leaves. Tussocks of these species keep old dead leaves that account for a high proportion of standing biomass.

DATA

In January 2001 we mapped a 27.4 × 13 m representative area of the shrub community (Fig. 1) with a spatial resolution of 10 × 10 cm, and categorized the cells according to the different shrub and grass species and dead material, the rest being bare ground. The area was located in a 2-year-old grazing enclosure, which had previously been moderately grazed (0.2 sheep ha⁻¹).

NULL HYPOTHESES AND NULL MODELS

Non-random spatial patterns caused by net positive or net negative plant–plant interactions are commonly reported for semi-arid vegetation in general (e.g. Aguiar & Sala 1998) and shrublands in particular (e.g. Wright 1982; Haase *et al.* 1996; Schenk *et al.* 2003; Schurr *et al.* 2004). Three cases are of particular interest: (i) where the pattern of all individuals of a given species shows aggregation or regularity; (ii) where the relationship between small (young) and large (adult) plants shows repulsion due to competition (Wright 1982; Haase *et al.* 1996) or attraction due to facilitation or dispersal;

and (iii) where the relationship between plants of different species (or functional groups) shows repulsion or attraction. To address these three general questions we performed five groups of analyses (Table 1).

Analysis 1: univariate shrub patterns

We used null model 1 (CSR) to analyse the spatial structure of the three different shrub species (Table 1, analysis 1). We hypothesized that shrubs would show regularity at smaller scales, due to intraspecific competition in this water-limited community, and a random pattern at larger scales.

Analysis 2: small shrubs vs. large shrubs

We divided the individuals of each shrub population into two classes: small individuals with a size of less than 10 cells (or 0.1 m²) and large individuals with a size of more than 10 cells (the smallest limit which gave reasonable sample sizes of small shrubs for all three species).

We first analysed the univariate patterns of small and large shrubs using null model 1 (CSR; Table 1, analyses 2a and 2b) to assess whether the univariate pattern of the two size classes differed from that determined for the entire population in analysis 1. To detect possible intraspecific competition or facilitation effects between small and large individual shrub plants we next analysed bivariate patterns between large shrubs (pattern 1) and small shrubs (pattern 2) (Table 1, analysis 2c). We used null model 3 (antecedent condition), which randomized the small plants without overlap and kept the large plants fixed. All shrubs of the other two dominant species and dead material were masked to account for the area of the study plot not accessible to small shrubs. However, we did not mask grasses.

Analysis 3: independence between shrub species

We tested for independence of pairs of shrub species using null model 2 (independence; Table 1, analysis 3). Note that this null model allows shrub species to overlap and might therefore introduce a bias for shrubs that are known not to overlap (as in our case).

Analysis 4: facilitation/competition between different shrub species

To detect small-scale interactions between shrubs of different species, which may indicate competition or facilitation, we investigated whether shrubs of species 2 are randomly distributed with respect to shrubs of species 1 (null model of antecedent condition; Table 1, analysis 4). For this null model we kept the locations of individual plants of species 1, but distributed the shrubs of species 2 randomly over the area not covered by shrubs of species 1. Shrubs of the third dominant species and dead material were masked.

Table 1 Null models, questions and methods used to investigate the spatial structure of dominant shrubs and grasses in the semi-arid Patagonian steppe, Argentina. Abbreviations: Ad = *Adesmia campestris*, Mu = *Mulinum spinosum*, Se = *Senecio filaginoides*, dead = dead material, Gr = grasses (all species). Null models: N1 = complete spatial randomness (CSR), N2 = independence (toroidal shift), N3 = antecedent condition (pattern 1 fixed, pattern 2 random)

Analysis	Pattern		Mask	Figure	Null model	Questions to be tested		
	1	2	Identifier					
<i>Univariate</i>								
1. Univariate shrub patterns								
	Ad	–	–	2a	N1: Randomization of shrubs without overlap	Is the spatial pattern random, aggregated, or regular?		
	Mu	–	–	2b				
	Se	–	–	2c				
2. Small shrubs and large shrubs								
(a) Small shrubs								
	Ad	–	–	3a	N1: Randomization of small shrubs without overlap	Is the spatial pattern random, aggregated, or regular?		
	Mu	–	–	3b				
	Se	–	–	3c				
(b) Large shrubs								
	Ad	–	–	3d	N1: Randomization of large shrubs without overlap	Is the spatial pattern random, aggregated, or regular?		
	Mu	–	–	3e				
	Se	–	–	3f				
<i>Bivariate</i>								
(c) Small shrubs vs. large shrubs								
	Ad	Ad	Mu, Se, dead	3g	N3: Large shrubs fixed, randomization of small shrubs without overlap	Facilitation or competition between small and large shrubs?		
	Mu	Mu	Ad, Se, dead	3h				
	Se	Se	Ad, Mu, dead	3i				
3. Independence between shrub species								
	Ad	Mu	–	4a	N2: Pattern 1 fixed, pattern 2 randomly shifted as a whole (toroidal shift)	Are shrub species independent of each other? (Overlap of shrubs allowed)		
	Ad	Se	–	4b				
	Se	Mu	–	4c				
4. Facilitation/competition between shrubs								
	Ad	Mu	Se, dead	4d	N3: Pattern 1 fixed, randomization of pattern 2 without overlap	Do shrubs of pattern 2 follow a random distribution with respect to shrubs of pattern 1?		
	Ad	Se	Mu, dead	4e				
	Se	Mu	Ad, dead	4f				
5. Facilitation of grasses through shrubs								
(a) All grasses vs. all shrubs								
	Ad, Mu Se	Gr	dead	5a	N3: Pattern 1 fixed, randomization of pattern 2 without overlap	Are grasses more aggregated around shrubs than random?		
(b) All grasses vs. <i>Senecio</i> shrubs (with mask)								
	Se	Gr	Ad, Mu, dead	5b			N3: Pattern 1 fixed randomization of pattern 2 without overlap	Are grasses more aggregated around <i>Senecio</i> shrubs than random?
(c) All grasses vs. <i>Senecio</i> shrubs (no mask)								
	Se	Gr	–	5c	N3: Pattern 1 fixed, randomization of pattern 2 without overlap	Are grasses more aggregated around <i>Senecio</i> shrubs than random?		

Analysis 5: facilitation of grasses by shrubs

To address the hypothesis of Soriano *et al.* (1994), that shrubs facilitate grasses in their immediate neighbourhood, we applied null model 3 (antecedent condition) where the respective shrub species were defined as pattern 1 (locations were kept fixed), grass tussocks as pattern 2 (randomly distributed), and dead material (in some analyses) as mask. In a first analysis we used all grasses vs. all shrub species to investigate the general effect of grass facilitation by shrubs (Table 1, analysis 5a). We then analysed how space competition might influence the results of spatial pattern analysis. We chose to consider the effects of all grasses vs. the shrub species

Senecio filaginoides, with and without masking of all other shrub species and dead material (Table 1, analyses 5b and 5c), as masking should have the strongest effect on the species with the lowest cover.

Settings during analyses

For all analyses we calculated approximate 99% confidence limits using 99 randomizations of the null model. We used the 'guard area' method to treat plants that fall partly outside the study rectangle. A four cell wide guard area along the border of the rectangle is excluded from analysis and the second-order statistics are calculated based only on the patterns of the plants inside this

border. This removed most of the biases but did not reduce the sample size of plants too much. The g -functions were always calculated with a ring width of three cells (see Appendix S1). For each null model we calculated both the L -function and the g -function. The L -function is, in general, sensitive to violation of a null model but does not provide correct information on the scale at which a null model is violated (i.e. the memory, see Wiegand & Moloney 2004). We therefore show the results of the pair-correlation function to demonstrate departures from a null model at specific spatial scales. Results of the L -function are shown either (i) to prove that the null model was satisfied at all spatial scales or (ii) if the number of points was low. In one analysis (Table 1, analysis 5) we used the O -ring statistic instead of the g -function because we needed a direct interpretation of a neighbourhood density. The analyses and null models used are summarized in Table 1. All statistical analysis was done with the Programita software (Wiegand & Moloney 2004).

Results

SIZE CLASS DISTRIBUTIONS

Our study plot contained 133 *Mulinum* individuals (covering *c.* 5% of the area), 126 *Adesmia* individuals (*c.* 3% of the area), 98 *Senecio* individuals (*c.* 3% of the area), and 4114 tussocks of dominant grass species (*c.* 11–12% of the area). Dead material covered approximately 8% of the area. Both *Adesmia* and *Mulinum* showed a skewed size-class distribution with many small individuals and few large individuals (not shown). The average diameter (calculated approximately as $d = 2(100n/3.14)^{0.5}$, with n being the number of cells occupied) of *Adesmia* shrubs, was 29.8 cm (standard deviation 15.5 cm, range 11.3–79.8 cm). Individual plants of *Mulinum* grew considerably larger than plants of the other two shrub species (average 36.2 cm, standard deviation 22.5 cm, range 11.3–101.6 cm), and showed both a skewed and a bimodal diameter distribution with an additional peak at larger diameters of about 80 cm (not shown). The *Senecio* population had the lowest number of small individuals in comparison with the other two shrub species and the average size of *Senecio* shrubs was 33.3 cm (standard deviation 14.8 cm, range 11.3–74.0 cm).

UNIVARIATE ANALYSES

The univariate analysis of the three dominant shrub species showed almost no evidence of non-random intraspecific interactions (Fig. 2). The pair-correlation function detected no departure from null model 1 (CSR, Fig. 2), except for *Adesmia*, where a slight clustering at a scale of 1.1 m was apparent (Fig. 2a). Analyses with the L -function yielded the same result (not shown). Our hypothesis of small-scale regularity due to intraspecific competition was thus not confirmed.

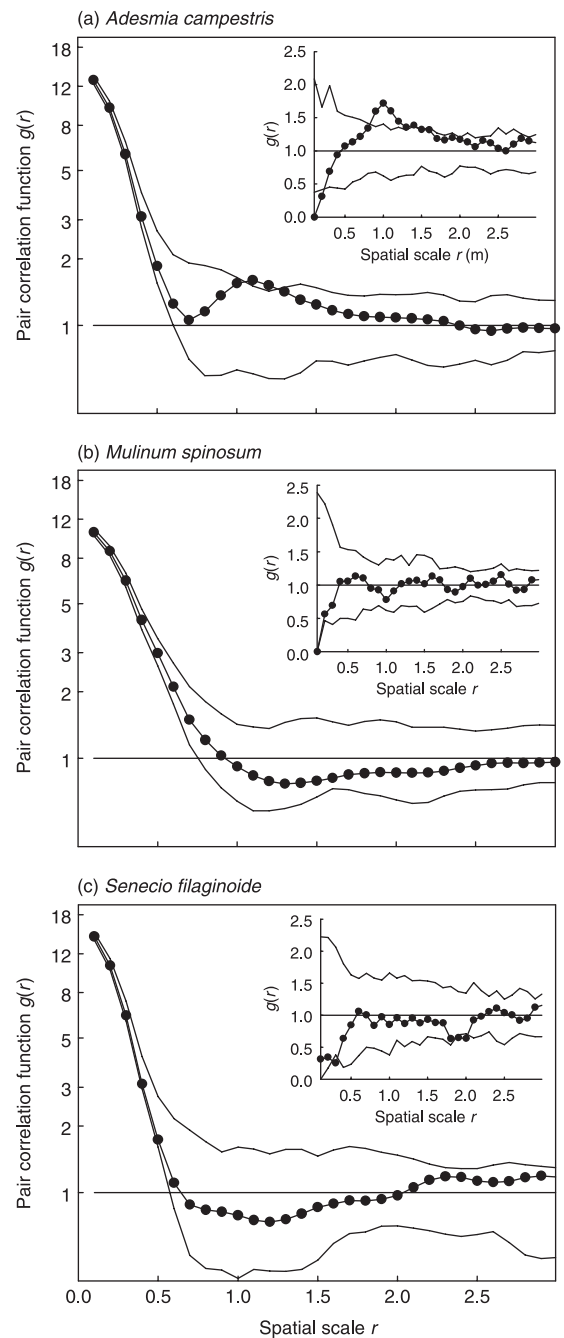


Fig. 2 Univariate analysis of the spatial pattern of three Patagonian shrub species using the pair-correlation function (filled circles) with confidence limits (lines) for null model 1 (CSR), which involved randomization of the locations of shrubs without overlap. The confidence limits were constructed using the highest and lowest $g(r)$ from 99 replicates of the null model. The horizontal line shows the value $g = 1$, which is the theoretical expectation for a random point pattern. Note that the y -axis is on a logarithmic scale. The insets show the same analysis under the point approximation.

The analysis for *Adesmia* using the point approximation showed marked differences from the results obtained with our method of finite objects. While the plants with finite size were mostly randomly distributed (the test depicts only slightly significant clustering at 1.1 m), the point approximation showed a clear clustering at scales

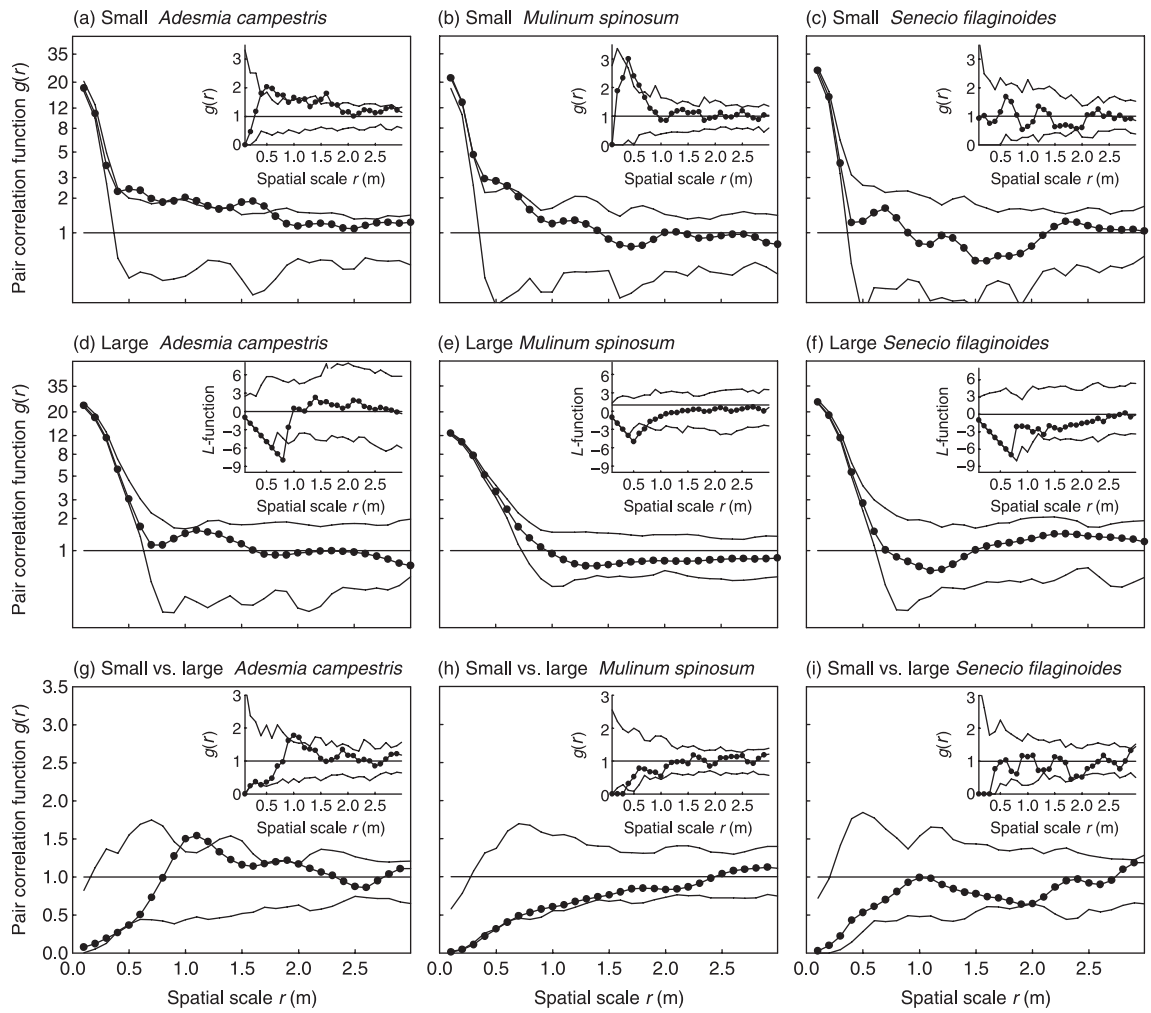


Fig. 3 Separate univariate analysis of small and large shrubs and bivariate analysis, testing for competition or facilitation. Uni- and bivariate (a–f and g–i, respectively) pair-correlation functions (closed circles) are shown together with their confidence limits (lines). Univariate analyses used null model 1 (CSR), which involved randomization of the locations of shrubs without overlap, and bivariate analyses used null model 3 (antecedent condition), which randomised the locations of small shrubs without overlap. Other conventions as in Fig. 2.

of 90–110 cm and repulsion at small scales of 10–20 cm (subplot in Fig. 2a). A closer look at the univariate patterns revealed that, for both approaches, smaller *Adesmia* and *Mulinum* individuals were significantly clumped at 0.5–1.8 m and 0.1–0.6 m, respectively (Fig. 3a,b). In contrast, the patterns of large shrubs of all species (Fig. 3d,e,f), as well as small *Senecio* shrubs (Fig. 3c), showed no significant deviations from our null model. The point approximation usually depicted significant effects that were weaker than in the approach using objects of finite size (subplots of Fig. 3), and the results of the two approaches often differed significantly at small scales (e.g. Figs 2a and 3d,e).

SMALL SHRUBS VS. LARGE SHRUBS

Bivariate analyses (null model 3, antecedent condition) testing for competition or facilitation between large and small shrubs showed differences between the three species. Only *Adesmia* showed a strong significant departure from the null model. Small *Adesmia* plants

occurred significantly more frequently at a distance of about 1 m from large plants (Fig. 3g). Small *Mulinum* plants showed a weakly significant tendency to occur less frequently in the neighbourhood of larger individuals up to 60 cm (Fig. 3h), whereas small *Senecio* shrubs were randomly distributed in relation to larger ones (Fig. 3i). Again, the point approximation indicated these effects to be much weaker, or did not reveal them at all.

INDEPENDENCE AND FACILITATION/COMPETITION OF SHRUBS

The bivariate analysis under the null model of independence (null model 2) showed that the spatial patterns of shrubs of different species were basically independent (Fig. 4a–c). We only found a significant departure from independence for the pair *Mulinum*–*Adesmia* at small scales (Fig. 4a). This effect, however, is a consequence of the bias introduced by the rule of the null model of independence, which allows shrubs of

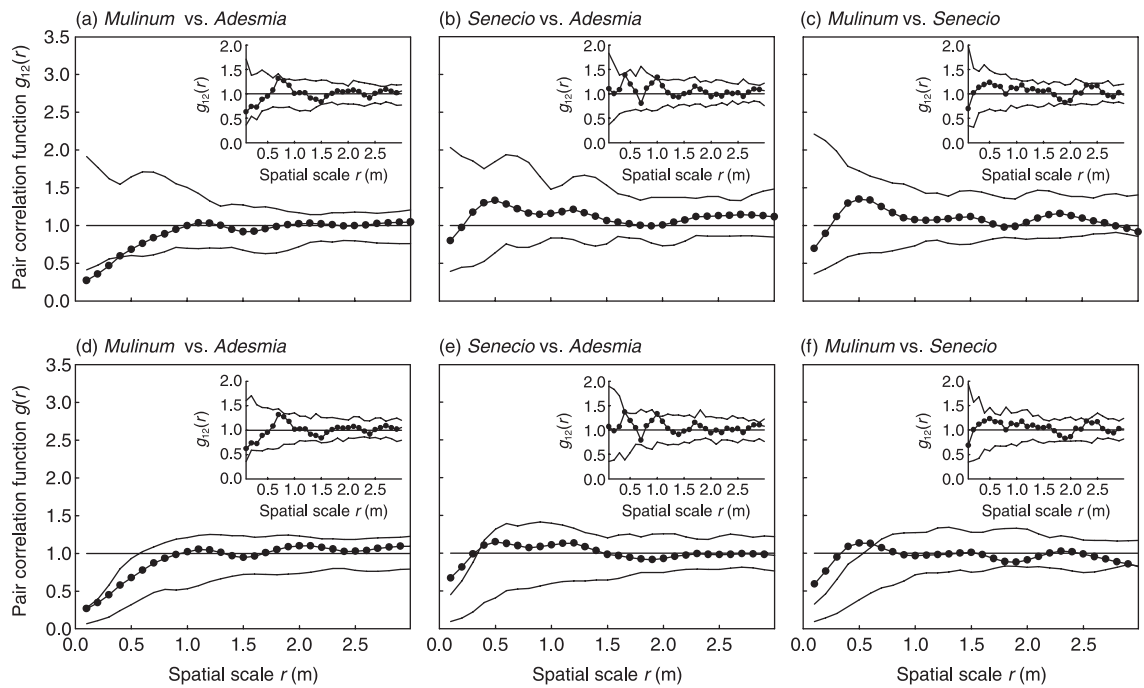


Fig. 4 Bivariate analyses using null models 2 (independence) and 3 (antecedent condition) testing for independence (a–c) and competition/facilitation (d–f) between pairs of shrub species. The null model of independence preserved the pattern of one shrub species (pattern 1) and performed random shifts of the pattern of the second shrub species (pattern 2) across the study region using a torus (toroidal shift), thus preserving the two patterns in their observed form but breaking its observed dependence. Note that this model allows overlap between individuals of the two shrub species. Null model 3 randomized the locations of pattern 2 without overlap and kept pattern 1 unchanged.

different species to overlap (shrubs did not overlap in the field). Absence of a significant effect for the two other pairs (Figs 4b,c), in turn, indicates that they may show attraction at small scales. The point approximation reflected our findings reasonably well except for the biased small-scale repulsion of *Mulinum*–*Adesmia*.

The bivariate null model 3 (antecedent condition, facilitation/competition between shrubs) revealed a random spatial relationship between *Adesmia* and *Mulinum* (Fig. 4d), but significant small-scale aggregation of the other two species combinations up to approximately 30 and 50 cm, respectively (Fig. 4e,f). This is in accordance with the results found under the null model of independence (see above) because those shrubs are known not to overlap in reality. The point approximation revealed the same pattern for the pair *Mulinum*–*Adesmia*, but failed to detect aggregation at small scales for the pairs *Senecio*–*Adesmia* and *Mulinum*–*Senecio*.

SHRUBS FACILITATE GRASSES

We found clear evidence in the main analysis for facilitation of grasses in the immediate neighbourhood of shrub cells, although the point approximation showed a significant repulsion at small scales of 10–20 cm and only a slightly significant attraction at the scale of 0.5 m (Fig. 5a). We also analysed the distribution of grasses around *Senecio* (Fig. 5b) and assessed the potential impact of masking inaccessible areas (Fig. 5c). The null model where other shrubs and dead material were

masked detected a weak repulsion at scales of about 1 m, but this effect was much stronger in the absence of masking, indicating significant repulsion at scales of 0.7–1.3 m. In both cases, the point approximation did not detect this effect and instead showed significant repulsion at scales of 10–20 cm.

Discussion

FINITE SIZE VS. POINT APPROXIMATION

We extended conventional point pattern analysis, where objects are approximated as points, to categorical raster maps, which allow an analysis of objects of finite size and irregular shape. This approach facilitates incorporation of real world structures and provides a powerful tool for the statistical analysis of plant spatial patterns that is not subject to the limitations of the point approximation. The comparison of our approach with point pattern analysis revealed sometimes subtle differences between the two approaches, often at small scales. Consideration of real plant size and shape might therefore be especially important where the small-scale spatial structure of a plant community is concerned (Purves & Law 2002). Based on our results, literature and general considerations we suggest that important determinants of spatial patterning are often not taken into consideration when mapping locations of plants as points, and may therefore produce misleading results (summarized in Fig. 6).

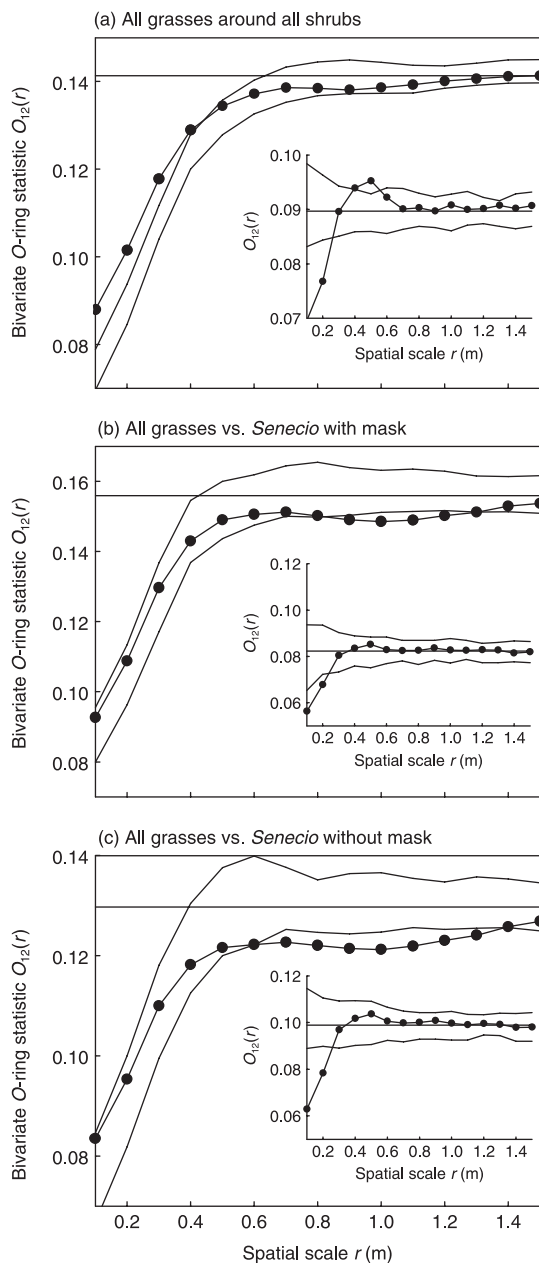


Fig. 5 Bivariate analyses to investigate the hypothesis of Soriano *et al.* (1994) that shrubs facilitate grass tussocks. (a) All grass tussocks vs. all shrubs masking the locations of dead material. (b) All grass tussocks vs. *Senecio* masking the other shrubs and dead material. (c) All grass tussocks vs. *Senecio* without masking. We used null model 3 (antecedent condition), which randomized the locations of the grass tussocks without overlap and kept the pattern of the shrubs unchanged. For better interpretation we used the bivariate O -ring statistics $O_{12}(r) = \lambda_2 g_{12}(r)$.

Hard core effect

A hard core effect arises if circular plants with diameter d_H do not overlap (Fig. 6a). In this case, the plant centres are always at least a distance d_H apart and the point approximation yields a pair-correlation function that is zero for distances $r < d_H$ and a L -function that decreases linearly for distances $r < d_H$. The hard-core effect produces small-scale regularity, as evident, for example, in Fig. 3(d).

Soft core effect

A soft core effect arises if non-overlapping plants have different sizes (Fig. 6b). As a consequence, smaller distances between plant centres occur less frequently than expected under random distribution of the corresponding plant centres. This results in a tendency to small-scale regularity, as evident in the univariate analyses of the different shrub species (Fig. 2).

Aggregation effect

A subtle aggregation effect may occur if the size of the plants varies greatly and if large plants occupy a considerable proportion of the study area. Larger numbers of smaller plants may occur within the gaps left by larger individuals (Fig. 6c). If all plants are randomly distributed (but without overlap), an analysis of the point pattern of the plant centres will indicate aggregation at scales above the size of the largest plants. This effect was responsible for the differences between the approaches noted in *Adesmia* (Fig. 2a), where shrub sizes differed by up to 50-fold. The point pattern of all individuals showed strong aggregation at a scale of about 1 m, whereas the finite size framework showed only weak aggregation (Fig. 2a). Separate analyses showed that these results were due to large *Adesmia* shrubs being randomly distributed (Fig. 3d) while small individuals showed aggregation up to 1.5 m (Fig. 3a).

Weighting effect

The point approximation puts the same weight on all plants regardless of their size. However, a large plant that covers, say, 50 times the area of a small plant should intuitively be given a higher weight than a small plant. Our approach of weighting according to projection (Fig. 6d) explains the differences between the approaches for *Adesmia*, where the random pattern of the more highly weighted large shrubs ‘overpowered’ most of the aggregation seen in smaller individuals. An opposite effect may occur if several small plants occupy the same grid cell, and the simplest way of avoiding this is to reduce the cell size. An alternative technique for considering size differences in point patterns is to introduce a ‘mark’ size and to analyse the correlation of these marks by means of the mark-correlation function (e.g. Penttinen *et al.* 1992).

Real shape effect

Processes that approximate a plant of finite size by a circle of the same size can account for effects caused by finite size (Fig. 6a–c), but not for effects introduced by the real shape of the plants. Such effects were evident in the analysis of facilitation/competition between different shrub species. The bivariate patterns of the pairs *Senecio*–*Adesmia* (Fig. 4e) and *Mulinum*–*Senecio* (Fig. 4f) showed significant attraction at smaller scales, indicating that

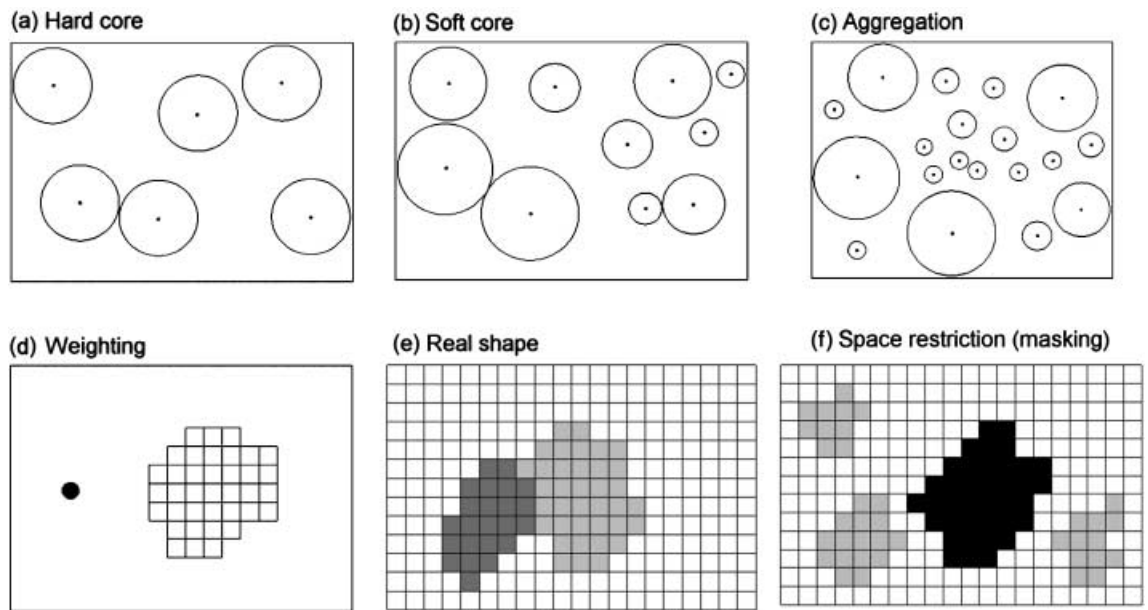


Fig. 6 Six important effects introduced (or obscured) by the point approximation. Each effect may obscure the real spatial dependence between objects of finite size and irregular shape. (a) Hard core effect causing regularity at scales smaller than the hard core distance d_H . (b) Soft core effect causing regularity at smaller scales. (c) Aggregation effect causing aggregation at small and intermediate scales. (d) Weighting effect causing regularity or aggregation. (e) Real shape effect (dark grey, species 1; light grey, species 2). (f) Space restrictions causing virtual aggregation (light grey, species 1; black, mask).

plants grow closer together than expected by random distribution of one of the patterns. This indicates a positive net balance between interspecific competition and facilitation effects.

Space restriction effect (masking)

Because of environmental heterogeneity there may be large areas of the ground that plants of the focal species cannot inhabit. This can have a strong impact on the outcome of a second-order analysis (i.e. virtual aggregation; Wiegand & Moloney 2004) and requires using an irregularly shaped study area (Pélissier & Goreaud 2001; Wiegand & Moloney 2004). Within the finite size framework it may be necessary to consider additional areas of ground that the focal species cannot inhabit because they are already occupied by other species (Fig. 6f). We expect an effect if the spatial structure of the other species is non-random at scales where possible facilitation or competition occurs (e.g. Fig. 5b,c). Accounting for the influence of this effect would be complicated with standard techniques.

NULL MODELS

The formulation of an appropriate null model is at the heart of successful application of second-order statistics. The approach presented here allows for testing specific null models adapted to the biology of the study system and provides a considerable degree of added realism. Besides accounting for the shape of the plants, this is achieved by a rule that either allows or prohibits overlap of plants of the two different patterns. This is relevant

for a bivariate null model to approximate, for instance, 'third dimension' effects that may occur if smaller plants such as grass tufts grow inside larger unpalatable shrubs. Additionally, prohibiting overlap of the focal species with plants of a third pattern (i.e. masking) provides additional flexibility for hypothesis testing. Our framework allows for a straightforward generalization of several other useful null models for more specific circumstances, which include a heterogeneous Poisson null model and random labelling (Wiegand & Moloney 2004). Random labelling may be applied, for example, if plants of different species form a complete mosaic of tiles rather than patches on a background, a situation that is difficult to analyse with the other null models presented here.

HOW IS THE PATAGONIAN SHRUB COMMUNITY STRUCTURED?

To our surprise we found that the shrub component in our study plot in the Patagonian shrub-grass steppe was basically randomly structured. Most analyses showed no evidence of intraspecific competition as all three dominant shrub species followed a random distribution in almost all cases (Figs 2 and 4d) or small-scale attraction (Figs 4e,f). Our results are surprising because marked non-random spatial patterns are commonly reported for semi-arid vegetation and shrublands. Net positive plant interactions are often found in arid and semi-arid areas because these environments are characterized by high abiotic stress and low productivity. Positive interactions may buffer effects of abiotic stress (Bertness & Callaway 1994; Callaway & Walker 1997;

Schenk *et al.* 2003) whereas net negative plant interactions arise through competition and may create spatial segregation (i.e. a 'regular' distribution) of individual plants. One possible explanation is that density-dependent processes (i.e. competition, facilitation) for shrub populations occurred at an early stage of individual plant growth. Since competition for soil water is the main limiting factor for plants in the semi-arid Patagonian steppe (Sala *et al.* 1989; Paruelo & Sala 1995; Aguiar & Sala 1998; Golluscio *et al.* 1998), differences in rooting depth and root systems, which are mostly restricted to the area under the canopy, may also account for the absence of the expected inter- and intraspecific competition and facilitation from our study system.

A clear exception to the non-random patterns, however, was that small *Adesmia* individuals, which were aggregated at scales of 0.5 m to 1.8 m (Fig. 3a), tended to occur less frequently in the immediate neighbourhood of large conspecifics, but occurred significantly more frequently in the 1.0–1.3 m neighbourhood of larger individuals (Fig. 3g). Competition with large *Adesmia* shrubs may prevent small *Adesmia* individuals from occurring in their immediate neighbourhood, with localized seed dispersal increasing the density of smaller individuals within 1 m.

The bivariate analyses under the null model of antecedent condition revealed that *Senecio* plants grew closer to *Mulinum* and *Adesmia* plants than expected by randomization without overlap (Figs 4e,f). The absence of competition may have allowed shrubs of the two species pairs to grow in close proximity and, when large, to grow around each other. *Mulinum*–*Adesmia* did not show this effect (Fig. 4d), which indicates that there may be small-scale competition that prevents these species from touching.

Our bivariate analysis of grass–shrub interactions supported the hypothesis of Soriano *et al.* (1994) that shrubs facilitate grasses in their immediate neighbourhood (Fig. 5a), possibly due to differences in root density, soil water potential and evaporation (Aguiar & Sala 1994; Soriano *et al.* 1994; Aguiar & Sala 1998). Protection from winds, accumulation of sand, silt and organic debris and production of litter might all enhance establishment and growth of grasses around shrubs because of their influences on water dynamics and heat flux (Soriano *et al.* 1994). On the other hand, Aguiar & Sala (1994) found that seeds of a grass species tend to accumulate in the close neighbourhood of individual shrub plants and propose that seed distribution can overcome the effects of plant interactions to determine the pattern of association between shrubs and grasses. We found repulsion of grasses at scales of about 1 m around *Senecio* (Fig. 5b,c), possibly because grass dynamics are relatively slow (i.e. it takes a long time to colonize gaps left by dead shrubs). The bivariate g_{12} between cells of *Adesmia* and *Mulinum* (pattern 2) and *Senecio* (pattern 1) showed a peak at 1–1.5 m (result not shown), which indicates that a cell occupied by a dead shrub will be slightly more likely than expected at

this distance. If this cell is not immediately filled by a grass tussock, grass density will be lower than expected at this distance from an arbitrary cell occupied by *Senecio*.

We found that considering the real shape of plants is important (i) if the size of the objects differs greatly, (ii) if the scale of interest is of the same order of magnitude as the size of the objects, and (iii) if the objects of a given pattern cannot occupy the entire study region, but are constrained by other objects competing for space. All of these circumstances may significantly change the biological interpretation of the spatial dependences of univariate or bivariate patterns, but in other cases the point approximation should work well.

As plants respond to the biotic and abiotic composition of some neighbourhoods (the 'plant's-eye view' of the community), plant size and shape may affect the analysis of many important questions in plant ecology, such as the balance between facilitation and competition. Our approach for plants of finite size and real shape is a natural extension of the traditional point pattern analysis (with which ecologists are familiar), and requires only slight modifications that arise directly out of the nature of finite objects. It facilitates more sophisticated analyses of the spatial relationship between plants, and can be broadly applied. Clearly, mapping plants with real shape instead of point coordinates takes considerably more effort (Hennie Snyman, personal communication), but is necessary if we are to consider real size and shape effects without severe approximations.

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com

Appendix S1 Description of point pattern analysis and grid-based estimators of second-order statistics.