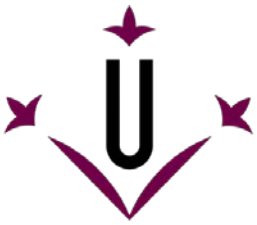

Analysing spatial correlation of weeds and harvester ants in cereal fields using point processes

Running title: Spatial correlation of weeds and harvester ants

Carles Comas[1], Aritz Royo-Esnal[2], Jordi Recasens[2], Joel Torra*[2]

[1]Department of Mathematics, AGROTECNIO, Universitat de Lleida, Avda. de l'Estudi General, 4 E-25001, Lleida, Spain.

[2]Weed Science and Plant Ecology Research Group, Department of Hortofructicultura, Botànica i Jardineria, AGROTECNIO, ETSEA, Universitat de Lleida, Avda. Rovira Roure 191, E-25198 Spain.

* Corresponding author. Email address: joel@hbj.udl.cat; tel. No. +34973702318; fax. No. +34973238264

Abstract

The interaction between the spatial distribution of weed richness and weed cover and the spatial location of harvester ant nets was investigated in cereal fields. The understanding of such interdependencies can be relevant to understand weed population dynamics in dryland cereal fields and may enhance management strategies for weed control. We used spatial statistical tools derived from point process theory. In particular, we compared the two spatial configurations by assuming two different point patterns. We did so by replacing the weed random fields by a related point pattern and comparing it with the point pattern of harvester ants. Our results suggest that areas with a high density of ant nests are in general areas with low weed richness and low weed cover, and that large nests have a greater impact on weed spatial configurations than small nests. Thus preserving and enhancing regular ant nest distributions, especially of large nests, would have a major impact on depleting weed density and consequently enhancing weed control.

Keywords Cross-pair correlation function, *Messor barbarus*, Point pattern, Random field, Weed plants.

Introduction

Weed species are distributed unevenly in arable fields and, consequently, diversity is not expected to be homogeneous within the fields (Izquierdo et al. 2009a). Weeds occur in patches because they tend to cluster where conditions favour propagule banks and seed dispersal (Colbach et al. 2000). Biotic, abiotic, and anthropogenic processes likely contribute to the expression of weed ‘‘patchiness’’ in agricultural fields (Williams et al. 2002). The spatial distribution may be related to the interaction of several of these factors, such as soil type (Burton et al. 2006; Di Virgilio et al. 2007; Dieleman et al. 2000), cultivation or tillage (Barroso et al. 2006; Burton et al. 2006; Colbach et al. 2000; Heijting et al. 2009), harvesting (Barroso et al. 2006; Blanco-Moreno et al. 2004; Heijting et al. 2009), herbicides (Barroso et al. 2004; Dieleman et al. 2000) and competition between crop and weeds (Blanco-Moreno et al. 2006). Spatially explicit factors affecting seed distribution, germination and survival have a big impact on weed spatial distribution and dynamics (Blanco-Moreno et al. 2004). However, differences in weed population dynamics and spatial distribution with respect to within-field heterogeneity are not well documented despite increasing interest in site-specific management of agro-ecosystems (Burton et al. 2006). Moreover, the evaluation of the spatial structure of weed diversity and factors that determine it (i.e. field management or landscape heterogeneity) can be extremely important in biodiversity studies (Izquierdo et al. 2009a). Finally, the understanding of spatial dynamics of weed patches is of fundamental importance for achieving realistic models of weed populations and for weed management (Blanco-Moreno et al. 2006).

Several reasons for weed patchiness have been proposed, but it is clear that the factors that influence weed mortality are among the most important (Dieleman and Mortensen 1999; Woolcock and Cousens 2000). One of the factors that is known to have a big impact on weed survival and population dynamics is epigeaic seed predation (Westerman et al. 2003). In dryland cereals of NE Spain the main seed predator is the harvester ant *Messor barbarus* L. (Baraibar et al. 2009). This species causes 46%-100% of post-dispersal seed losses before weed seeds enter the seedbank (Westerman et al. 2012). Harvester ants can cause significant losses of weed seeds

84 in dryland cereals and can thus contributing to weed control (Baraibar et al. 2011). However,
85 harvester ant nests are not evenly distributed on the field (Díaz 1992), because factors such as
86 soil characteristics (Wiernasz and Cole 1995), field management (Díaz 1991) and interaction
87 between nests (Ryti and Case 1992) affect these distribution patterns. A previous study in NE
88 Spain indicated that the origin of spatial trends (4-12 m) of harvester ants in cereal fields should
89 be sought in biotic factors, such as seed availability or intrinsic ones (Blanco-Moreno et al.
90 2014). Because harvester ant abundances are not constant in fields, seed predation rates are not
91 equal within a dryland cereal field (Torra et al. in press). Therefore, if there is spatial variability
92 in the seed predation by harvester ants, we hypothesize that there can also be a spatial
93 relationship between this process and the spatial distribution of weeds in these cereal fields.
94 This could partially explain the spatial and temporal dynamics of weeds and seed losses in the
95 life cycle of annual weeds highlighted by Dicke et al. (2007), at least in the study area.
96 This paper analyses the interaction between the spatial distribution of weeds and the
97 spatial location of ant nets. In particular, it considers weed richness and weed cover samples
98 over a rectangular grid, and the spatial location and size of ant nests. These two sampling
99 processes result in two different sets of spatial data, i.e. point referenced data (lattice) for the
100 weed samples and a point pattern for the ant nests (Cressie 1993). Since the pioneering paper of
101 Ford (1975), who studied the effect of between-plant competition on *Tagetes patula* L.
102 (marigolds) planted on a regular grid, several studies have used lattice data to analyse the spatial
103 distribution of plants, including the spatial and temporal structures of weeds (Barroso et al.
104 2004; Blanco-Moreno et al. 2006; Colbach et al. 2000; Izquierdo et al. 2009a). The spatial
105 analysis of ant nets has also been investigated by regarding their nests as a point pattern (see
106 among others, Harkness and Isham 1983; Nicolai et al. 2010; Tanner and Keller 2012), also in
107 cereal fields (Blanco-Moreno et al. 2014). A spatial point process is a stochastic mechanism that
108 generates a countable set of events x_i in a bounded region A (see, for instance, Diggle 2003); a
109 point pattern is a stochastic realization of a point process. Animal and plant ecology has applied
110 numerous statistical methods belonging to point processes (Diggle 2003; Illian et al. 2008;

Stoyan and Penttinen 2000; Wiegand et al. 2006) to tackle ecological management questions (Comas 2009; Comas and Mateu 2011; Law et al. 2009). However, few approaches (if any) have combined both sets of sample data to analyse the interaction between spatial structures of weeds and ants. The analysis of these interactions may be valuable for interpreting the processes governing the spatial relationship between weed plants and harvester ants, thus providing key information on the life cycle for future control management of weed species in cereal fields.

The main objective of this study was to investigate the spatial interdependencies between spatial locations of harvester ant nests and the spatial configuration of weed richness and coverage. To do so we considered a novel methodology based on spatial statistical tools derived from point process theory. To the best of our knowledge this the first time that the space spatial structure of weeds and ants are analysed using point processes.

Materials and Methods

Study area

A no-tillage dryland cereal field was surveyed to analyse the relationship between the spatial distribution of its weeds and harvester ant nests. The selected field (2 ha), located in Bellmunt d'Urgell, Spain, was managed following the usual practices of the region. Barley was sown at a rate of 180 kg/ha in late October. Broad-leaved weeds were controlled with a mixture of herbicides (florasulam + 2,4-D at 0.75 l//ha) on 10 March 2011.

Data

Weed species and abundance were evaluated in early May 2011 after herbicide spraying. The percentage of total weed cover and the number of species were recorded in 50 x 50 cm quadrats located every 10 m in a 150 x 50 m grid placed on the field, resulting in 96 sampling units. In each quadrat, weed cover of each species was determined using a scale from 0 to 100. Nodes were georeferenced using a differential global positioning system (DGPS), model GS02, with centimetre precision (Leica Geosystems AG, Heerbrugg, Switzerland). Moreover, *Messor*

barbarus nest abundance and spatial distribution was recorded in the experimental area in early August 2011 after harvest. In this case, we recorded nest abundance in a 50 x 50 m small region of the rectangular area where weed species and abundance were evaluated. The nests were usually determined by counting one opening per nest, though large nests were assumed to have more than one entrance. Nests were only included if ants were detected, to prevent counting of abandoned nests. Therefore, counting was done from sunrise until around noon, because high temperatures limit ant activity (Azcárate et al. 2007). All nests were marked with spray-paint to prevent double counting, and nest size was determined using a subjective scale ranging from 1 (smallest) to 5 (largest), according to the area occupied by the colony, the number of entrances, worker size and the number of active ants (Baraibar et al. 2011). This classification is based on the assumption that larger colonies will have more reproductive adults and that there will be more openings for their release. Four nest sizes were therefore classified into four main categories: categories 1 and 2 for nest sizes <0·4 m^2; category 3 for nest sizes in the range 0.4-1 m^2; category 4 for nest sizes in the range 1-2 m^2; and category 5 for nest sizes >2 m^2. This classification distinguishes between nests with a single entrance (category 1) and nests with more than one entrance (categories 2, 3, 4 and 5) (Baraibar et al. 2011). Finally, each marked nest was georeferenced with the DGPS mentioned above.

Spatial statistics

Analysing the spatial point structure of ant nests

The spatial structure of a point pattern can be described by various summary characteristics. To analyse the spatial structure of ant nests (point locations) we used a spatial correlation function derived from point process theory. We considered the pair correlation function (Illian et al. 2008), an estimator of which can be obtained as

$$\hat{g}(r) = \frac{1}{2\pi\hat{\lambda}^2|A|}\sum_{(x_1,x_2)\in\varphi}^{\neq}\frac{\kappa(\|x_1-x_2\|-r)}{e(x_1,\|x_1-x_2\|)} \quad (1)$$

for a given observation region A with area $|A|$ and inter-point distance r. Here φ is the observed point pattern, $\hat{\lambda}$ is an estimator of the point intensity, i.e. the number of points (i.e. nests) per unit space, $\kappa(\cdot)$ is the Epanechnikov kernel function, $\sum^{\neq}$ stands for the summation over all pairs such that $x_i \neq x_j$, where $x_i = \{x_{i1}, x_{i2}\}$ is a point in the Euclidian plane, and $e(\cdot)$ is the Ripley's factor (Ripley 1976) to correct edge effects. Broadly speaking, this function indicates point inhibition when $\hat{g}(r) < 1$, $\hat{g}(r) = 1$ denotes the Poisson case (i.e. a random point process) with no interaction between points, while $\hat{g}(r) > 1$ implies point clustering for any $r > 0$.

Analysing the spatial dependence between ant nets and weed richness and coverage weeds based on point process correlation functions

To analyse the spatial dependences between the distribution of ant nests and the spatial configuration of weed richness and coverage, we used spatial statistical tools derived from point process theory. In particular, we adopted an approach initially formulated by Illian et al. (2008) to analyse the spatial correlation between point patterns and random fields. This statistical approach is based on comparing some summary statistics associated with these spatial structures. Consider a stationary and isotropic space point process Φ in two dimensions with point intensity λ and a random field $Z = Z(x)$, where x is any location in the Euclidian plane, both processes over an observation window A (i.e. the area of study). The basic idea of this approach is to replace Z by a point pattern with point intensity determined by Z. In this way, a spatial correlation function is obtained to compare and evaluate the existing dependences between the ant point pattern and the derived point pattern determined by Z.

Let us now replace Z (random fields for weed data) by a point pattern and consider the correlation between two point patterns. So if the random field Z is positive (as it is in our case), we can assume this function as the intensity field function of a Cox process (a family of point processes driven by a random point intensity; see for instance Stoyan et al. 1995), and then

192 generate point realizations based on this point intensity. To obtain the resulting random field Z
193 from the n field weed samples, we used an ordinary kriging approach based on the gloval
194 variogram matrix (Isaaks and Srivastava 1989). Notice that other spatial procedures can be
195 considered to obtain this random field Z (see for instance, Cressie 1993). Now Z is derived
196 from values $Z_i = Z(y_i)$ at the points y_i in a grid B (i.e. the prediction values after ordinary
197 kriging). Note that Z_i can be multiplied by a scaling factor if necessary. Moreover, assuming
198 that for each cell c_i centred at point location y_i the random field value is constant and equal
199 to Z_i, we can generate point realizations based on this grid. Now points are located at random
200 over B and accepted only if $U \leq Z_i / \max(Z_i)$, where $U \sim U(0,1)$, i.e. a uniform random
201 number. Therefore, areas with large values of Z_i (high-intensity values) are expected to have
202 greater numbers of points than areas with small values of Z_i, and so on. This procedure will
203 generate a point pattern based on the intensity function Z_i. After that, label 1 was assigned to
204 the original point pattern of ant nests and label 2 to the resulting Cox pattern based on Z_i,
205 thereby resulting in a bivariate point pattern. Then, summary statistics involving a bivariate
206 point pattern can be used to evaluate the dependences of both point patterns. Here, we used the
207 *partial* or *cross-pair correlation* function $g_{12}(r)$ (Illian et al. 2008), for a given inter-point
208 distance $r > 0$ to evaluate this spatial structure. This correlation function is a bivariate
209 derivation of the pair correlation function to study the spatial dependences of point classes for
210 bivariate point patterns. This function indicates point-type inhibition when $g_{12}(r) < 1$,
211 $g_{12}(r) = 1$ is the Poisson case (i.e. point-types are independently distributed from each other),
212 while $g_{12}(r) > 1$ implies point-type clustering. An estimator function for this function can be
213 defined (Illian et al. 2008) as
214
215 $$\hat{g}_{12}(r) = \frac{1}{2\pi\hat{\lambda}_1\ \hat{\lambda}_2 |A|} \sum_{x_1 \in \varphi_1, x_2 \in \varphi_2} \frac{\kappa(\|x_1 - x_2\| - r)}{e(x_1, \|x_1 - x_2\|)}, \qquad (2)$$

where φ_1 and $\hat{\lambda}_1$ are the point pattern and the point intensity of the point class 1 (say), respectively, for a given inter-point distance r. For the Epanechnikov kernel function, we chose the bandwidth to be equal to $c/\sqrt{\hat{\lambda}}$, where typically $c = 0.1-0.2$ (here $c = 0.2$), as suggested by Stoyan and Stoyan (1994).

In order to choose the variogram model that provides the best goodness of fit, we used a cross-validation procedure based on the standardized prediction residuals (Cressie 1993, page 102). The spherical and exponential parametric models provided the best mathematical fit for the empirical variograms (see also Table 1). Given that both models provide similar parametrizations, we finally considered the spherical model to be in concordance with similar studies carried out in the same geographic region in which the spherical model also provided the best goodness of fit for similar datasets (Izquierdo et al. 2009a and b). Therefore, this model was considered to provide a valid parametric representation for the ordinary kriging procedures. All the geostatistical and point processes procedures have been computed using the GeoR and the Spatstat statistical packages, respectively, for the R statistical environment (R Development Core Team, 2007).

Testing for spatial independence for (bivariate) point patterns

For each kind of spatial correlation function, we tested for spatial independence following a Monte Carlo approach based on the random simulation of (marked) point patterns from the null hypothesis (Poisson). We simulated 999 (bivariate) point patterns under the null hypothesis of spatial independence, and for each one, an estimator of one of the correlation functions defined above was obtained. These set of functions were then compared with the resulting estimator of this correlation function for the point pattern under analysis. Under this test, we rejected the null hypothesis (spatial independence) if the resulting estimator of this correlation function lay outside the 25th largest and/or smallest envelope values obtained from the set of simulated functions with an exact significant level of $\alpha = 2 \times 25/(999+1) = 0.05$. Tests for each

(bivariate) point pattern considered here are defined as follows. For the point pattern of ant nets we tested against spatial point independence based on the random simulation of Poisson point configurations (see for instance, Stoyan and Stoyan 1994). Whilst, under the bivariate point patterns (i.e. two point classes i and j) we considered a *random labelling* approach (see, Illian et al. 2008).

Table1 around here

Results

The total number of weed species was 12 and *Papaver rhoeas* L. and *Bromus diandrus* Roth were the most abundant species (Table 2). The number of species per sampling unit ranged from 0 to 4.

Table 2 around here

In total, 237 (948 nests/ha) nests were identified and the nest size class two was by far the most abundant in the experimental area (Table 3).

Table 3 around here

Are the locations of ant nests spatially correlated?

Figures 1a and 1b show the spatial positions of ant nests for the five size classes and the related bivariate point pattern assuming only two size classes, namely small (classes 1 and 2) and large (classes 3, 4 and 5) classes, respectively. This size classification is chosen since it provides a reasonable number of points for each class, 185 small nests and 52 large nests, and distinguishes between nests with a single entrance (classes 1 and 2) and nests with more than one entrance (classes 3, 4 and 5). Visual inspection of these point patterns does not provide much information about the spatial dependence of these two point patterns. The resulting pair correlation function

(1) for the point pattern of ant nests is shown in Figure 1c together with their respective 25th largest and smallest envelope values based on 999 Poisson point randomizations. This suggests an inhibitory structure for short inter-nest distances of less than 1 m.

How are small and large nests related to each other in space?

Similarly, when analysing the spatial configuration of ant nests assuming small and large nest sizes via the resulting cross-pair correlation function (2) (Figure 1d), we reject the null hypothesis of independence and accept that small and large nests are spatially correlated. In particular, this indicates repulsion between nest classes, i.e. large nests (say) are unlikely to be surrounded by small classes at short inter-event distances (<2 m).

Figure 1 around here

Does the presence of ant nets affect weed richness and coverage assuming point process correlation functions?

Figures 2 shows the resulting prediction maps $Z(y_i)$ based on an ordinary kriging approach for weed richness and weed cover, together with the spatial locations of the two nest size classes. To perform these ordinary krigings we considered a spherical variogram model for the two empirical variograms (i.e. weed richness and cover) (see Table 4 for the parameter values), based on 96 sampling points, which is an enough number of points to obtain reliable empirical variograms. Once again, visual inspection of these figures does not highlight any apparent spatial structure between ant nests and weed spatial configurations, so the comparison of summary statistics associated with these spatial structures is clearly necessary if we are to detect spatial correlations. Notice that resulting weed richness and cover random fields are visually very similar, thereby suggesting that areas with large number of weed species are also areas with large weed coverage.

Table 4 around here

Let us now consider the spatial correlation between nest locations and the weed random fields based on the cross-pair correlation function (2). Figure 3 shows the resulting cross-pair correlation for ant nest locations (large and small sizes) and the Cox point patterns for the weed random fields, highlighting that ant nest locations and weed richness are negatively correlated for inter-event distances of less than 8 m. This finding suggests that for short inter-event distances high intensities of ant nests results in low weed richness. Note that this result is more evident for large nest sizes than for small ones (see Figure 3c). Moreover, the resulting cross-pair correlations for nest locations and weed cover indicate that these variables are spatially uncorrelated regardless of the nest size (Figure 3d, e and f).

Figure 3 around here

Discussion

To analyse the spatial dependences between the distribution of ant nests and the spatial configuration of weeds, we used spatial statistical tools derived from point process theory. In particular, we compared the two spatial configurations by assuming two different point patterns. We did so by replacing the weed random fields by a related point pattern, and analysing it with the ant point pattern.

Our results suggest that, in general, areas with a high density of large ant nests are areas with low weed richness. In direct contrast, small nest classes do not apparently affect the resulting structure of weed richness. Our results also suggest that ant nest density does not affect too much weed coverage. Moreover, when analysing the spatial configuration of ant nests we found that small and large nest classes are also negatively correlated, indicating that large nests (say) are unlikely to be surrounded by small classes at short inter-event distances. This spatial inhibition of nests can probably be explained by the killing of smaller colonies by workers

belonging to large colonies or by the lower probability of nest initiation success in the proximities of long-established colonies (Hölldobler 1981; Ryti and Case 1992), as pointed out by previous research in cereal fields in NE Spain (Blanco-Moreno et al. 2014). This fact, together with the results obtained in the analysis of the spatial interaction between weed random fields and ant point patterns, suggests that weeds were able to survive in zones with small nests, areas with probably lower ant pressure, and areas where large nests were not found. Seed predation pressure in areas with small ant nests is lower than that in areas with larger nests, because in these areas there are fewer workers and less foraging activity (Crist and Macmahon 1992). So, in areas with small nests it is expected that there will be more weed cover than in areas with large nests. Therefore, the presence of large nests apparently regulates the richness and cover of weeds, limiting them to areas with smaller ant nests.

There are several factors that could explain ant nest distribution and weed distribution. Among those extrinsic, soil characteristics should be one of the main factors. In this sense however, one study carried out in the same area (Baraibar et al. 2011) showed that none of the studied soil properties could explain ant nest densities in the studied fields. The appointed paper did not perform a spatial analysis relating both variables, but it already highlighted that soil could not be an important factor explaining ant nest distribution. That research and another one in the same study area (Blanco-Moreno et al. 2014), elucidated that other factors not considered, such as seed availability, intraspecific competition or the distribution of landing sites of founding queens, may play an additional role in determining ant density and spatial variability. Anyway, the apparent correlation between ant nests and weed richness found here could be just because large nests occupy a large space, of at least 1 m in diameter, where nest entrances are kept free of plants (Torra, pers. observ.).

Regarding the weed cover, some reasons could partially explain its uncorrelation with the spatial arrangement of harvester ant nests. By far, the most abundant and regularly distributed species were *B. diandrus* and *P. rhoeas*. *P. rhoeas* has a very short exposure time to ants on the soil surface because small-sized seeds have a faster seed burial (Westerman et al. 2003). This fact, together with its highly persistent seeds, would allow the presence of an

important seedbank, which could buffer the regulation exerted by harvester ants on its abundance. In the case of *B. diandrus*, this species is less preferred by harvester ants than other weed species (Westerman et al. 2012).

We conclude that large nests of *M. barbarus* can have a bigger impact on weed spatial configurations than small nests. Therefore, preserving and enhancing regular ant nest distributions, especially those of large nests, would have a major negative impact on weed survival, and simultaneously improve weed control measures. Management strategies to promote this effect are desirable, but further research is required to understand the factors affecting ant nest distribution in cereal fields. For example, long-term no-tillage systems in dryland cereal fields would promote bigger nests and higher nest densities compared with tilled fields (Baraibar et al. 2011) or irrigated fields (Baraibar et al. 2009). This research only considered one cereal field. Once the spatial dependencies between weeds and harvester ants are possible to study, the findings of this research should be corroborated in more cereal fields in the study area. Moreover, understanding how management factors affect these spatial interdependencies would be key for improving weed control. Finally, a future research line can be the modelling of such structures, such as ant nests as a Cox process with weed parameters as a covariate. A such work may open up new and promising research lines.

Acknowledgements

We wish to thank the funding of research by the Ministry of Education and Science of Spain (projects AGL 2007-60828 and AGL 2010-22084-C02-01).

References

Azcárate FM, Kovacs E, Peco B (2007) Microclimatic conditions regulate surface activity in harvester ants *Messor barbarus*. J Insect Behav 20:315-329.

Baraibar B, Westerman PR, Carrión E, Recasens J (2009) Effects of tillage and irrigation in cereal fields on weed seed removal by seed predators. J Appl Ecol 46:380-387.

Baraibar B, Torra J, Westerman PR (2011) Harvester ant (*Messor barbarus* (L.)) density as related to soil properties, topography and management in semi-arid cereals. Appl Soil Ecol 51:60-65.

Barroso J, Fernández-Quintanilla C, Ruiz D, Hernáiz P, Rew LJ (2004) Spatial stability of *Avena sterilis* ssp. *ludoviciana* populations under annual applications of low rates of imazamethabenz. Weed Res 44:178-186.

Barroso J, Navarrete L, Sánchez del Arco MJ, Fernández-Quintanilla C, Lutman PJW, Perry NH, Hull RI (2006) Dispersal of *Avena fatua* and *Avena sterilis* patches by natural dissemination, soil tillage and combine harvesters. Weed Res 46:118-128.

Blanco-Moreno JM, Westerman PR, Atanackovic V, Torra J (2014) The spatial distribution of nests of harvester ants *Messor barbarus* (L.) in dryland cereals. Insect Soc 22:145-152.

Blanco-Moreno JM, Chamorro L, Sans FX (2006) Spatial and temporal patterns of *Lolium rigidum–Avena sterilis* mixed populations in a cereal field. Weed Res 46:207-218.

Blanco-Moreno JM, Sans FX, Chamorro L, Masalles RM, Recasens J (2004) Spatial distribution of *Lolium rigidum* seedlings following seed dispersal by combine harvesters. Weed Res 44:375-387.

Burton MG, Mortensen DA, Lindquist JL (2006) Effect of cultivation and within-field differences in soil conditions on feral *Helianthus annuus* growth in ridge-tillage maize. Soil Till Res 88:8-15.

Colbach N, Forcella F, Johnson GA (2000) Spatial and temporal stability of weed populations over five years. Weed Sci 48:366–377.

Comas C (2009) Modelling forest regeneration strategies through the development of a spatio-temporal growth interaction model. Stoch Environ Res Risk Assess 23:1089-1102.

Comas C, Mateu J (2011) On the Takacs-Fiksel estimation method for forest field observations. Stoch Environ Res Risk Assess 25:287-300.

408 Crist TO, Macmahon JA (1992) Harvester ant foraging and shrub-steppe seeds: interactions of
409 seed resources and seed use. Ecology 73:1768-1779.
410 Cressie N (1993) Statistics for Spatial Data. John Wiley and Sons, New York, USA.
411 Di Virgilio N, Monti A, Venturi G (2007) Spatial variability of switchgrass (*Panicum virgatum*
412 L.) yield as related to soil parameters in a small field. Field Crop Res 101:232–239.
413 Díaz M (1991) Spatial patterns of granivorous ant nest abundance and nest site selection in
414 agricultural landscapes of Central Spain. Insect Soc 38:351-363.
415 Díaz M (1992) Spatial and temporal patterns of granivorous ant seed predation in patchy cereal
416 crop areas of central Spain. Oecologia 91:561-568.
417 Dicke D, Gerhards R, Büchse A, Hurle K (2007) Modeling spatial and temporal dynamics of
418 *Chenopodium album* L. under the influence of site-specific weed control. Crop Prot
419 26:206-211.
420 Dieleman JA, Mortensen DA (1999) Characterizing the spatial pattern of *Abutilon theophrasti*
421 seedling patches. Weed Res 39:455-467.
422 Dieleman JA, Mortensen DA, Buhler DD, Ferguson RB (2000) Identifying associations among
423 site properties and weed species abundance. II. Hypothesis generation. Weed Sci 48:576-
424 587.
425 Diggle PJ (2003) Statistical Analysis of Spatial Point Patterns. Hodder Arnold, London, UK.
426 Ford ED (1975) Competition and stand structure in some even-aged monocultures. J Ecol
427 63:311–333.
428 Harkness RD, Isham V (1983) A Bivariate Spatial Point Pattern of Ants' Nests. J Appl Stat
429 3:293-303.
430 Heijting S, Van der Werf W, Kropff MJ (2009) Seed dispersal by forage harvester and rigid-tine
431 cultivator in maize. Weed Res 49:153-163.
432 Hölldobler B (1981) Foraging and spatiotemporal territories in the honey ant *Myrmecocystus*
433 *mimicus* wheeler (*Hymenoptera*: *Formicidae*). Behav Ecol Sociobiol 9:301-314.
434 Illian J, Penttinen A, Stoyan H, Stoyan D (2008) Statistical analysis and modelling of spatial
435 point patterns. Wiley, New York, USA.

436 Isaaks EH, Srivastava RM (1989) An Introduction to Applied Geostatistics. Oxford University
437 Press, New York, USA.
438 Izquierdo J, Blanco-Moreno JM, Chamorro L, González-Andújar JL, Sans FX (2009a) Spatial
439 distribution of weed diversity within a cereal field. Agron Sustain Dev 29:491-496.
440 Izquierdo J, Blanco-Moreno JM, Chamorro L, Recasens J, Sans FX (2009b) Spatial Distribution
441 and Temporal Stability of Prostrate Knotweed (*Polygonum aviculare*) and Corn Poppy
442 (*Papaver rhoeas*) Seed Bank in a Cereal Field. Weed Sci 57:505-511.
443 Law R, Illian J, Burslem DFRP, Gratzer G, Gunatilleke CVS, Gunatilleke IAUN (2009)
444 Ecological information from spatial patterns of plants: insights from point process theory. J
445 Ecol 97:616-628.
446 Nicolai N, Feagin RA, Smeins FE (2010) Spatial Patterns of Grass Seedling Recruitment Imply
447 Predation and Facilitation by Harvester Ants. Environ Entomol 39:127-133.
448 R Development Core Team (2007) R: A Language and Environment for Statistical Computing.
449 R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org.
450 Ripley BD (1976) The second-order analysis of stationary point processes. J Appl Probab
451 13:255-266.
452 Ryti RT, Case TJ (1992) The role of neighborhood competition in the spacing and diversity of
453 ant communities. Am Nat 139:355-374.
454 Stoyan D, Stoyan H (1994) Fractals, Random Shapes and Point Fields: Methods of Geometrical
455 Statistics. Wiley, Chichester, UK.
456 Stoyan D, Kendall WS, Mecke J (1995) Stochastic Geometry and its Applications. John Wiley
457 and Sons, New York, USA.
458 Stoyan D, Penttinen A (2000) Recent applications of point process methods in forestry statistics.
459 Stat Sci 15:61-78.
460 Tanner CJ, Keller L (2012) Nest distribution varies with dispersal method and familiarity-
461 mediated aggression for two sympatric ants. Anim Behav 84:1151-1158.
462 Torra J, Atanackovic V, Blanco-Moreno JM, Royo-Esnal A, Westerman PR (2015) Effect of
463 patch size on seed removal by harvester ants. Weed Res. (in press).

Wackernagel H (1998) Multivariate geostatistics. Springer, Berlin, Germany.

Westerman PR, Wes JS, Kropff MJ, Van der Werf W (2003) Annual losses of weed seeds due to predation in organic cereal fields. J Appl Ecol 40:824-836.

Westerman PR, Atanackovic V, Royo-Esnal A, Torra J (2012) Differential weed seed removal in dryland cereals. Arthropod-Plant Inte 6:591-599.

Wiegand T, Kissling WD, Cipriotti PA, Aguiar MNR (2006) Extending point pattern analysis for objects of finite size and irregular shape. J Ecol 94:825-837.

Wiernasz DC, Cole BJ (1995) Spatial Distribution of *Pogonomyrmex occidentalis*: Recruitment, Mortality and Overdispersion. J Anim Ecol 64:519-527.

Williams II MM, Mortensen DA, Marx DB (2002) Within-field soil heterogeneity effects on herbicide-mediated crop injury and weed biomass. Weed Sci 49:798-805.

Woolcock JL, Cousens RA (2000) Mathematical analysis of factors affecting the rate of spread of patches of annual weeds in an arable field. Weed Sci 48:27-34.

Table 1 Values of a cross-validation procedure based on the standardized prediction residuals for two variogram parametrization initially considered; smaller values indicates better goodness of fit for the model under analysis (Cressie, 1993)

	Weed richness	Weed cover
Spherical	0.00108	0.00002
Exponential	0.00127	-0.00009

Table 2 Weeds species found in a sampled area of 50 x 50 m in May 2011 after herbicide spraying in a no-till cereal field in Bellmunt d'Urgell, Spain.

Species	Frequency (nº of sampling units)	Mean percentage coverage ±SE per sampling unit
Bromus diandrus	63	7.2 ± 1.2
Papaver rhoeas	17	4.6 ± 0.7
Veronica hederifolia	7	3.4 ± 0.5
Fumaria densiflora	9	2.7 ± 0.5
Fumaria officinalis	1	5.0
Avena sterilis ssp. *ludoviciana*	1	1.0
Anacyclus clavatus	3	0.5 ± 0.0
Galium aparine	1	1.0
Galium parisiense	2	0.3 ± 0.0
Lolium rigidum	1	1.0
Herniaria hirsuta	1	0.1
Sonchus oleraceus	1	0.1

Table 3 Abundances of harvester ant nests in an area of 50 x 50 m in August 2011 for five different nest sizes in a no-till cereal field in Bellmunt d'Urgell, Spain.

Nest size class*	Number
1	37
2	148
3	37
4	9
5	6

* Subjective scale of nest size from 1 (smallest) to 5 (largest); see Material and Methods.

Table 4 Estimated variogram parameter values obtained for weed richness and cover empirical variograms under a spherical variogram model.

	Nugget	Sill	Range
Weed richness	0.083	0.077	20.001
Weed cover	0.699	0.293	13.350

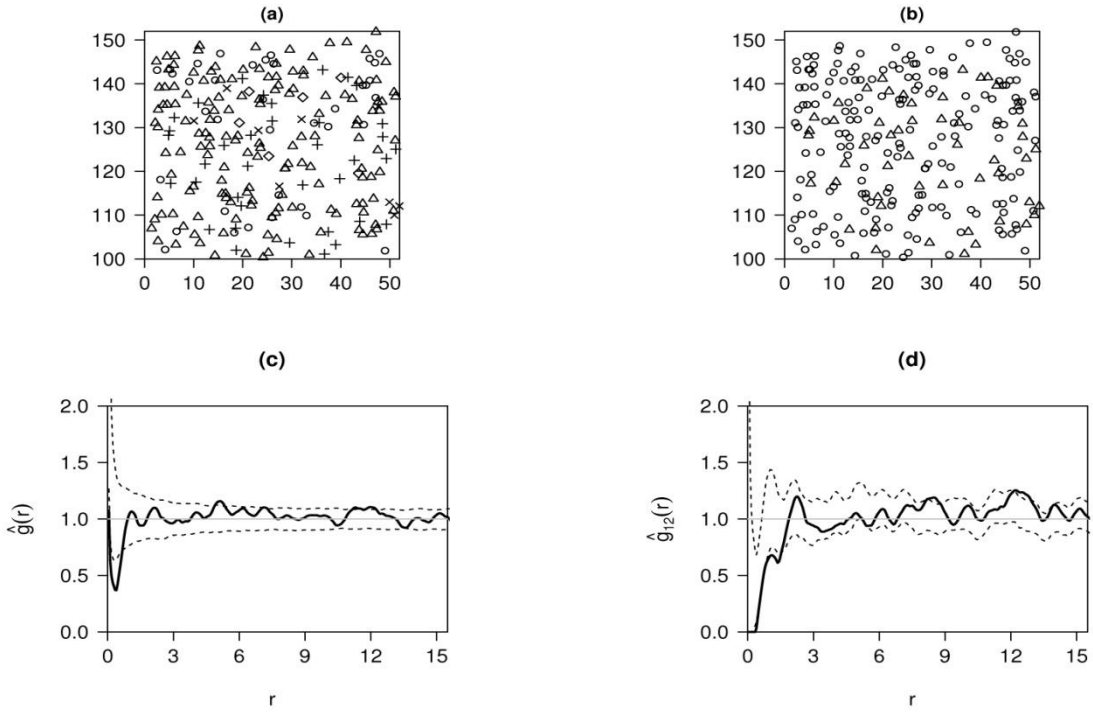

Fig. 1 (a) Point patterns of ant nest positions for five size classes (x and y axes are the nest positions coordinates): class 1 (circle, smallest class), class 2 (triangle), class 3 (cross), class 4 (multiplication sign), and class 5 (diamond). (b) The related bivariate point pattern assuming only two size classes: small (circle, classes 1 and 2), and large (triangle, classes 3, 4 and 5) sizes in a cereal field in Bellmunt d'Urgell, Spain. (c) Resulting estimator of the pair correlation function (see equation (1)) for all the ant nest positions along with the resulting fifth largest and smallest envelope values based on 199 Poisson point randomizations (dashed lines). (d) Resulting estimator of the cross-pair correlation function (see equation (2)) for the ant nest bivariate point pattern together with the resulting fifth largest and smallest envelope values based on 999 random labelled (i.e. independent) bivariate point configurations (dashed lines).

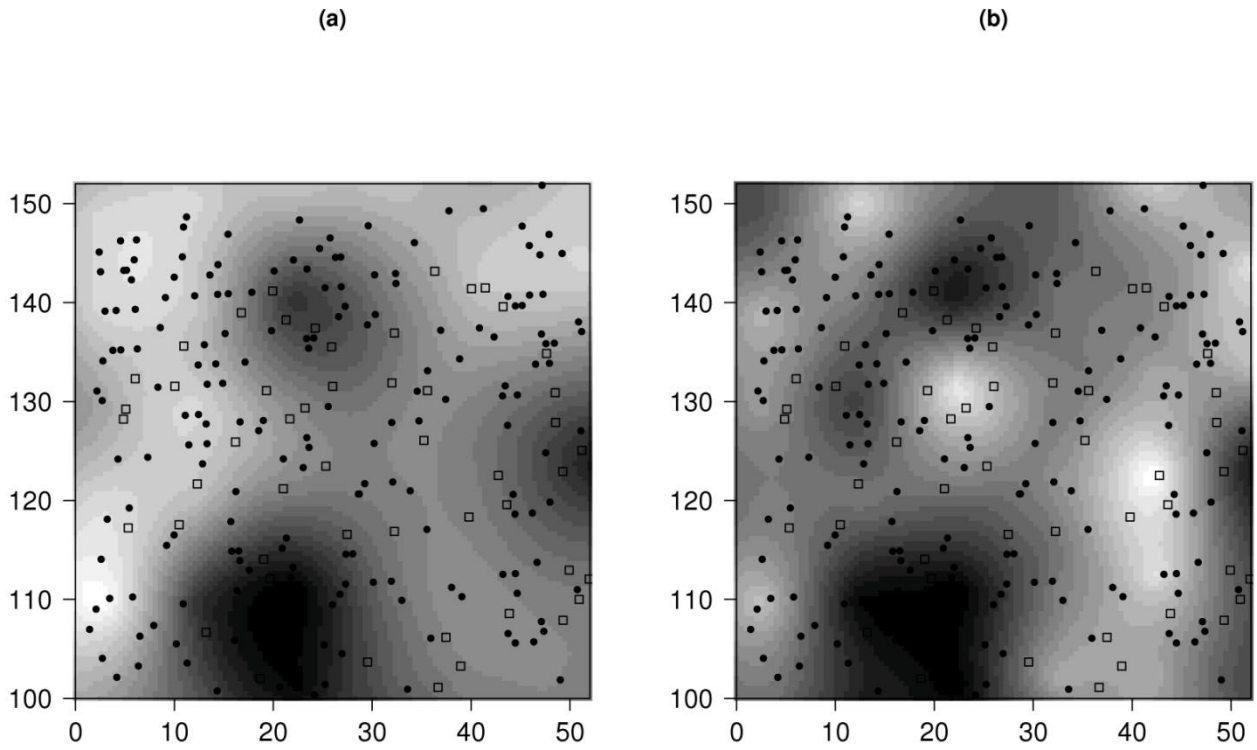

Fig. 2 Resulting maps $Z(y_i)$ based on an ordinary kriging approach for weed richness (a) and cover (b), together with spatial locations of the two nest size classes, large (square) and small (bullet).

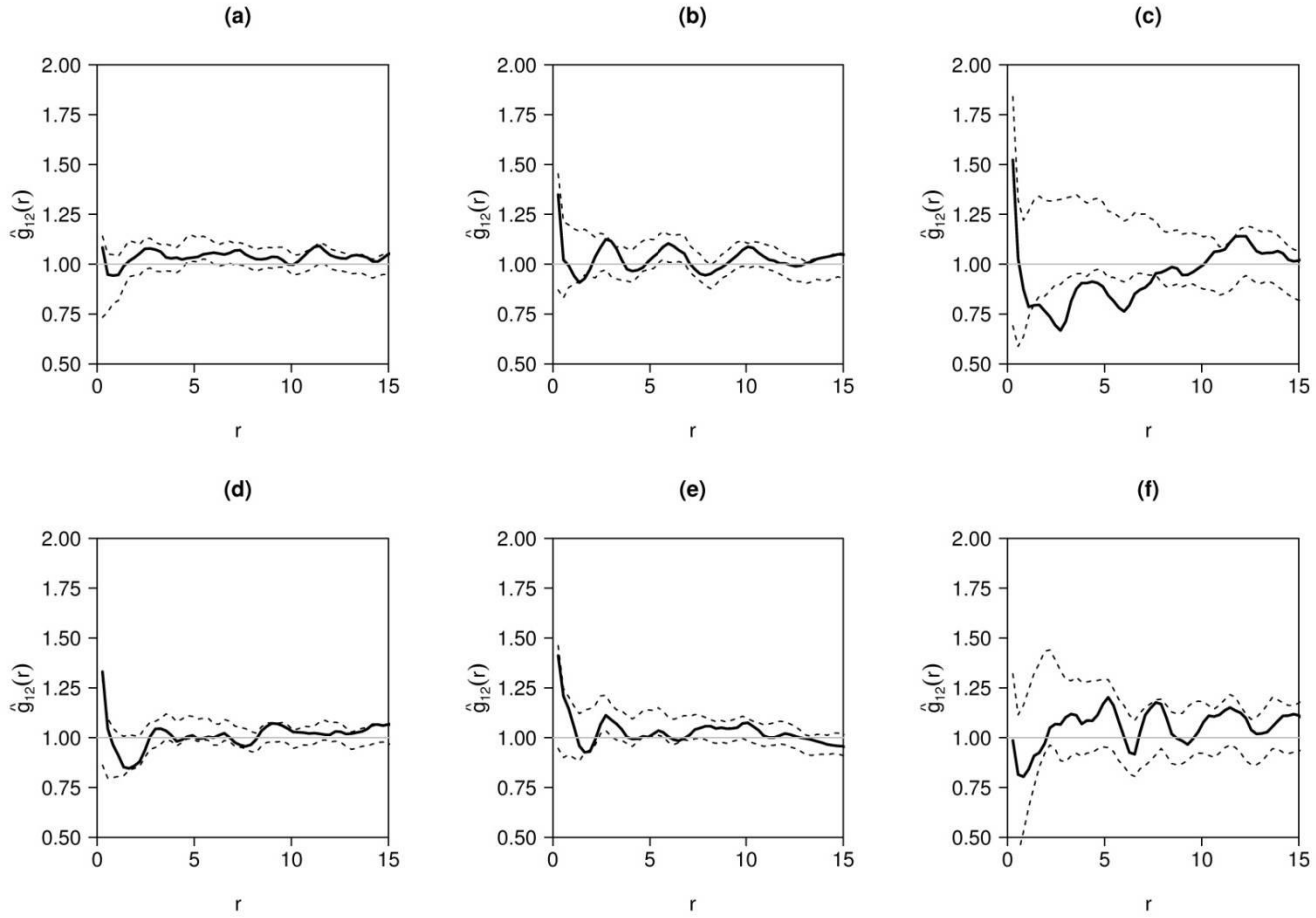

Fig. 3 Resulting estimator of the cross-pair correlation function (see equation (2)) for all the ant nest locations (a) and (d), small nest locations (b) and (e), and large nest locations (c) and (f), and the Cox point patterns of weed richness (top row) and weed cover (bottom row), together with the resulting fifth largest and smallest envelope values based on 999 random labelled (i.e. independent) bivariate point configurations (dashed lines).