RESEARCH ARTICLE

The role of landscape structure on the abundance of a disease vector planthopper: a quantitative approach

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Abstract Studies of patchily distributed insect populations have made clear the importance of host patch size and degree of isolation in determining the distribution of these populations. For such populations, patch connectivity will have an effect on patterns of patch occupancy and regional dynamics. In the present study we performed a series of observations to estimate the effect of landscape structure on the abundance of *Delphacodes kuscheli* (Homoptera: Delphacidae), vector of "Mal de Río Cuarto" disease to maize. Actively dispersing *D. kuscheli* individuals were collected in 19 sampling sites during the spring of 2004, using sticky traps placed at 2 m above ground level. Land use and landscape pattern were quantified, using Landsat 5 TM images for the area where each sampling site was placed. Four land use categories were considered in the analysis; winter pastures, winter cereals, perennial pasture and stubble. The spatial pattern analysis program FRAGSTATS was employed to estimate the patch area, patch proximity index, Total Class Area and the Mean Proximity Index for each of the land use categories in those sites where insect samples were taken. Partial Least Squares Regression analysis techniques were employed to relate the mean abundance of *D. kuscheli* and the landscape measures. Eighty percent of the variation of the mean insect abundance was explained by two first PLSR components. The proximity index of the local host patches, the amount of area left to stubble, local host patch area and total area of winter pastures were the most important variables affecting the abundance of dispersing *D. kuscheli* individuals. We found that the abundance of the dispersive fraction of the population of *D. kuscheli* is affected mostly by the surrounding landscape, particularly by the proximity of other host patches, and the permeability of the matrix represented by the stubble.

Keywords Delphacid planthopper ·
Delphacodes kuscheli · Landsat 5 TM ·
Landscape fragmentation

Introduction

Insect herbivore populations within an agroecosystem tend to be spatially structured into discrete local populations, depending on the distribution of their habitat patches in the landscape (Fahrig and Jonsen 1998; Grilli and Bruno 2007). For these populations, the transfer of individuals between patches is a key process that will finally influence their spatial

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structure and regional dynamics (Tilman and Kareiva 1997; Hanski 1999; Cronin 2003). This transfer of individuals between patches is the main reason for the persistence of populations in poor quality habitats as they receive immigrants from good, productive ones. This is the basis of source-sink dynamics theory (Shmida and Ellner 1984; Pulliam 1988; Pulliam and Danielson 1991), which has been empirically demonstrated (Pulliam 1996), and is considered one of the mechanistic foundations for landscape ecology (Wiens et al. 1993).

A landscape consists of several types of elements. The matrix is the most extensive and most connected landscape element, playing a dominant role in the exchange of energy, materials and species. However, when observing the landscape it is sometimes difficult to estimate the role each landscape element plays (Forman and Godron 1986).

Among all the delphacids species present in Argentina, *Delphacodes kuscheli* is the economically most important because of its ability to transmit what was initially thought to be a local strain of the Maize Rough Dwarf Virus (MRDV–RC) named Río Cuarto Disease (Conci and Marzachi 1993; March et al. 1995). This insect has a limited range of hosts, and can breed on winter cereals such as rye (*Secale cereale* L.) or wheat (*Triticum aestivum* L.) and winter pastures such as oats (*Avena sativa* L.). The latter are the most important overwintering hosts as they are sown by the end of the summer and not harvested until spring, becoming the main source from which *D. kuscheli* migrates to maize fields, as it does not reproduce in this crop (Tesón et al. 1986; Virla and Remes Lenicov 1991; Ornaghi et al. 1993; Garat et al. 1999; Remes Lenicov et al. 1999).

Delphacodes kuscheli has two wing forms: macropters, which can fly, and brachipters, which are flightless, and, as observed in other delphacids species, the production of migratory forms is a density-dependent process, related to crowded conditions and intensified by nutritionally inadequate host plants (Denno et al. 1991; Ornaghi et al. 1993). High population densities are strongly associated with land use management and the presence, condition, and distribution of host vegetation (Grilli and Gorla 1997, 1998). The abundance of planthoppers is related to the distribution and abundance of host plants: the higher the environmental diversity in terms of crop species per unit area, the lower the

abundance of individual planthopper species (Grilli and Gorla 1999). Dispersive individuals are particularly affected by the configuration of host patches in the surrounding landscape (Grilli and Bruno 2007).

For patchily distributed populations, patch connectivity is a critical factor affecting patterns of patch occupancy and regional population dynamics (Hanski 1994, 1999; Stacey et al. 1997). The composition of the matrix will influence not only the among-patch distribution of insects, but also the within-patch abundance by affecting the movement pattern of individuals (Haynes and Cronin 2003) and can surpass patch quality in its effect on individuals' dispersal (Haynes et al. 2007). In those species that show different movement response depending on the matrix cover type, the movement paths of individuals through the landscape will depend on the occurrence and pattern of these cover types (Bender and Fahrig 2005).

Planthoppers and grasshoppers dominate the insect herbivore fauna of gramineous ecosystems (Haddad et al. 2001; Cronin 2003). Our own previous studies showed that *D. kuscheli* regional abundance is affected not only by the host area in a region, but also by the phenology and fragmentation of the different host species, but no attention was put on the role of other landscape elements (Grilli 2006; Grilli and Bruno 2007). In this study, we made a series of observations to evaluate the effect of the configuration of host patches and surrounding elements of the landscape on the abundance of the dispersive fraction of populations of this planthopper species.

Methods

Study area

The study was carried out in the western area of Argentina's central plain (Fig. 1). The area is flat agricultural land with almost uniform farming activity. The most abundant delphacid species is *D. kuscheli* (Grilli and Gorla 1998). Insect abundance and disease incidence vary from 1 year to the next, and is mainly affected by the land use of the area and the presence and abundance of host plants patches (Grilli and Gorla 1997; Grilli and Gorla 1998; Grilli 2006; Grilli and Bruno 2007). It is not completely

Fig. 1 Sampling sites in the study area (Cordoba Province, Argentina). Each site has been identified by a *number*
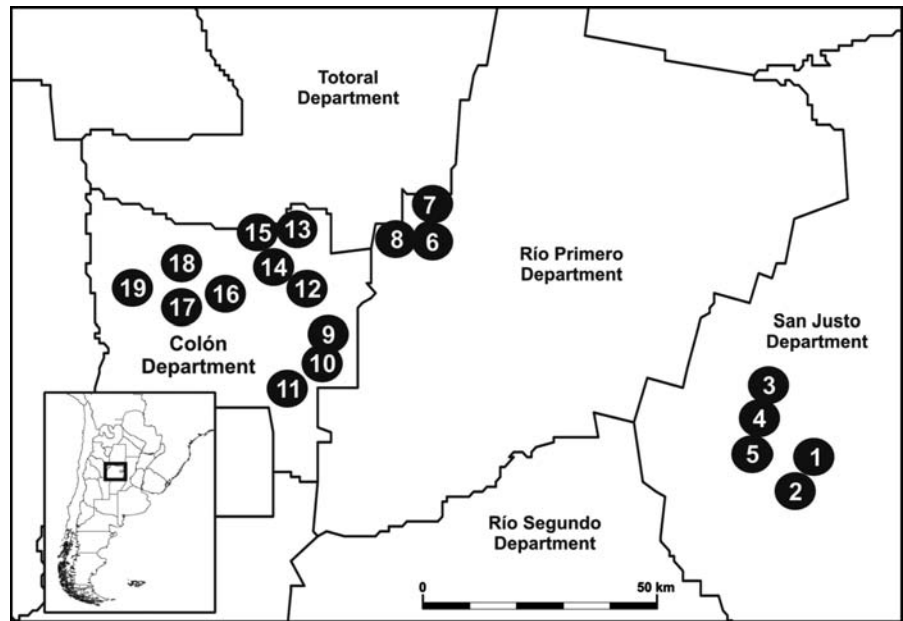
clear what the local mechanisms are that affect abundance of the vector at a regional level.

Delphacodes kuscheli data collection

Macropterous, actively dispersing *D. kuscheli* individuals were collected in 19 gramineous patches randomly distributed in the central region of Córdoba province (Argentina) in an area of 16,000 km^2. Insect sampling was performed using sticky traps that were placed inside the host patches (focal patches). Individuals collected in the sticky traps are formed by those that emigrate from and immigrate to the focal patch. Nevertheless our own previous results indicate that the individuals inhabiting focal patches have a relative minor effect on sticky traps captures (Grilli 2008). The traps were made from a metal cylinder with a 30 cm base diameter and 36 cm in height, supporting a plastic film coated with lithium grease (YPF® EP 62) as an adhesive, and were placed at 2 m above ground level. The plastic film was replaced with a clean one every 10 days from mid-September to the end of October 2004. All traps were painted yellow. Sampling dates were the same for all sites, and all the traps were replaced simultaneously. Films were transported to the laboratory, where *D. kuscheli* individuals were identified according to Remes Lenicov and Virla's identification key (1999). Insect

abundance was expressed as insects/trap/day for each of the 19 sampling sites (Fig. 2).

Host patches assessment

The spatial position of host patches was established using a GPS. Afterwards in the lab, each of the 19 patches was identified on a Landsat 5 TM image.

Nineteen Landsat 5 Thematic Mapper (TM) scenes provided by CONAE (National Aerospace Commission of Argentina) path/row 229/82, 229/81, 228/82 of May, June and November 2004 were used to estimate the spatial distribution of the host patches in which dispersing individuals were sampled. For this purpose, a supervised classification was used to determine land use based on spectral brightness, for six spectral bands in the visible and reflected infrared regions of the electromagnetic spectrum. 27,384 training sites were identified from site visits and four classes were considered in the analysis: winter pastures, winter cereals (host patches), perennial pasture and stubble. Training site areas were digitized and signatures were created, describing each informational class. Images were classified using Fisher's Linear Discriminant classifier (Landgrebe 2003). Finally, accuracy was assessed by generating a random set of locations for verifying the true land cover type. An error matrix was applied to compare

Fig. 2 Areas around the sampling site with host patches extracted from Landsat 5 TM classified images. Different land uses are identified by different colours
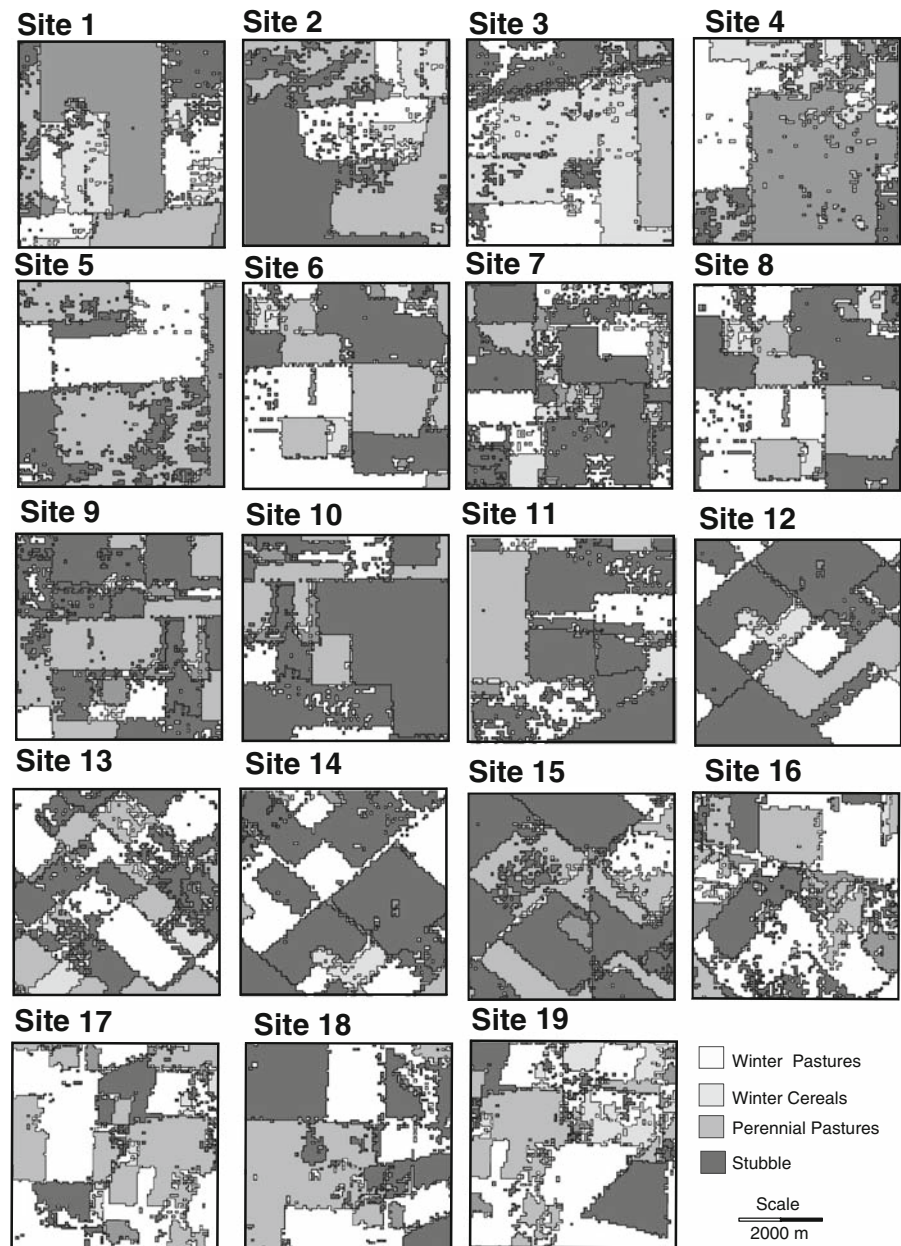
the classes obtained with the real classes found in the field and to tabulate the overall proportional error (Congalton and Green 1999).

The Thematic Mapper Imaging System is a cross-track scanner with an oscillating scan mirror and arrays of 16 detectors for each of the visible and reflected IR bands. Data are recorded on both eastbound and westbound sweeps of the mirror, which allows a slower scan rate, longer dwell time, and higher signal-to-noise ratio than with MSS

images (MSS was the primary imaging system in the first generation of Landsat) (Sabins 1997). A major advantage of Landsat 5 TM over the MSS imaging system is not only its spectral resolution but also its spatial resolution, which is of 30 m in TM. Each of the Landsat images was georeferenced to the latitude/longitude reference system and atmospheric and radiometrically corrected. Georeferencing was performed applying a quadratic algorithm for geometric rectification to modify the plane geometry of

the original images to a latitude/longitude grid using 57 ground control points obtained from the terrain (Eastman 2006).

Atmospheric and radiometric calibrations were performed and consisted in the transformation of the Digital Numbers of the original Landsat images to reflectance values in order to make comparable the classification of different scenes and different dates. All the image processing was performed using Idrisi Andes® (Eastman 2006).

Landscape metrics

Each of the agricultural plots where traps were placed was identified in the field using a GPS and these were defined as focal patches. Later in the lab their area in hectares was measured from the Landsat images. Using this information, the most representative of composition and configuration metrics for each of the landscape component that could have an effect on planthopper dynamics were estimated (Grilli and Gorla 1997; Grilli 2006; Grilli and Bruno 2007). All the landscape metrics were estimated using FRAG-STATS 3.3 (McGarigal and Marks 1995).

Focal patch proximity index

The Proximity Index, a patch-based metric, was estimated to test for the effect of landscape configuration on the abundance of dispersing *D. kuscheli* individuals in the study area. This metric was calculated for the focal patch (the patch where the traps were placed), identifying the other surrounding host patches from the classified images (Fig. 2). The Proximity Index discriminates isolated patches from aggregated patches and is focused on the host patch studied. This index will equal 0 if the focal patch has no neighbours of the same patch type; in our case the proximity index increases as the number of neighbour patches of the same class within the 1,500 m searching radius increases, and as those patches become closer and more contiguous. It is estimated by:

$$\text{PROX} = \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2} \tag{1}$$

where: a_{ijs} = area (m^2) of patch ijs within the specified neighborhood (m) of patch ij. h_{ijs} = distance (m)

between patch ijs and patch ijs, based on patch edge-to-edge distance, computed from cell centre to cell centre.

We obtained one Proximity Index per focal patch, based on the proximity of the other surrounding patches of the same class (Fig. 1).

Class metrics

Four Class metrics were estimated for each of the land covers identified from the Landsat Images. Each of these class metrics represents different landscape pattern properties.

Total class area

Total Class Area is a metric that is affected by the number and size of patches and the amount of edge generated by these patches. It is a direct measure of the amount of landscape comprised of a particular patch type. This metric approaches zero as the patch type becomes increasingly rare in the landscape (McGarigal and Marks 1995).It is estimated by:

$$\text{TCA} = \sum_{j=1}^{n} a_{ij} \left(\frac{1}{10000} \right) \tag{2}$$

where; a_{ij} = area (m^2) of the patch ij

Mean proximity index

Mean Proximity Index (MPI) is based on the spatial and temporal context of habitat patches. This index discriminates isolated patches from those that are part of a complex of patches. It is equal to zero if a patch has no neighbours of the same class within a 3,000 m diameter area and increases as this neighbourhood is more occupied by patches of the same class, and as those patches become closer and more contiguous. The index is dimensionless, so the absolute value of the index has little interpretive value; it is used as a comparative index (Gustafson and Parker 1992). MPI is estimated by;

$$\text{MPI} = \frac{\sum_{j=1}^{m} \left(\sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2} \right)}{N} \tag{3}$$

where; a_{ijs} = area (m^2) of patch ijs within the specified neighborhood (m) of patch ij. h_{ijs} = distance (m)

between patch ijs and patch ijs, based on patch edge-to-edge distance, computed from cell centre to cell centre. N = Total number of patches.

Data analysis

Partial Least Squares Regression (PLS) analysis techniques (Martens and Naes 1989) were employed to relate the mean abundance of *D. kuscheli* with the landscape measures obtained with FRAGSTATS 3.3. All the statistical analyses were performed using Statistica 7.0 software (StatSoft, Inc. 2001). Ten landscape metrics were the independent variables (Table 1) and the insect mean abundance during the sampling period was the dependent variable.

Partial Least Squares Regression is a recently developed generalization and combination of multiple lineal regression and principal component analysis (Wold et al. 1982; Tenenhaus 1998). It is particularly useful because, unlike multiple lineal regression, it can analyze data with strongly correlated, noisy and numerous independent variables, and also simultaneously model several dependent variables (Wold et al. 2001). In empirical models it is fundamental to establish the correct complexity of the model. The inclusion of excessive factors will certainly increase the accuracy of description but may decrease the predictivity because the model starts to represent not just the true pattern of relation

between independent and dependent variables but also random noise. In PLSR analysis both, the independent and the dependent variables (X and Y) are reduced to principal components. The components of X are used to predict the scores on the Y component, and the predicted Y component scores are used to predict the scores on the Y variable. The main output of PLSR analysis is the model coefficients for the variables, called PLS weights or loadings. X weights, denoted w, indicate how much they participate in the modelling of Y. The weights for the Y-variables, denoted by c, indicate which Y-variables are modelled in the respective PLS model dimensions. When these coefficients are plotted in a $w \times c$ plot, we obtain a picture showing the relationships between X and Y, those X-variables that are important, and which Y-variables are related to which X (Wold et al. 2001).

When determining how many principal components to include in the model it is important to take into account not only the goodness of fit but also the complexity taken to achieve that fit. The trade off between model complexity and the goodness of fit is deeply rooted in the *Lex parsimoniae*, which states that if two models with different complexities explained the data equally well, the simpler one should be taken. In this case the quantity used to find the optimal complexity of a model is the predicted variation Q^2. The value of Q^2 will increase as more

Table 1 Landscape metrics estimated from the Landsat images for the whole area and land uses

Metric	Unit	Description
Area	Hectares	Measures the area of the host patch where the individuals were collected
ProxPatch	Dimensionless	Measures the proximity of other patches of the same class of the patch where individuals were collected
WPastCA	Hectares	Indicates how much of the landscape is comprised winter pastures
WPastProx	Dimensionless	Is the mean value of all the proximity indexes estimated for all the winter pastures in the studies area
WCerCA	Hectares	Indicates how much of the landscape is comprised by winter cereals
WCerProx	Dimensionless	Is the mean value of all the proximity indexes estimated for all the winter cereal in the studies area
StubCA	Hectares	Indicates how much of the landscape is comprised by stubble
StubProx	Dimensionless	Is the mean value of all the proximity indexes estimated for all the stubble patches in the studies area
PPastCA	Hectares	Indicates how much of the landscape is comprised perennial pastures
PPastProx	Dimensionless	Is the mean value of all the proximity indexes estimated for all the perennial pastures in the studies area

Metric: Landscape metric used; Unit: Spatial unit of the landscape metric; Description: Characteristic of the landscape metric

components are added to the model until a point in which this trend will eventually give way to a decrease in Q^2. This point of inflection in the value of Q^2 provides an estimate of how many principal components to include in the model. A way to make this estimation is by a method called cross-validation that determines if a principal component is significant or not. In this procedure calculation is repeated in times and a sample of observations is not used in the model construction. The activity is predicted for excluded compounds using such partial model. Each compound is excluded exactly once, and normalized total error of prediction for them serves as a measure of predictivity for the full model (Wold et al. 2001). In this case the amount of Y predicted is represented by Q^2 and represents the cross-validated R^2.

Results

Land use in this area of the country has changed little in the last 20 years. Estimations from Landsat 5 TM showed that there is considerable local variability in land management, in particular as regards the proportion and spatial distribution of host patches (Fig. 2). Mean abundance of *D. kuscheli* appears to be variable in the different host patches during the study period. Values ranged from 0.017 insects/trap/day in host patch 3, to 1.39 insects/trap/day in host patch 8 (Fig. 3).

Classification of land use by Fisher's Linear Discriminant classifier proved very precise. The error matrix accounted for 97% of overall accuracy of the land use classification for the period studied. Host

and non-host areas were seen to be very variable between sites. Land use classification showed that 49% of the study area was classified as stubble, 33% classified as host (winter cereals and winter pastures) and 18% classified as perennial pastures (Fig. 2). The area of host patches where dispersing individuals were collected was also very variable, ranging from 33.32 to 7.74 ha.
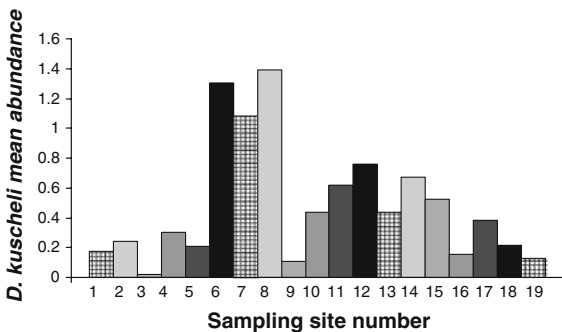
Partial least squares regression analysis

Based on the dependent matrix and the explanatory matrix obtained, PLSR was used to analyze the relationship between mean insect abundance during the sampling period (September–October) period, and the group of 10 landscape metrics described in Methods (Table 1).

The first PLSR component explained 38% of the explanatory matrix (landscape elements) and 74% of the dependent matrix ($Q^2 = 0.65$). The second component explained 19% of the explanatory matrix and 6% of the dependent matrix ($Q^2 = 0.57$). Overall, 80% variation of the mean insect abundance throughout the study period was explained by the first and second PLSR components (Table 2).

PLSR loadings analysis

The loadings plot shows the first PLS component dominated by the proximity of other host patches to the focal patch, the total area of stubble surrounding the focal patch and the mean proximity winter cereals and stubble patches (ProxPatch and StubCA on the positive side and WCerProx and StubProx on thengative). The second component is dominated by patch


Fig. 3 Mean *D. kuscheli* abundance during the study period (spring 2004) in each of the sampling sites. Each site has been identified by its *number*

Table 2 Partial least squares analysis summary

Comp.	R^2 X	R^2 X (Cumul.)	R^2 Y	R^2 Y (Cumul.)	Q^2	Significance
1	0.38	0.38	0.74	0.74	0.65	S
2	0.19	0.58	0.06	0.80	0.57	S

Comp: Principal Component; R^2 X: Amount of the independent variable explained by the principal component; R^2 Y: Amount of the dependent variable explained by the principal component; Q^2: Amount of Y predicted by the principal component; Significance: Significance of the principal component (S = Significant). Number of significant components is 2, 80% of sum of squares of the dependent variables has been explained by all the independent variables
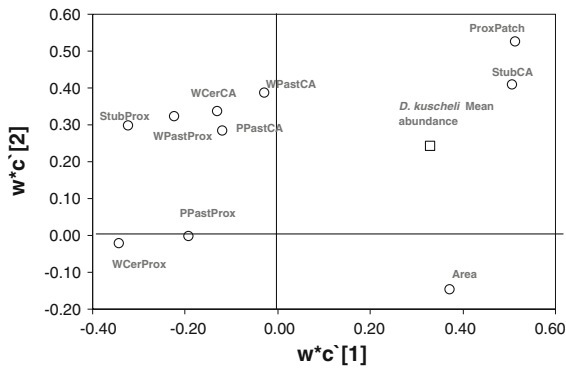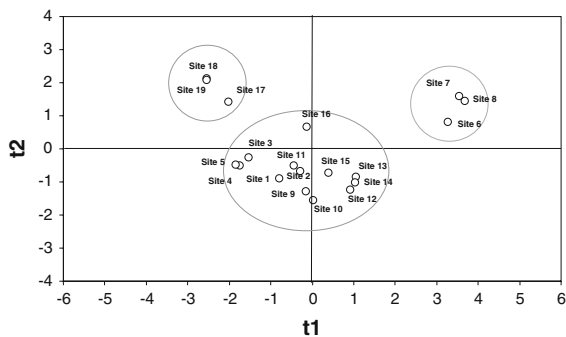
Fig. 4 PLS weight, w^* and c' for the first two dimensions of the model

metrics, the proximity of other host patches to the focal patch where the individuals were collected (ProxPatch) on the positive (high) side and the area of the focal patch (Area) on the negative (low) side. The c-values of the dependent variable, y, are proportional to the linear variation of Y explained by the corresponding dimensions, this is R^2. They define one point per response, in our case having a single response this point (*D. kuscheli* mean abundance) sits approximately in the centre of the first quadrant of the plot. The importance of a given X-variable for Y is proportional to its distance from the origin in the loading space (Fig. 4).

PLSR scores analysis

X scores (t) show object similarities and dissimilarities (Wold et al. 2001). The plot of the X scores (Fig. 5), shows three clear groups of the sampling sites; the most distinctive group placed in the first quadrant formed by sites 6, 7 and 8; a second group formed by sites 1, 2, 3, 4, 5, 8, 9, 10, 11, 12, 13, 14, 15, 16 in the second and third quadrant; and a third group in the fourth quadrant formed by sites 17, 18 and 19 (Fig. 5).

Partial Least Squares Regression coefficients indicate the importance of an independent variable (X) for the dependent variable (Y) in the model (Wold et al. 2001). It can be considered as the directions in the explanatory variables space that result in the largest increase in the dependent attribute (Cheng and Sun 2005).

Our results show that the variable that had the greatest influence on the abundance of dispersing *D. kuscheli* individuals was the proximity of the patch where individuals were collected to other host patches (ProxPatch), followed by the amount of area left to stubble, host patch area and winter pasture total area (SubCA, Area and WPastCA). Winter cereals mean proximity also shows an important influence, but with negative PLSR coefficients (WCerProx,) (Fig. 6).

Discussion

The study area is a typical agricultural and cattle-breeding region. The estimation of the distribution of host patches in each of the sampling sites showed that the spatial distribution and size of these patches is very variable. Regional abundance of *D. kuscheli* is affected not only by the condition and distribution of

Fig. 5 Partial Least Squares scores ($t1$ and $t2$) for each of the sampling sites where *D. kuscheli* individuals were collected
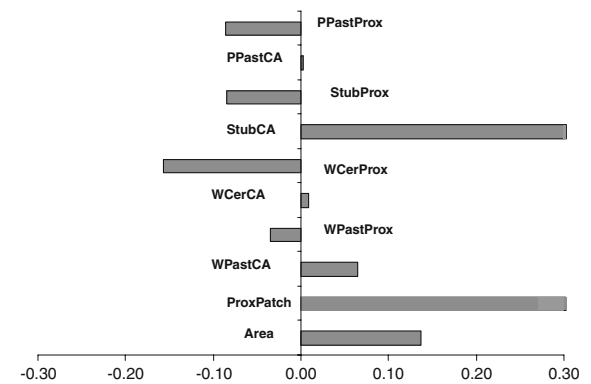
Fig. 6 Estimated regression coefficients for the predicted *D. kuscheli* mean abundance. Independent variables names are explicated in Table 1

the vegetation at a regional scale (Grilli and Gorla 1997), but also by regional host area (Grilli 2006) and patch isolation (Grilli and Bruno 2007). Plants, in natural systems, are distributed forming discrete patches. In agricultural systems, this situation is more evident, and every year the pattern of distribution of these patches will change modifying the landscape, which will finally affect the distribution and abundance of the insects that develop in those patches.

Spatial structure of landscapes will influence the abundance and distribution of species in several ways (Forman and Godron 1986; Wiens 1997). For specialist herbivorous insects, habitat in an agricultural landscape will be distributed in patches (crop fields) of different sizes, at varying distances from each other and with varying frequencies of disturbance (Hanski and Gilpin 1997; Fahrig and Jonsen 1998).

We analyzed the abundance of individuals dispersing over host patches at very low altitude from the ground (only 2 m). Although *D. kuscheli* populations are formed of long-winged and short-winged individuals, only the macropterous ones are capable of active flying (Ornaghi et al. 1993; Grilli and Gorla 1997) and are those mainly responsible for Rio Cuarto Disease Epidemics as almost 90% of the populations are formed of macropterous individuals (Ornaghi et al. 1993). In a previous work we found that only 36% of the variation of the abundance of *D. kuscheli* registered in traps placed above 1.5 m from the ground can be explained by the abundance of the individuals living in the patch immediately bellow the trap (Grilli 2008). So 64% of the variation of the individuals caught in the traps are arriving to the trap from other source, this is host patches surrounding the trap.

Planthopper density in a particular habitat patch will depend on the area, isolation, quality, and surrounding landscape structure of the patch (Biedermann 2002; Grilli and Bruno 2007). Studies of patchily distributed insect populations made clear the importance of host patch size and degree of isolation in determining the distribution of insect populations (Hanski 1999). We described the landscape using metrics with different characteristics, some of which quantify landscape composition, while others quantify landscape configuration. Configuration and composition of the landscape will affect

ecological processes independently and interactively (Gustafson 1998). Four aspects of landscape pattern were considered when deciding which class metrics to use; the spatial context of focal patches (Proximity Index); the area of the focal patch (Area); the total area of a particular class (TCA) and the general context of patches in the landscape (Mean Proximity Index; McGarigal and Marks 1995).

The abundance of dispersing *D. kuscheli* individuals is positively correlated with the proximity of host patches (ProxPatch), the total area left with stubble surrounding the host patch (StubCA) and the area of the host patch where the dispersing individuals were collected (Area). The regression coefficients of the predicting model also show that the proximity of host patches (ProxPatch) is the most influential variable, followed by the total area left with stubble in the landscape (StubCA) and the area of the host patch (Area) in the third place. This means that the abundance of the dispersive fraction of the population of *D. kuscheli* over a host patch is mostly driven by the surrounding landscape, particularly by the proximity of other host patches, and the total area of the matrix, represented by the stubble. Short distances between host patches and the focal patch, high area of stubble in the surrounding landscape and big focal patches will bring an increase in the amount of dispersing individuals over a particular focal patch. All the other variables show little effect on the insect abundance, except for the mean proximity index of winter cereals patches that show a negative relationship. This is, as mean proximity of winter cereals patches increase, *D. kuscheli* mean abundance decrease.

Patch connectivity is a critical factor affecting patterns of patch occupancy and regional dynamics in patchily distributed populations (Hanski 1994, 1999; Stacey et al. 1997). Patch isolation is frequently predicted to have a negative effect on population density since isolated patches will have lower immigration, reducing rescue and recolonization rates (Sjögren Gulve 1994; Dunning et al. 1995; Enoksson et al. 1995; Hinsley et al. 1995). Isolation of habitat patches is relative (Wiens 1992) and the characteristics of the matrix between other host patches plays an important role in the connectivity of fragmented landscapes (Taylor et al 1993; Ricketts 2001; Bender and Fahrig 2005). The isolation of host patches by distance is still an influential factor of dispersal

among animal populations in fragmented habitats. But distance is not independent of the nature of the matrix in fragmented landscapes. In those cases where the matrix is very different to the primary habitat, the distance between host patches, will have a strong effect on the colonization of fragmented habitats (Goodsel and Connell 2008). Considering the high dispersal capacity if *D. kuscheli* a possible explanation for the role of the matrix is the "nearest refuge hypothesis" that states that mobile invertebrates disperse over areas of non habitat and then concentrate in isolated host patches because habitats in isolation are the nearest available refugee (Virnstein and Curran 1986). Movement paths of planthoppers are more linear on simplex matrices than on complex ones (Haynes and Cronin 2003), and their populations often escape natural enemy controls when the dispersal ability of the predator is limited and their aggregative response hampered (Döbel and Denno 1994; Denno et al. 2002). This explanation may be also applicable to the negative relationship found between dispersal individuals and most of the winter cereals metrics coefficients. These individuals are probably attracted to winter cereal patches as these patches are at the peak of their greenness because they have been sown at the beginning of the winter (end of June). Winter cereal patches are probably acting as ecological traps, with an increase of predation probability for the individuals that arrive in them. Patches that are perceived as stepping stones can become ecological traps. Corridors or stepping stones can function as traps or drift fences for specialist insects moving through the matrix, driving the individuals toward connected or very close habitat patches (Haddad and Baum 1999; Tewksbury et al. 2002). Therefore, as in our case, corridors and stepping stones may be enhanced if embedded in a low resistance matrix (Roland et al. 2000; Ricketts 2001; Haynes and Cronin 2003).

The measurement of landscape connectivity needs not only a species approach (Hansen and Urban 1992) but also has to be site specific. Our results show that landscape structure and *D. kuscheli* response is not regionally determined. Similarities in response between sites, represented by the *t* scores, showed that in some cases, sites that are on opposite sides of the study region, have many more similarities between them than with sites that are spatially closer.

For most metapopulation studies, patch size and isolation are driving variables in the determination of immigration or colonization events (Hanski 1999). Most of the empirical studies suggest that immigration increases with patch size and decreases with increasing isolation (Hanski 1999). These studies generally ignore the effect of the matrix in this process (Taylor et al. 1993; Wiens 1997; Tischendorf and Fahrig 2000). Our results suggest that patch size and isolation alone are not good predictors of the interpatch movement without considering the role of the matrix (Ricketts 2001; Cooper et al. 2002; Gobeil and Villard 2002; Goodwin and Fahrig 2002; Tischendorf et al. 2003; Bender and Fahrig 2005), making it at least difficult to generalize results obtained from models that ignore these aspects.

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