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RESEARCH ARTICLE

The effect of landscape structure on two species of different trophic levels in an arid environment

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Abstract

Context Insect species of different trophic level will respond differently to landscape configuration.

Objective In this context we explore the way landscape structure affects the distribution and abundance of the whitefly *Siphoninus phillyreae* and its predator *Clitostethus arcuatus* in olive orchards.

Methods Adult individuals of these two species were collected using sticky traps placed in 12 olive host patches in Argentina. Host patches were detected and quantified using Landsat 5 TM images. Different landscape metrics were estimated for the study area land covers. PLSR analysis techniques were employed to relate the mean abundance of the studied species and the landscape measures.

Results The Landsat land use estimations showed that most of the vegetation is limited to particular irrigated spots or urban areas. 89 % of the land cover is exposed soil, 10 % is xerophytic vegetation, 0.56 % is introduced urban vegetation and 0.31 % is occupied by olive orchards. *S. phillyreae* was positively affected by total area of olive orchards, followed by total area of urban vegetation, and negatively affected by the perimeter of olive focal patch and the proximity of other urban vegetation patches. *C. arcuatus* was positively affected by the perimeter of the host patch, the total area of olive orchards and the mean proximity of urban vegetation patches.

Conclusion We concluded that although the total area of the herbivore host was the most influential variable affecting the two species, each of them was affected in different way by other landscape elements.

Keywords *Siphoninus phillyreae* · *Clitostethus arcuatus* · Olive patches · Dry land · Landscape configuration

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Introduction

We can define habitat fragmentation as the process in which a large area of habitat is divided into a number of smaller patches embedded in a matrix that is different from the original (Wilcove et al. 1986). Under this definition a landscape can be categorized as continuous or fragmented, and a fragmented landscape is the end point of a process of fragmentation. The patchy nature of populations can be accentuated by human activities imposing a temporal pattern of habitat on a landscape. The most obvious example is the conversion of a landscape into a patchwork of crop fields by agricultural activity, interspersed with remnant forest, grassland or even dry zones.

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In general, a suitable habitat for herbivore insects, specialized on particular plant species, may be distributed in patches (crop fields) of different sizes and different separation distances between patches (degree of isolation) with various frequencies of disturbance through farming operation. Different species may be expected to respond at different spatial and temporal scales on a particular landscape (Wiens 1989; Milne et al. 1992). Populations of many insects seem to respond to the scale of the agricultural field. Insect populations tend to be spatially structured in discrete local populations, especially in agroecosystems depending on the distribution of their habitat patches (Fahrig and Jonsen 1998; Grilli and Bruno 2007; Grilli 2010).

The resource concentration hypothesis stated by Root (1973) predicts that specialist herbivorous insects will be more abundant in large host patches, because they would find them more easily and stay there longer than in smaller host plant patches (Root 1973). Underlying this is an increase of emigration rates from smaller patches and an increase of immigration rates into larger patches. Since the hypothesis was originally formulated, many studies have empirically quantified these relationships for a diverse set of organisms, but the results of these studies have been quite variable (Bowers and Matter 1997; Bender et al. 1998; Connor et al. 2000; Hamback and Englund 2005).

Patch isolation will also have an effect on species abundance. The effects of habitat isolation will depend on the dispersal ability of a species, the distance to the nearest colonized habitat, and the landscape matrix between habitats including barriers, corridors and stepping stones (Murphy and Lovett-Doust 2004; Tscharntke and Brandl 2004).

Like the herbivores, predators can also be generalist or specialist depending on the number of prey species they use. Specialist predators are assumed to generally feed on one prey species only (Prakash and De Roos 2002; Nakagiri and Tainaka 2004), while omnivorous and generalist predators feed and survive on a variety of prey species (Swihart et al. 2001; Melian and Bascompte 2002). The effect of fragmentation on the survival rate of omnivorous predators will depend on the degree of polyphagy and on the quality of the alternative prey (Swihart et al. 2001). On the other hand generalist predators are assumed to obtain most of their resources from sources other than a focal prey species and they feed only by chance on the focal prey species that is experiencing habitat fragmentation (Laurance and Yensen 1991; Cantrell et al. 2001; Swihart et al. 2001; Cantrell et al. 2002; Ryal and Fahrig 2006), however in some cases they can also have in some particular cases preferred preys (Venzon et al. 2002; Boivin et al. 2010).

The use of habitat also differs between different predator types. Specialist predators tend to be restricted to the same habitat as their prey, and so loss of prey habitat is therefore also a loss of predator habitat (Bascompte and Sole 1998; Swihart et al. 2001; Prakash and De Roos 2002). In general, specialist predators can survive in patches without prey only if they have an influx of the focal prey (Nakagiri et al. 2001; Kondoh 2003; Nakagiri and Tainaka 2004). They are limited or regulated by the abundance of the population of their prey (Bascompte and Sole 1998; Nakagiri et al. 2001; Swihart et al. 2001; Prakash and De Roos 2002).

Omnivorous predators are considered to be responsible for the increase of the rate of prey extinction in predator–prey patches (Swihart et al. 2001; Melian and Bascompte 2002). They can persist in habitats not used by their focal prey, but at the cost of elevated mortality rates. Omnivorous predators are thus “matrix tolerant” (Swihart et al. 2001).

The response of generalist predators is more complex as they may be able to use matrix habitats (if favorable) (Holt et al. 1999; Tscharntke and Kruess 1999). This spillover of generalist predators benefiting from the surrounding favorable landscape can result in increased predation within a focal patch (Rand and Louda 2006).

Siphoninus phillyreae (Haliday) (Hemiptera: Aleyrodidae) is a generalist whitefly, commonly known as the “ash whitefly”. It has a wide distribution all over the world and in all continents, from Europe, the Indian subcontinent to the Middle East, Asia and the Americas (Bellows et al. 1990; Peña 1994; Viscarret and Botto 1996). This species is an important pest of numerous ornamental and fruit crops and in many cases causes economic damage to agricultural production (Bellows et al. 1990; Gerling et al. 2004). It was introduced into Argentina sometime prior to 1996, when it was first described infesting ornamental trees in Mendoza City (Mendoza Province, Argentina) (Viscarret and Botto 1997). By the end of 2004, the pest was already detected as infesting olive plantations in Mendoza province (Holgado et al. 2005) and, from that year, the pest extended to the whole olive production area of Argentina. *S. phillyreae* has important pest potential, mainly because of its rapid reproduction and short egg-to-adult developmental time. Among the many effects of heavy infestation on host plants, the most common are early leaf drop, leaf wilt and in some cases smaller fruit. In many cases, *S. phillyreae* is not reported as a pest until its natural enemy populations are disrupted by pesticide treatments (Bellows et al. 1990).

Clitostethus arcuatus (Rossi) (Coleoptera: Coccinellidae) is one of the most important predators of *S. phillyreae* and is considered a very useful natural controller of this whitefly (Gerling 1990). It generally feeds on eggs, nymphs and adult whiteflies, showing a wide range of feeding behaviours (Priore 1969; Bathon and Pietrzik 1986).

In Argentina, *C. arcuatus* has the same distribution as *S. phillyreae*, and was first mentioned on olive trees infested with *S. phillyreae* in 2007 (Gasparini et al. 2007). The records show this predator as introduced into Chile in 1995 for the natural control of *S. phillyreae* (González 1996), so this is probably the source of this species in Argentina, as it was mentioned in Mendoza Province, which borders Chile. Both species are now present in the whole olive production area of Argentina.

As mentioned previously, landscape does not influence all species in the same way as interacting communities are formed by species with different spatial strategies (With et al. 2002; Thies et al. 2003). Spatial distribution of habitat patches can affect whole communities even if only some of the species respond directly to fragmentation. This particular response is caused by the interaction between species: the chance of a particular species to persist in a habitat patch will be strongly affected by the presence or absence of other species (Elzinga et al. 2007). We propose as a working hypothesis that in this arid environment two species of different trophic levels, *S. phillyriae* and its predator *C. arcuatus*, will show a differential response to landscape composition.

Methods

Study area

The study was carried out in the north west of Argentina, between La Rioja and Catamarca provinces (Fig. 1), which is the main olive production region of the country, mainly because of its arid environment. In the North West, La Rioja is the largest province in terms of surface under production (20,503 ha), followed by Catamarca (16,354 ha), San Juan (14,868 ha), and Mendoza (14,643 ha) provinces (INDEC 2002). Mean annual precipitation in the area ranges from 130 (Aimogasta, La Rioja Province) to 440 mm (La Rioja Capital, La Rioja Province) (Searles et al. 2011), and most of the plantations are irrigated.

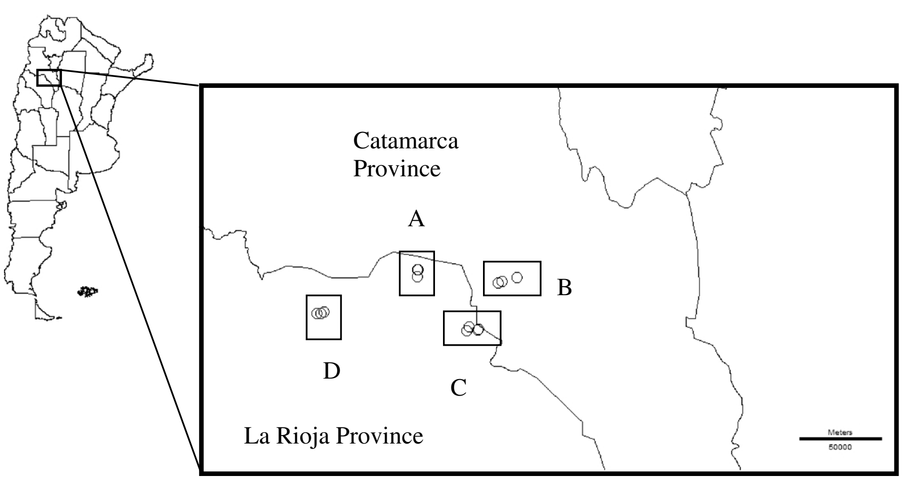

Fig. 1 Sampling sites in the study area. Area *A* contains sampling sites 1, 2 and 3; area *B* contains sampling sites 4, 5 and 6; area *C* contains sampling sites 7, 8, 9 and 10; and area *D* contains sampling sites 11 and 12

Insect data collection

Adult *Siphoninus phillyreae* and *Clitostethus arcuatus* were collected in 12 olive plots distributed between industrial olive production (sites 1, 2, 3, 5, 6, 7, 8) and urban farming plots (sites 4, 9, 10, 11, 12) in four settlements placed in the north-west region of Argentina (La Rioja and Catamarca provinces) in an area of 3700 km^2. Sampling sites distances ranged between 1 km (in the same settlement) to 100 km (in different settlements) (Fig. 1). Sampling was performed with 10 yellow sticky traps placed inside each of the 12 host patches (olive plots). Yellow sticky traps were chosen for they effectiveness for monitoring whiteflies (van-Lenteren and Noldus 1990) and coccinellids (Honek 2012).

Individuals collected in the traps were adult flying individuals of both study species (*S. phillyreae* and *C. arcuatus*). The traps were made from a plastic board of 15 cm × 20 cm, coated with lithium grease (YPF® EP 62) as an adhesive. In each sampling field (host patch), ten traps were placed in a line from one of the borders of the plot, at 1.50 m above ground level, hanging from branches of the olive trees. Traps were replaced with clean ones every 7 days from the beginning of October to mid-November 2008. Sampling dates were the same for all sites, and all the traps were replaced simultaneously. Traps were transported to the laboratory, where *S. phillyreae* and *C. arcuatus* individuals were identified. Insect activity density was expressed as insects/trap/day for each of the 12 sampling sites (Fig. 2).

Landscape assessment

The spatial position of host patches was established using a GPS. Each of the 12 patches was then identified in the lab on a Landsat 5 Thematic Mapper (TM) image. Two Landsat 5 TM scenes provided by CONAE (National Aerospace Commission of Argentina), path/row 231/80, 232/80 of October and November 2008, were employed to estimate the spatial distribution of the host patches in which individuals of the two groups were sampled. 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. In supervised classification, the software system delineates specific land-cover types based on statistical characterization data drawn from known examples in the image (known as training sites). Different training sites were identified from site visits and four classes were considered in the analysis: exposed soil, natural vegetation, urban vegetation and olive orchards. 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

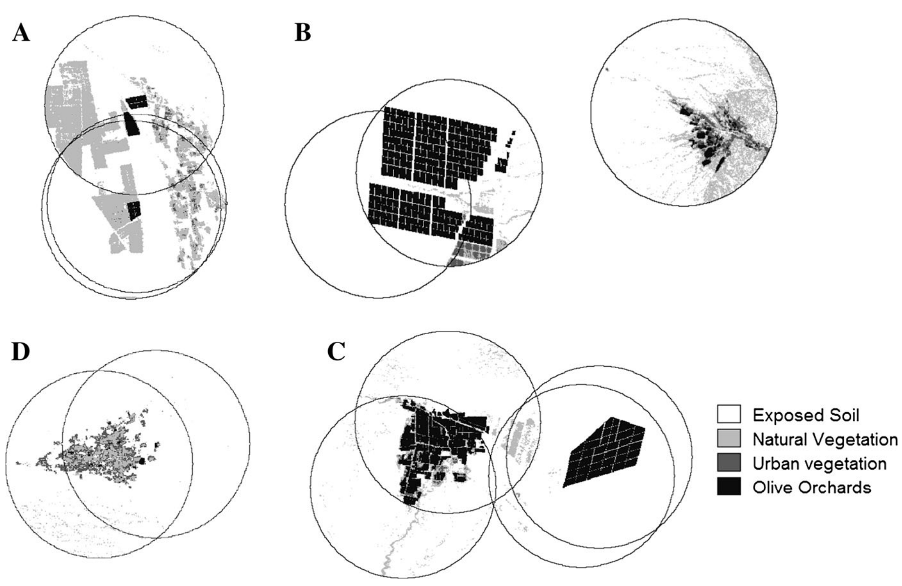

Fig. 2 Areas around the sampling site with host patches extracted from Landsat 5 TM classified images. Area (**a**) contains sampling sites 1, 2 and 3; area (**b**) contains sampling sites 4, 5 and 6; area (**c**) contains sampling sites 7, 8, 9 and 10; and area (**d**) contains sampling sites 11 and 12. Different land uses are identified by different colours

cover type. An error matrix was applied to compare 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 on board Landsat Satellites 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). Landsat 5 TM images have a spatial resolution of 30 m. Each of the Landsat images was georeferenced to the latitude/longitude reference system and atmospherically 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).

Radiometric calibrations were performed, consisting in the transformation of the digital numbers of the original Landsat images to reflectance values, in order to make the classification of different scenes and different dates comparable. All the image processing was performed using Idrisi Andes® (Eastman 2006).

For the analysis of supervised classification results, a confusion matrix (or named error matrix), an almost universally accepted image classification accuracy report, was applied (Congalton and Green 1999). This is a symmetrical array to express the number of classified pixels in the assigned category relating to the actual category from the ground truth data. Ground truth data are an alternative set of sampled area delineated independently in an image. The overall accuracy of the confusion matrix, which is computed by the weighting of the percentage of all corrected-classified pixels in each assigned category, is used to quantify the classification accuracy. The Kappa coefficient, which is the sum of the off-diagonal elements in the confusion matrix, was also employed in this study to calculate the actual classification agreement and the chance agreement (Congalton and Green 1999).

Landscape quantification

Each of the olive orchard plots where traps were placed was identified in the field using a GPS and these were defined as focal patches, and their area (in ha) was measured from the Landsat images. Using this information, we extracted the most representative composition and configuration metrics for each landscape component that we estimated could have an effect on *S. phillyreae* and *C. arcuatus* populations. All the landscape metrics were estimated using FRAGSTATS 3.3 (McGarigal and Marks 1995). For landscape analysis, we computed several patch metrics and class metrics. Patch metrics are defined for individual patches and show the spatial character and context of patches. Class metrics are values integrated over all the patches of a given type (class) in a certain area (McGarigal et al. 2012). We estimated all the patch and class metrics based in an area of 3500 m searching radius centred in the focal patch (Table 1).

Patch metrics

Focal patch area

This metric is basically the area in hectares of the olive patches in which individuals of the two species were collected.

Focal patch perimeter

This metric was also calculated for each of the focal patches, i.e., the olive patches where both species were collected. It represents the perimeter in metres of each patch (McGarigal and Marks 1995).

Focal patch proximity index

The focal proximity index, also a patch-based metric, was estimated to analyze the effect of landscape configuration within the study area on the activity density of individuals of both insect populations. This metric was estimated for the focal olive patch, identifying the other surrounding host patches from the classified images. Basically, the proximity index discriminates isolated patches from aggregated ones, and is focused on the local patch where individuals were collected. The proximity index will be equal to zero if the focal patch has no neighbours of the same type. In this case the proximity index increases as the number of neighbour patches of the same class within the 3500 m searching radius increases, and as those patches become closer and more contiguous. It is estimated by:

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
Perimeter	Metres	Measures the perimeter of the host patch (olive)
ProxPatch	Dimensionless	Measures the proximity of other patches of the same class of the patch where individuals were collected (olive)
OCA	Hectares	Indicates how much of the landscape is comprised by olive orchards
UVMNProx	Dimensionless	Is the mean value of all the proximity indexes estimated for all the urban vegetation patches in the studies area
UVCA	Hectares	Indicates how much of the landscape is comprised by urban vegetation
ESCA	Hectares	Indicates how much of the landscape is comprised by exposed soil

Metric landscape metric used; *unit* spatial unit of the landscape metric; *description* characteristic of the landscape metric

$$Prox = \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2}$$

where a_{ijs} = area (m^2) of patch ijs within the specified neighbourhood (m) of patch ij; h_{ijs} = distance (m) between patches, based on patch edge-to-edge distance, computed from cell centre to cell centre (McGarigal and Marks 1995).

We obtained one proximity index per focal patch, based on the proximity of the other surrounding patches of the same class (olive patches) (Fig. 2).

Class metrics

Total class area (CA)

Total class area is a metric that is a direct measure of the amount of landscape comprised by a particular patch type. This metric approaches zero as the patch type becomes increasingly rare in the landscape (McGarigal and Marks 1995).

It is calculated by:

$$\mathrm{CA} = \sum_{j=1}^{n} a_{ij} \left(\frac{1}{1000} \right)$$

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

In our case, we estimated the total class area for olive orchards (*OCA*), for urban vegetation (*UVCA*) and for exposed soil (*ESCA*).

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 3500 meter 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;

$$MNProx = \frac{\sum_{j=1}^{m} \left(\sum_{i=1}^{n} \frac{a_{ijs}}{h_{ijs}^2} \right)}{N}$$

where a_{ijs} = area (m^2) of patch ijs within the specified neighbourhood (m) of patch ij; h_{ijs} = distance (m) between patches, based on patch edge-to-edge distance, computed from cell centre to cell centre; N = total number of patches.

We estimated the mean proximity index for urban vegetation patches (*UVMNProx*).

Data analysis

Partial least squares regression (PLS) analysis techniques (Martens and Naes 1989) were employed to relate the mean activity density of both insect species (*S. phillyreae* and *C. arcuatus*) with the landscape measures obtained with FRAGSTATS 3.3. All the statistical analyses were performed using Statistica 8.0 software (StatSoft Inc. 2001). The seven landscape metrics were the independent variables (Table 1), and the insects' mean activity densities during the sampling period were the dependent variables.

Partial least squares regression is a generalization and combination of multiple linear 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 as in our case (Wold et al. 2001).

With numerous, correlated independent variables, there is a higher risk of getting a model with little or no predictive power. One way to solve this problem is monitoring its predictivity after including each successive factor by means of a *cross-validation procedure*. In this procedure, the calculation is repeated various times and a sample of observations is not used in the model construction. The activity is predicted for excluded compounds using this partial model. Each compound is excluded exactly once, and the normalized total error of prediction for these 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 and land cover in this area of the country is mainly determined by the climate as the area is dry, with less than 100 mm of rainfall per year. Estimations from Landsat 5 TM showed that there was very little local variability in land management, particularly as vegetation is limited to urban areas or specially irrigated plantations (Fig. 2).

The mean activity density of *S. phillyreae* and *C. arcuatus* appeared to be variable in the different host patches during the study period. Values ranged between 6.29 insects/trap/day to 423 insects/trap/day in *S. phillyreae* and 0.02 insects/trap/day to 2.9 insects/trap/day in *C. arcuatus*, and there was a clear correlation of the activity densities of the two species during the study period (Fig. 3).

Classification of land use by Fisher's linear discriminant classifier proved very precise. The error matrix accounted for 94 % of overall accuracy of the land use classification for the study period. Considering the land use of the entire study area, we found that most of it was classified as dry land. 89 % of the area

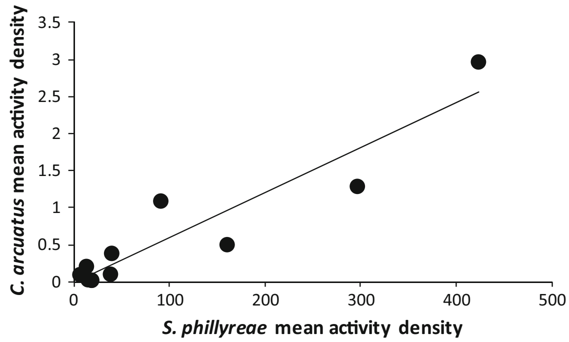

Fig. 3 Relationship between *Clitostethus arcuatus* mean activity density and *Siphoninus phillyreae* mean activity density captured in each sampling site. $R^2 = 88$ %; $P < 0.001$, lineal model (adjusted)

was classified as exposed soil, 10 % as natural vegetation, which is mainly non-host as it is xerophytic, 0.56 % as urban vegetation that includes potential hosts, and only 0.31 % of the whole area was occupied by the olive orchards that are the main host of *S. phillyreae*.

Partial least squares regression analysis

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

The first partial least square regression component explained 47 % of the explanatory matrix (landscape elements) and 63 % of the dependent matrix ($Q^2 = 0.21$). The second component explained 31 % of the explanatory matrix and 19 % of the dependent matrix ($Q^2 = 0.28$). In general, 82 % of the mean activity density of the two species throughout the study period was explained by the first and second PLSR components (Table 2).

PLSR loadings analysis

The first PLSR component was defined by the local patch metrics (*Area*, *Perimeter* and *ProxPatch*) and one Olive orchard class metric, total class area (*OCA*), on the positive side, and the other landscape component class metrics (*UVMNProx*, *UVCA* and *ESCA*) on the negative side. The relationship of the variables with the second component was more diffuse (Fig. 4). The c values of the response variables (y) are proportional to the linear variation of Y explained by the corresponding dimension, i.e., R^2. They define one point per response, and in this case we have one point for *S. phillyreae*, and one point for *C. arcuatus*, and both sit in the first quadrant very close to each other, as there is a very high correlation between them (Figs. 2, 4). In PLSR analysis, the importance of a particular X-variable for Y is represented by the distance from the origin in the loading space (Fig. 4).

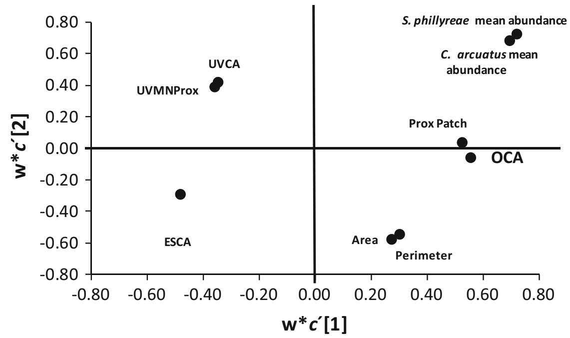

Fig. 4 PLS weight, w^* and c' for the first two dimensions of the model

Scores analysis

In PLSR analysis, scores (t) show object similarities and dissimilarities (Wold et al. 2001). In our case, the plot of the X scores (Fig. 5) shows similarities and dissimilarities based in geographical position and the type of production management of the sampling plot (urban farming plot or industrial farming plot). Five groups of sampling sites were defined: the most distinctive group placed in the first quadrant formed by sites 5 and 6 (industrial farming, North East); a second group formed by sites 1, 2, 3 (industrial farming, Centre North) and 4 (but separated, urban farming) in the second quadrant; a third group formed by sites 11 and 12 (urban farming) also in the second quadrant; a fourth group formed by sites 7, 8 (industrial farming) in the third quadrant and a fifth group formed by sites 9 and 10 (urban farming), in the fourth quadrant (Figs. 1, 5).

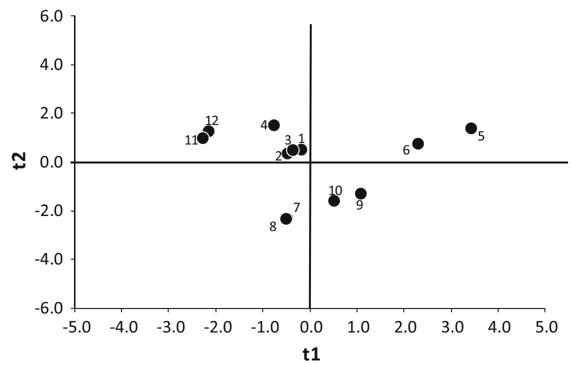

Fig. 5 Partial least squares scores ($t1$ and $t2$) for each of the sampling sites *Clitostethus arcuatus* and *Siphoninus phillyreae* individuals were collected

Coefficient analysis

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 with the greatest influence on the activity density of *S. phillyreae* is the total class area of olive orchards (*OCA*), followed by the total area of urban vegetation (*UVCA*). On the other hand host patch perimeter (*Perimeter*), host

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	0.47	0.47	0.63	0.63	0.21	S
2	0.31	0.78	0.19	0.82	0.28	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 2.82 % of sum of squares of the dependent variables has been explained by all the independent variables

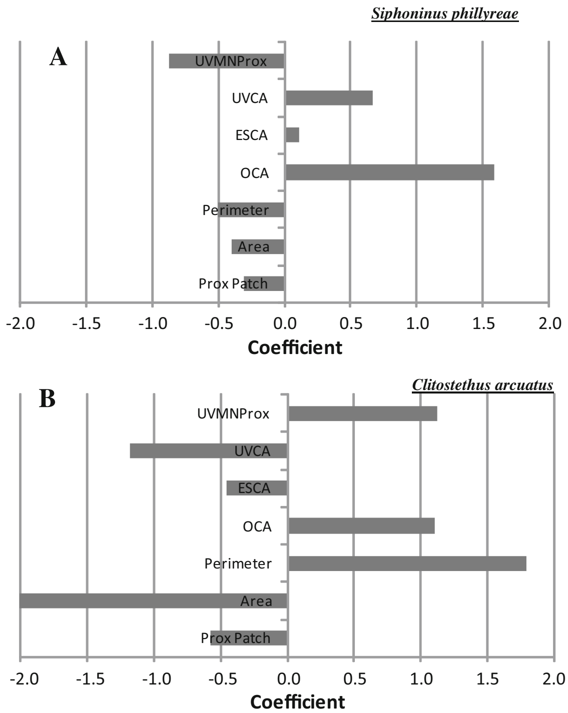

Fig. 6 Estimated regression coefficients for the predicted *Siphoninus phillyreae* (**a**) and *Clitostethus arcuatus* (**b**) mean activity density. Independent variables names are explicated in Table 1

patch area (*Area*), proximity to other olive patches (*ProxPatch*), and mean proximity between urban vegetation patches (*ProxMNUrb*), all show negative PLSR coefficient, being perimeter of host patches (*Perimeter*) and proximity between urban patches (*ProxMNUrb*) those more influential (Fig. 6a).

The situation with *C. arcuatus* is a bit different. Although total class area of olive orchards (*OCA*) is also a variable with a positive PLSR coefficient, now the perimeter of the host patch (*Perimeter*) and the mean proximity of urban vegetation patches (*UVMN-Prox*) show to be more influential. The host patch area (*Area*) from which samples were collected is also very important but with a negative PLSR coefficient (Fig. 6b).

Discussion

Our study region is situated in north western Argentina and is an arid land with less than 100 mm of rainfall per year (Biurrun et al. 2012). Vegetation is concentrated in irrigated spots some in urban areas where small farmers have small olive plots, and in olive industrial production plots. Landscape is less fragmented and less diverse in the big industrial production plots, and more fragmented and more diverse in urban areas (Fig. 2).

Different species will experience the landscape in a different way depending on their needs, behaviours, and trophic level. It is expected different ecological responses to landscape changes among species based on the amplitude of their resourced needs and behaviour.

Some species may be dispersive and long lived, moving at such large scale that do not perceive the landscape as patchy, or if using a broad range of resources, perceiving the landscape as continuous. At the opposite extreme there are sedentary species which individuals usually spend their entire life within a single habitat patch (van Nouhuys 2005). If the resource requirements of a species are very narrow, it will perceive the landscape as highly fragmented because just a small fraction of the total area will be useful (MacArthur and Levins 1964). Species in different trophic levels will show different responses to habitat fragmentation (van Nouhuys 2005). This is this way, because preys are limited to a subset of the suitable locations in the landscape, and because population dynamics of the prey species make them an unstable resource for the predator (Holt 2002; van Nouhuys and Hanski 2005).

The ash whitefly, *S. phillyreae* is a polyphagous invasive species that affects many ornamental plants such as ash trees, wild or fruit trees (pear, apple, orange, olive, pomegranate etc.) (Abd-Rabou 2006). It generally causes severe damage to its hosts directly by feeding, and its heavy infestation causes leaf wilt, early leaf drop and smaller fruit (Bellows et al. 1990) and in extreme cases small trees may die (Bellows et al. 1990; Gerling et al. 2004). As mentioned in the introduction, this species was first reported as heavily infesting ash trees in Mendoza city in 1997 (Viscarret and Botto 1997) and was probably introduced from Chile. On the other hand *C. arcuatus* was mentioned for the first time in the same area 10 years later (Gasparini et al. 2007). This species is one of the most important natural enemies of *S. phillyreae*, feeding on its eggs, nymphs, and adults (Priore 1969; Bathon and Pietrzik 1986; Bellows et al. 1992). The agricultural system where this study was performed is particular in terms of distribution and tenure. Olive orchards are distributed either in urban areas or in irrigated plots far away from urban areas and surrounded by an almost desert matrix. The spatial structure of landscapes influences the abundance and distribution of species in several ways (Forman and Godron 1986; Wiens 1997). For 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). Some 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). Both theoretical and empirical landscape studies show how the spatial arrangement and composition of landscape elements affect insect dynamics inside the host patch, the response of the species to the edge, the spillover among adjacent elements and the distribution of organisms between patches (Tscharntke 2000; Tscharntke and Brandl 2004; With 2004). Many studies on herbivores show that the composition of the matrix has an effect on animal movement and connectivity between patches (Crist et al. 1992; Ricketts 2001; Revilla et al. 2004), but until now there are very few studies showing how the matrix affects predators or parasitoids (Morrison 1996; Elliott et al. 2002; Cronin 2003; Cronin and Haynes 2004; Grez et al. 2005).

Generalist coccinellids have two principal kind of food: essential that guarantees oviposition and completion of larval development, and alternative that only serves as source of energy (Hodek and Evans 2012). Although *Clitostethus arcuatus* is a generalist predator, there is evidence that prefers Aleyrodid species (Mills 1981) and has been employed to control *S. phillyreae* in some parts of the United States (Bellows et al. 1990). It is documented that it preys on other species of Homoptera, like *Aleurothrixus floccosu*s (Maskell) (Liotta 1981a; Katsoyannos et al. 1997), *Aleurotrachelus jelinekii* (Frauenfeld) (Mills 1981), *Aleyrodes proletella* L. (Bathon and Pietrzik 1986), *Dialeurodes citri* (Ashmead) (Agekian 1977; Liotta 1981b), *Siphoninus immaculata* (Heeger) (Hodek and Honek 2009), *Trialeurodes vaporariorum* (Westwood) (Agekian 1977), which are also considered as essential preys or even in aphids (Gerling et al. 2001). All these prey species feed on different ornamental plants, fruit trees or other vegetables that can be found in the area surrounding the olive patches of different size. The relationship between patch size and animal density is a key subject for pest control (Bommarco and Banks 2003; Bukovinszky et al. 2005), and many researchers have attempted to explore its underlying mechanisms (Bach 1988a, b). As mentioned in the introduction, among herbivorous insects there will be a direct relationship between abundance and patch size (Capman et al. 1990). Nevertheless, in some cases herbivores seem not to show this behaviour, e.g. they can be more abundant in large patches, in small patches, or may simply not discriminate between patches of different sizes (Bowers and Matter 1997). This is why we approached the description of the landscape using metrics with different characteristics, some of which quantify landscape composition, while others quantify landscape configuration. Predators and prey respond differently to landscape configuration and to specific landscape elements. Configuration and composition of the landscape will affect ecological processes independently and interactively (Gustafson 1998). Five 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 perimeter of focal patch (*Perimeter*); the total area of a particular class (*CA*), and the general context of patches in the landscape (*Mean Proximity Index*) (McGarigal and Marks 1995). We quantified these metrics not only for the herbivore host (olive orchards) but also for other landscape elements; i.e. urban vegetation (*UVCA* and *UVMNProx*) and exposed soil (*ESCA*), as the latter can be considered as the matrix. We found that the regression coefficients of the model for the predicted activity density of the herbivore *S. phillyreae*, showed that the total area of olive trees was the most influential variable (*OCA*), followed by the total area of urban vegetation in the landscape (*UVCA*). The activity density of the herbivore also had a negative relationship with the area of the focal patch (*Area*), host patch proximity (*ProxPatch*), host patch perimeter (*Perimeter*) and the mean proximity between urban vegetation patches (*UVMNProx*). This is the response expected of a generalist herbivorous insect in an area surrounded by a very hostile environment. In the case of generalist species, it is difficult to apply most of the predictions derived from theories based on islands or patches, as these organisms can use other hosts or even the matrix to survive and reproduce (Sheehan 1986; Holt et al. 1999; van Nouhuys and Hanski 2002; Rand et al. 2006; Ryal and Fahrig 2006). Moreover, there is evidence that population densities of specialist species increase with host patch size, while generalists tend to diminish (Steffan-Dewenter and Tscharntke 2000; Ostergard and Ehrlen 2005; Rand and Tscharntke 2007). According to the metapopulation theory, populations densities will diminish in small, isolated habitats, due to a decrease in immigration (Hanski 1994), which is confirmed by experimental results (González et al. 1998). This seems to be the reason for the decreasing densities of monophagous insects in small habitats. Higher densities of oligophagous and polyphagous insects in small fragments may be an effect of the accumulation of individuals in the landscape surrounding the patch, which may be considered an edge effect (Steffan-Dewenter and Tscharntke 2000). And this seems to be what is going on in our system. The activity density of *S. phillyreae* is weakly negatively related with the host patch area, but strongly correlated with the total area of the host in the landscape. The total area of olive trees within each study site is clearly a key factor affecting population activity density in each of the study patches. There is evidence that the positive relationship between patch area and insect density occurs mainly in systems embedded in highly fragmented landscapes (Andren 1994), but that is not our case. The whole area behaves like a single host patch, even with a negative effect of the proximity of other host patches. This is also what the PLSR scores indicate: each isolated region, separated by a very hostile desert matrix, is behaving as an individual island. Generalist herbivores do not generally show a clear relationship with host patch proximity, as in many cases they can use other resources (Jonsen and Fahrig 1997). This is normal behaviour among whiteflies, which in general make only short range flights, probably within the same tree (Cohen 1990; van-Lenteren and Noldus 1990; Byrne 1999). As mentioned before, we found that the perimeter of olive trees patches had a negative effect on the activity density of whiteflies in the study host patch. This can be read as an edge effect (Ries et al. 2004): trees at the border of the patch are probably more affected by predation in general and in particular that caused by *C. arcuatus*, as shown by the direct relationship between the activity density of these two species. The activity density of the predator *C. arcuatus* on the other hand is seen to be negatively correlated with the area of the host patch where individuals were collected (*Area*), the proximity of host patches (*ProxPatch*), and the total area of other, mostly urban, vegetation (*UVCA*). In this case the regression coefficients of the predicted model for *C. arcuatus* also show that, although the total area of olive trees is an influential variable (*OCA*), the most influential variable on the activity density of this species within the host patch is the perimeter (*Perimeter*) with a strong positive effect on activity density, followed by the proximity of other vegetation in the landscape (*UVMNProx*). That the perimeter of the host patch has a strong positive regression coefficient with *C.arcuatus* and negative with *S. phillyreae* suggests that there is some effect of the host patch border in the interaction between these two species. Edge effects have been widely studied as they are a key factor for understanding the effect of landscape structure on habitat quality. In fact, the effect of the edge on predation is one of the most extensively studied classes of species interactions within the edge literature (Paton 1994; Lahti 2001; Chalfoun et al. 2002; Ries et al. 2004). Even when *Clitostethus arcuatus* is considered one of the most important natural biological control agents of *Siphoninus phillyreae,* it is well-documented as a polyphagous species, feeding especially on the eggs and nymphs and sometimes on the adults of *Siphoninus phyllyridae* and many other homopteran species (Mills 1981; Bellows et al. 1992). So the positive effect on *C. arcuatus* of the proximity to other vegetation spots (*UVMNProx*) indicates that the predator probably uses this other vegetation as a refuge, and gets into the olive patch to feed on nymphs and eggs of *S. phillyreae.*

Our results showed that although the total area of the herbivore host plays a primary roll for the studied species, the landscape structure has a differential effect in each of these species. Sites are grouped for affinity of land management and geographical position. Nearby sites with similar farming practice are more similar between them. In terms of pest management, it is important to consider that any control measure of this whitefly should be approached within a more general strategy, considering not only the olive production patch but the surrounding vegetation area too.

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References

Abd-Rabou S (2006) Biological control of the pomegranate whitefly, *Siphoninus phillyre*ae (Homoptera: Aleyrodidae: Aleyrodinae) by using the bioagent, *Clitostethus arcuatus* (Coleoptera: Coccinellidae). J Entomol 3(4):331–335

Agekian NG (1977) *Clitostethus arcuatus* Rossi (Coleoptera, Coccinellidae)—predator of citrus whitefly in Adzharia. Entomologicheskoye Obozrenie 56:31–33

Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366

Bach CE (1988a) Effect of host plant patch size on herbivore density: patterns. Ecology 6:1090–1102

Bach CE (1988b) Effect of host plant patch size on herbivore density: underlying mechanisms. Ecology 69:1103–1117

Bascompte J, Sole RV (1998) Effects of habitat destruction in a prey predator metapopulation model. J Theor Biol 195:383–393

Bathon VH, Pietrzik J (1986) On the food consumption of *Clitostethus arcuatus* (Rossi) (Col.: Coccinellidae), a predator of *Aleurodes proletella* L. (Hom.: Aleyrodidae). J Appl Entomol 102:321–326

Bellows TS, Paine TB, Arakawa KY, Meisenbacher C, Leddy P, Kabashim J (1990) Biological control sought for ash whitefly. Calif Agric (Berkeley) 44:4–6

Bellows TS, Paine TD, Gerling D (1992) Development, survival, longevity, and fecundity of *Clitostethus arcuatus* (Coleoptera: Coccinellidae) on *Siphoninus phillyreae* (Homoptera: Aleyrodidae) in the laboratory. Environ Entomol 21(3):659–663

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533

Biurrun F, Agüero N, Walter D, Teruel, DF (2012) Consideraciones fitogeográficas sobre la vegetación de los llanos de La Rioja. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina

Boivin G, Roger C, Coderre D, Wajnberg E (2010) Learning affects prey selection in larvae of a generalist coccinellid predator. Entomol Exp Appl 135:48–55

Bommarco R, Banks JE (2003) Scale as modifier in vegetation diversity experiments: effects on herbivores and predators. Oikos 102:440–448

Bowers MA, Matter SF (1997) Landscape ecology of mammals: relationships between density and patch-size. J Mammal 78:999–1013

Bukovinszky T, Potting RPJ, Clough Y, van Lenteren JC, Vet LEM (2005) The role of pre- and post-alighting detection mechanisms in the responses to patch size by specialist herbivores. Oikos 109:435–446

Byrne D (1999) Migration and dispersal by the sweet potato whitefly, *Bemisia tabaci*. Agric For Meteorol 97:309–316

Cantrell RS, Cosner C, Fagan WF (2001) How predator incursions affect critical patch size: the role of the functional response. Am Nat 158:368–375

Cantrell RS, Cosner C, Fagan WF (2002) Habitat edges and predator—prey interactions: effects on critical patch size. Math Biosci 175:31–55

Capman WC, Batzli GO, Simms LE (1990) Responses of the common sooty wing skipper to patches of host plants. Ecology 71:1430–1440

Chalfoun AD, Thompson FR, Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and metaanalysis. Conserv Biol 16:306–318

Cheng Q, Sun DW (2005) Application of PLSR in correlating physical and chemical properties of pork ham with different cooling methods. Meat Sci 70:691–698

Cohen S (1990) Epidemiology of whitefly-transmitted viruses. In: Gerling D (ed) Whiteflies: their bionomics, pest status and management. Intercept, Andover, UK, pp 210–225

Congalton RG, Green K (1999) Assessing the accuracy of classifications of remotely sensed data: principles and practices. Lewis Publishers (CRC Press Inc.), New York, p 209

Connor EF, Coutney AC, Yoder JM (2000) Individuals–area relationship: the relationship between animal population density and area. Ecology 81:734–748

Crist TO, Guertin DS, Wiens JA, Milne BT (1992) Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. Funct Ecol 6:536–544

Cronin JT (2003) Movement and spatial population structure of a prairie planthopper. Ecology 84:1179–1188

Cronin JT, Haynes KJ (2004) An invasive plant promotes unstable host–parasitoid patch dynamics. Ecology 85:2772–2782

Eastman RJ (2006) IDRISI Andes guide to GIS and image processing. Clark Labs, Clark University, Worcester, MA, p 328

Elliott NC, Kieckhefe RW, Michels GJ, Giles KL (2002) Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. Environ Entomol 31:253–260

Elzinga JA, van Nouhuys S, van Leeuwena DJ, Biere A (2007) Distribution and colonisation ability of three parasitoids and their herbivorous host in a fragmented landscape. Basic Appl Ecol 8:75–88

Fahrig L, Jonsen I (1998) Effect of habitat patch characteristics on abundance and diversity of insects in an agricultural landscape. Ecosystems 1:197–205

Forman RTT, Godron M (1986) Landscape ecology. Wiley, New York

Gasparini ML, Holgado MG, Rodriguez F (2007) Presencia de *Clitostethus arcuatus* (Coleoptera: Coccinellidae) sobre olivos infestados con *Siphoninus phillyreae* (Hemiptera: Aleyrodidae) en Argentina. Revista de la Sociedad Entomológica Argentina 66:169–170

Gerling D (1990) Natural enemies of white flies: predators and parasitoids. In: Gerling D (ed) White flies: their bionomics, pest status and management. Intercept, Andover, Hants, UK, pp 147–185

Gerling D, Alomar O, Arno J (2001) Biological control of *Bemisia tabaci* using predators and parasitoids. Crop Prot 20:779–799

Gerling D, Rottenberg O, Bellows TSJ (2004) Role of natural enemies and other factors in the dynamics of field populations of the whitefly *Siphoninus phillyreae* (Haliday) in introduced and native environments. Biol Control 31:199–209

González G (1996) Los Coccinellidae de Chile. http://www.coccinellidae.cl. Accessed 18 March 2015

González A, Lawton JH, Gilbert FSM, Blackburn T, Evans-Freke I (1998) Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047

Grez AA, Zaviezo T, Rios M (2005) Ladybird (Coleoptera: Coccinellidae) dispersal in experimental fragmented alfalfa landscapes. Eur J Entomol 102:209–216

Grilli MP (2010) The role of landscape structure on the abundance of a disease vector planthopper: a quantitative approach. Landscape Ecol 25:383–394

Grilli MP, Bruno MA (2007) Regional abundance of a planthopper pest: the effect of host patch area and configuration. Entomol Exp Appl 122:133–143

Gustafson EJ (1998) Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1:143–156

Gustafson E, Parker GR (1992) Relationships between land cover proportion and indices of landscape spatial pattern. Landscape Ecol 7:101–110

Hamback PA, Englund G (2005) Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. Ecol Lett 8:1057–1065

Hanski I (1994) A practical model of metapopulation dynamics. J Anim Ecol 63:151–162

Hanski I (1999) Metapopulation Ecology. Oxford University Press, New York

Hanski I, Gilpin ME (1997) Metapopulation biology: ecology, genetics, and evolution. Academic, San Diego, CA

Hodek I, Evans EW (2012) Food relationships. In: Hodek I, van Emden HF and Honek A (eds) Ecology and behaviour of the ladybird beetles (*Coccinellidae*). Wiley-Blackwell, UK, pp 141–274

Hodek I, Honek A (2009) Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. Biol Control 51:232–243

Holgado M, Saez C, Llera J, Gasparini M, Anzorena G, Bataglia M, Cid P, Pasquale N (2005) Fluctuación poblacional de *Siphoninus phillyreae* (Hemiptera-Aleyrodidae) en olivos de Mendoza. Libro de Resúmenes VI Congreso Argentino de Entomología, San Miguel de Tucumán, Argentina

Holt RD (2002) Food webs in space: on the interplay of dynamic instability and spatial processes. Ecol Res 17:261–273

Holt RD, Lawton JH, Polis GA, Martinez ND (1999) Trophic rank and the species–area relationship. Ecology 80:1495–1504

Honek A (2012) Distribution and habitats. In: Hodek I, van Emden HF and Honek A (eds) Ecology and behaviour of the ladybird beetles (*Coccinellidae*). Wiley-Blackwel, UK, pp 110–140

Inc StatSoft (2001) STATISTICA for Windows (computer program manual). StatSoft Inc., Tulsa, Oklahoma (StatSoft Inc., 2300 East 14th Street, Tulsa, Oklahoma)

Indec (2002) Censo Nacional Agropecuario 2002. http://www.indec.mecon.gov.ar/agropecuario/cna_principal.asp. Accessed 18 March 2015

Jonsen ID, Fahrig L (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecol 12:185–197

Katsoyannos P, Ifantis K, Kontodimas DC (1997) Phenology, population trend and natural enemies of *Aleurothrixus floccosus* (Hom.: Aleyrodidae) at a newly invaded area in Athens, Greece. Entomophaga 42:619–628

Kondoh M (2003) Habitat fragmentation resulting in overgrazing by herbivores. J Theor Biol 225:453–460

Lahti DC (2001) The "edge effect on nest predation" hypothesis after twenty years. Biol Conserv 99:365–374

Landgrebe DA (2003) Signal theory methods in multispectral remote sensing. Wiley Interscience, New York

Laurance WF, Yensen E (1991) Predicting the impacts of edge effects in fragmented habitats. Biol Conserv 55:77–92

Liotta G (1981a) La mosca bianca fioccosa degli agrumi. Informatore Fitopatologico 32:11–15

Liotta G (1981b) Osservazioni bio-ecologiche su *Clitostethus arcuatus* (Rossi) (Col. Coccinellidae) in Sicilia. Redia 64:173–185

MacArthur RH, Levins R (1964) Competition, habitat selection, and character displacement in a patchy environment. Proc Natl Acad Sci USA 51:1207–1210

Martens H, Naes T (1989) Multivariate calibration. Wiley, New York

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 18 March 2015

Melian CJ, Bascompte J (2002) Food web structure and habitat loss. Ecol Lett 5:37–46

Mills NJ (1981) Essential and alternative foods for British Coccinellidae (Coleoptera). Entomol Gaz 32:197–202

Milne BT, Turner MG, Wiens JA, Johnson AR (1992) Interactions between the fractal geometry of landscapes and allometric herbivory. Theor Popul Biol 41:337–353

Morrison JA (1996) Infection of *Juncus dichotomus* by the smut fungus *Cintractia junci*: an experimental field test of the effects of neighbouring plants, environment, and host plant genotype. J Ecol 84:691–702

Murphy HT, Lovett-Doust J (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105:3–14

Nakagiri N, Tainaka K (2004) Indirect effects of habitat destruction in model ecosystems. Ecol Model 17:103–114
Nakagiri N, Tainaka KI, Tao T (2001) Indirect relation between species extinction and habitat destruction. Ecol Model 137:109–118
Ostergard H, Ehrlen J (2005) Among population variation in specialist and generalist seed predation, the importance of host plant distribution, alternative hosts and environmental variation. Oikos 111:39–46
Paton PWC (1994) The effect of edge on avian nest success—how strong is the evidence. Conserv Biol 8:17–26
Peña MA (1994) *Siphoninus phillyrae* (Haliday, 1835), una nueva mosca blanca para la fauna canaria (Homoptera, Aleyrodidae). Boletín de sanidad vegetal—Plagas 20(3):601–604
Prakash S, De Roos AM (2002) Habitat destruction in a simple predator–prey patch model: how predators enhance prey persistence and abundance. Theor Popul Biol 62:231–249
Priore R (1969) *Dealeurodes citri* (Ashmead) (Homoptera: Aleyrodidae) in Campania. Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri 27:287–316
Rand TA, Louda SM (2006) Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. Conserv Biol 20:1720–1729
Rand TA, Tscharntke T (2007) Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. Oikos 116:1353–1362
Rand TA, Tylianakis JM, Tscharntke T (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecol Lett 9:603–614
Revilla E, Wiegand T, Palomares F, Ferreras P, Delibes M (2004) Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation level parameters. Am Nat 164:130–153. doi:10.1086/424767
Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99. doi:10.1086/320863
Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol 35:491–522
Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Monogr 43:95–124
Ryal LK, Fahrig L (2006) Response of predators to loss and fragmentation of prey habitat: a review of theory. Ecology 87(5):1086–1093
Sabins F (1997) Remote sensing principles and interpretation. W. H. Freeman and Company, New York
Searles PS, Agüero Alcarás M, Rousseaux MC (2011) El consumo del agua por el cultivo de olivo (*Olea europaea* L.) en el noroeste de Argentina: una comparación con la Cuenca Mediterránea. Ecología Austral 21:15–28
Sheehan W (1986) Response by Specialist and Generalist Natural Enemies to Agroecosystem Diversification: a Selective Review. Environ Entomol 15(3):456–461
Steffan-Dewenter I, Tscharntke T (2000) Butterfly community structure in fragmented habitats. Ecol Lett 3:449–456
Swihart RK, Feng Z, Slade NA, Mason DM, Gehring TM (2001) Effects of habitat destruction and resource supplementation in a predator–prey metapopulation model. J Theor Biol 210:287–303
Tenenhaus M (1998) La Regression PLS: theorie et pratique. Technip, Paris
Thies C, Steffan-Dewenter I, Tscharntke T (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101:18–25
Tscharntke T (2000) Parasitoid populations in agricultural landscapes. In: Hochberg ME, Ives AR (eds) Parasitoid population biolog y. Princeton University Press, Princeton, NJ, pp 235–253
Tscharntke T, Brandl R (2004) Plant–insect interactions in fragmented landscapes. Annu Rev Entomol 49:405–430. doi:10.1146/annurev.ento.49.061802.123339
Tscharntke T, Kruess A (1999) Habitat fragmentation and biological control. In: Hawkins BA, Cornell HV (eds) Theoretical approaches to biological control. Cambridge University Press, Cambridge, UK, pp 190–205
van Nouhuys S (2005) Effects of habitat fragmentation at different trophic levels in insect communities. Ann Zool Fennici 42:433–447
van Nouhuys S, Hanski I (2002) Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. J Anim Ecol 71:639–650. doi:10.1046/j.1365-2656.2002.00627.x
van Nouhuys S, Hanski I (2005) Metacommunities of butterflies, their host plants and their parasitoids. In: Holyoak M, Leibold MA, Holt RD (eds) Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, pp 99–121
van-Lenteren JC, Noldus LP (1990) Whitefly–plant relationships: behavioural and ecological aspects. In: Gerling D (ed) Whiteflies: their bionomics, pest status and management. Intercept, Andover, UK, pp 47–89
Venzon M, Janssen A, Sabelis MW (2002) Prey preference and reproductive success of the generalist predator *Orius laevigatus*. Oikos 97:116–124
Viscarret MM, Botto EN (1996) Descripción e identificación de *Trialeuroides vaporariorum* (westwood) y *Bemisia tabaci* (Gennadius), (Hemiptera, Homoptera: Aleyroididae). Revista chilena de Entomología 23:51–58
Viscarret MM, Botto EN (1997) Presencia de *Siphoninus phillyreae* (Haliday), “la mosca blanca de los fresnos” (Homptera: Aleyrodidae), en la Argentina. Revista de la Sociedad Entomológica Argentina 56(1–4):90
Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397
Wiens JA (1997) Metapopulation dynamics and landscape ecology. In: Hanski IA, Gilpin ME (eds) Metapopulation biology: ecology, genetics, and evolution. Academic, San Diego, California, USA, pp 43–67
Wilcove DS, McLellan C, Dobson A (1986) Habitat fragmentation in the temperate zone. In: Soule ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, MA, pp 237–256
With KA (2004) Metapopulation dynamics: perspectives from landscape ecology. In: Hanski I, Gaggiotti OE (eds) Ecology, genetics, and evolution of metapopulations. Elsevier Academic, Boston, MA, pp 23–44
With KA, Pavuk DM, Worchuck J, Oates RK, Fisher JL (2002) Treshold effects of landscape structure on biological control in agroecosystems. Ecol Appl 12:52–65

Wold S, Albano C, Dunn WJ, Edlund U, Eliasson B, Johansson E, Norden B, Sjöström M (1982) The indirect observation of molecular chemical systems. In: Jöreskog KG, Wold H (eds) Systems under indirect observation, vol I and II. North-Holland, Amsterdam, pp 177–207

Wold S, Sjöström M, Eriksson L (2001) PLS-regression: a basic tool of chemometrics. Chemometr Intell Lab Syst 58:109–130