



Local predator composition and landscape affects biological control of aphids in alfalfa fields



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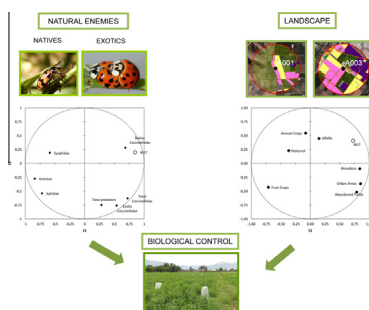
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HIGHLIGHTS

- We studied landscape and predator effects on biocontrol (BSI) of aphids in alfalfa.
- BSI was positively associated with native coccinellids and syrphids.
- BSI was positively associated with woodlots and urban habitats in the landscape.
- BSI was negatively associated with fruit crops in the landscape.
- Landscape effects on biological control only become important when local predator abundance is low.

GRAPHICAL ABSTRACT



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ABSTRACT

The biological control service supplied to croplands is a result of the predator community present within a focal crop, which is likely influenced by surrounding landscape composition and configuration. In this study, using cage experiments in two regions near Santiago, we determined if predator communities supplied a significant biological control service in alfalfa fields, examined how the abundance of exotic and native coccinellids, as well as other key predator groups, influenced biological control of aphids and measured how landscape composition and heterogeneity at three spatial scales influenced this service. We found that predators significantly suppressed aphid populations in both regions, but the relative importance of predators versus landscape variables on biological control differed between regions. In the region where predators were abundant, biological control was higher and related to the abundance of native coccinellids and syrphids, highlighting the importance of native species as providers of crucial ecological services. In the region where predators were not abundant, biological control was lower, and it was related to landscape composition, being positively associated with the abundance of woodlots and urban habitats, and negatively associated with fruit crops in the landscape. Therefore, landscape effects on biological control service may be weaker than local factors, and only become important when local predator abundance is low.

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1. Introduction

Arthropods provide multiple ecosystem services within agroecosystems including decomposition, pollination and biological control that influence the sustainability of crop production (Losey

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and Vaughan, 2006; Isaacs et al., 2009). In general, species rich communities are predicted to support the greatest combined capture of resources such as pollen or prey (Cardinale et al., 2006). However, species may vary in their contribution to an ecosystem service and interactions among guild members may affect the combined provision of a beneficial arthropod community. For predators and biological control services, many interactions such as facilitation and intraguild predation occur commonly (Losey and Denno, 1999; Finke and Denno, 2002; Cardinale et al., 2003) and can modify relationships between predator abundance, diversity, and function (Ives et al., 2005; Caballero-López et al., 2012).

Understanding how variation in predator community composition influences biological control is particularly important when exotic generalist predators are introduced into agricultural landscapes (Crowder and Snyder, 2010). Exotic predators can have varying impacts on populations of competitors through both direct mortality and indirect competition for shared resources (Evans, 2004; Crowder and Snyder, 2010; Tapia et al., 2010; Grez et al., 2012; Smith and Gardiner, 2013, in press). Thus, the addition of exotic generalist predators to agroecosystems may or may not enhance resource capture of prey within croplands (Elliott et al., 1996). For example, the introduction of exotic coccinellids has coincided with the rapid decline of several native taxa worldwide (Koch et al., 2006; Brown et al., 2011; Gardiner et al., 2012; Roy et al., 2012). While exotic generalist predators such as coccinellids are effective biological control agents in several cropping systems (Lucas et al., 2007; Soares et al., 2007; Koch and Galvan, 2008) it cannot be assumed that they will provide the same level of biological control services as potentially displaced native competitors.

Additionally, natural enemies in a given crop can be influenced by the characteristics of the surrounding landscape (Tscharntke et al., 2007; Werling et al., 2011). The heterogeneity of the landscape at different spatial scales, as well as the composition of vegetation have all been shown to influence natural enemy abundance, interactions, and the provision of biological control services (Bianchi et al., 2006; Gardiner et al., 2009a,b, 2011; Grez et al., 2010a; Holzschuh et al., 2010; Gagić et al., 2011; Médiène et al., 2011; O'Rourke et al., 2011; Caballero-López et al., 2012; Amaral et al., 2013). First, not all habitats within a landscape are equally suitable for natural enemies. By comparing coccinellid communities across habitats ranging from natural matorral and riparian habitats to cultivated croplands, Grez et al. (2013) illustrated that habitat disturbance favors exotic coccinellids. The proportion of the coccinellid community composed of exotic species increased with level of habitat disturbance, with the greatest dominance in alfalfa crops compared with the other habitat types mentioned. Second, exotic and native predators can vary in their use of the available resources present within crop patches and edges. For example, Amaral et al. (2013) found that the native coccinellid *Cycloneda sanguinea* (Coleoptera: Coccinellidae) commonly utilized non-crop weed strips as a source of alternative food resources, whereas *Harmonia axyridis* (Coleoptera: Coccinellidae) was rarely found foraging within these strips. Further, variation in landscape composition can influence the abundance of native versus exotic predators present within agroecosystems. For example, Gardiner et al. (2009b) found that native coccinellid abundance in soybean fields was positively related to the abundance of native grassland habitat in surrounding landscapes whereas exotic lady beetle abundance in soybean was greatest in forest-dominated landscapes. In contrast to the many examples showing that landscape composition and heterogeneity affects natural enemy populations, very few report how landscape affect biological control (but see Gardiner et al., 2009a; Woltz et al., 2012). Additionally, the effects of landscape variables related to configuration heterogeneity (the spatial arrangements of habitats, Fahrig et al., 2011), such as mean patch size, shape and edge density, on natural enemies and

biological control services have rarely been studied. Configurational heterogeneity affects the migration of natural enemies to and from crops, their searching efficiency and consequently may affect biological control (Grez and Prado, 2000; With et al., 2002; Bianchi et al., 2006; Zaviezo et al., 2006; Tscharntke et al., 2007; Werling et al., 2011).

In alfalfa fields in regions surrounding Santiago, Chile, there is a diverse community of native and exotic species of coccinellids and other predators that feed on the exotic pea aphid, *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) (Zaviezo et al., 2004, 2006; Grez et al., 2008, 2010a; Ximenez-Embun et al., 2014). Recently, in 2008, the exotic invasive lady beetle, *H. axyridis*, was detected in Chile. Within a few years *H. axyridis* has become common within alfalfa and may alter the outcome of aphid biological control (Grez et al., 2010b, 2013). This system provided an opportunity to test the hypothesis that the predator community within the crop and landscape composition and configuration impact biological control services. Our specific aims were to (1) Determine if predator communities supplied a significant biological control service to alfalfa fields, (2) Examine how the abundance of exotic and native coccinellids and other key predator groups influenced biological control services and (3) Measure how landscape composition and heterogeneity influenced biological control services.

2. Materials and methods

2.1. Study sites

The study was carried out in two regions near Santiago, Chile, in two consecutive springs (September–October): Pirque (33°38'S; 70°33'W) in 2012, and Calera de Tango (33°37'S; 70°46'W) in 2013. This time of the year is when aphids are most abundant in alfalfa fields (Apablaza and Stevenson, 1995). Both of these regions comprise agricultural landscapes with a diversity of production systems including vineyards, orchards, wheat and alfalfa fields with an average field size of less than 3 ha. Both regions also include remnants of native matorral and other semi-natural habitats such as hedgerows and eucalyptus woodlands (Grez et al., 2013). In each of these regions, we conducted experiments in ten alfalfa fields separated by at least 2 km.

2.2. Estimation of biological control services in alfalfa fields

Similar to previous studies (Costamagna and Landis, 2006, 2011; Gardiner et al., 2009a; Caballero-López et al., 2012; Costamagna et al., 2013) biological control was measured by comparing aphid population growth in the presence and absence of predators using exclusion cages. In the center of each alfalfa field, we established four plots which were each separated by 10 m. A plot consisted of three 1 m² subplots in a row separated by 1 m. Within each of these subplots, we isolated an alfalfa plant (approximately 15 cm diameter × 20 cm tall) by removing all surrounding stems. Each of these plants was randomly assigned to one of the following three treatments: (1) Exclusion Cage (no access for predators), (2) Sham Cage (allowed predator access, lowered dispersal probability of apteorus aphids and measurement of cage effects such as microclimatic changes and aphid crowding), and (3) Open Plant (un-caged plant allowing predator access). The exclusion cage consisted of a 0.4 m diameter × 0.7 m tall cylindrical framework of wire, covered by a white fine mesh (openings of 1 mm) tied at the top and buried in the soil. Additionally, to prevent access of carabids and other ground-dwelling predators to the excluded plant, we surrounded each cage with a 10 cm high metal ring, buried in the soil. The sham cage was identical to the exclusion cage except that the mesh had six rectangular openings (2 × 20 cm)

distributed in all directions (following Costamagna and Landis, 2011). Also, sham cages had no metal ring buried at the soil surface. Open plants consisted of un-caged plants marked by wire flags.

To establish each of the treatments, aphids and all other arthropods were removed through repeated vacuuming with a D-Vac. Next, each plant was stocked with 20 fourth instar or adult apterous aphids (*A. pisum*), to represent common spring infestation levels. The number of aphids (apterous and alate) present on each plant was counted 7 and 14 d after establishment. The study was limited to this time period to measure the influence of biological control shortly following aphid establishment and also to prevent unnatural build-up of alate aphids within the Exclusion Cage treatment or influencing emigration of apterous aphids due to overcrowding (Montgomery and Nault, 1978; Cronin et al., 2004; Costamagna and Landis, 2006, 2011; Gardiner et al., 2009a).

To quantify the influence of predators on aphid populations, we calculated a Biological Control Service Index (BSI, Eq. (1)) following Gardiner et al. (2009a). Given that there was no significant difference in aphid populations in Sham Cage and Open Plant treatments (see results), we estimated the relative suppression of aphid population found in each alfalfa field by expressing the proportional change in aphid number in the Open Plant versus Exclusion Cage treatments, where A_c is the number of aphids on the caged plant, A_o is the number of aphids on the open plant, p is the plot, and n is the number of plots for a given alfalfa field ($n = 4$). The resulting BSI varies from 0 to 1, with values increasing as the level of aphid predation increases. BSI values were calculated from aphid data at both 7 and 14 d after treatment establishment.

$$BSI = \frac{\sum_{p=1}^4 \frac{(A_c.p - A_o.p)}{A_c.p}}{n} \quad (1)$$

In some cases, negative values of BSI were found due to higher aphid populations on the Open Plant than in the corresponding Caged Plant (i.e., same plot). In these cases we assumed a lack of effective biological control, so we assigned a value of zero to these plots (from Gardiner et al., 2009a). In some cases, aphid populations failed to establish within the Exclusion Cage treatment, thus replicates with a count of zero aphids after 7 or 14 d were discarded from the analyses because we assumed that factors other than predation affected the survival of aphids. We found three instances of this for Pirque and two for Calera de Tango.

2.3. Predator and aphid sampling in alfalfa fields

Associated with the biological control experiment, we also measured aphid and predator populations within each alfalfa field site on day 7 and day 14 of the BSI study. Aphid predators were sampled using yellow sticky card traps, sweep samples and pitfall traps in five different locations in each field, close to the BSI experimental plants and separated among them by a minimum of 10 m. Unbaited yellow sticky traps (15 × 28 cm) were placed at foliage level (40 cm above ground) and pitfall traps (8 cm diameter) were sunk to ground level, and left operating during the whole experimental period. Sweep samples consisted of ten sweeps each. Predators collected were counted and identified to species level when possible. Syrphids were not counted in yellow sticky traps on day 7. The number of predators captured by all three sampling techniques was pooled for analyses. Field aphid abundance was also estimated in five different locations by counting the number of individuals on five alfalfa stems.

2.4. Landscape composition and heterogeneity

Natural enemies respond to landscape at several spatial scales (Rand and Tschardtke, 2007; Gardiner et al., 2009b), so we quantified the landscape surrounding each of the ten alfalfa fields sampled in Pirque and ten in Calera de Tango at spatial scales of 250, 500 and 1000 m radii from the center of each site. A buffer of 250 m was chosen to evaluate the local effects of adjacent cover types surrounding the alfalfa focal field on BSI while 1000 m was chosen to evaluate the effects of the variety of cover types surrounding the alfalfa field at landscape scale on BSI. We also include a 500 m radius analysis to assess intermediate scale effects. To characterize composition, we identified the area covered by the following 11 cover types: urban areas (dense residential and industrial areas), semi-urban areas (rural residential properties with yardspaces of approximately 0.5 ha or larger), roads, annual crops, alfalfa fields, orchards, vineyards, abandoned fields (non-cultivated fields composed of annual grasses and perennial weeds), hedgerows (perennial linear structures usually composed of bramble and poplar trees), woodlands (eucalyptus), and matorral. Cover types were digitized on screen using Google Earth Images SPOT 5 and DigitalGlobe. Cover types interpretation and delineation were verified using 150 and 254 field points in Pirque and Calera de Tango, respectively. The overall accuracy of the map was slightly above 95% (details in Grez et al., 2013). We also calculated landscape indexes that describe their compositional and configurational heterogeneity (Fahrig et al., 2011) at each of the three spatial scales: Simpson's diversity Index, mean patch size, edge density and mean shape index. Patch Analyst for ArcGIS® was used for all calculations.

2.5. Data analysis

To compare the number of aphids (apterous and alate) in the Exclusion Cage, Sham Cage, and Open Plant treatments a mixed effects model with the fixed effects Treatment and Time (7 and 14 d) and the random effects Site (alfalfa field) and Plot within Site was conducted. Time (7 and 14 d) was included in the model as a repeated factor. Mean separations were measured using a Tukey's means separation procedure (LS MEANS). Aphid counts were $\log(x + 1)$ transformed prior to analysis to meet the assumption of normality and homogeneity of variances. Each region (Pirque and Calera de Tango) was analyzed separately.

To determine if variation in landscape composition or configuration existed among the two regions an analysis of variance (ANOVA) model with region (Pirque and Calera de Tango) as a fixed effect was used. Our response variables included each landcover class (Alfalfa, Annual Crops, Fruit Crops and Vineyards, Woodland and Hedgerows, Abandoned Fields, Matorral, Semi-Urban, Urban and Roads) as well as each configuration variable (Landscape Diversity, Edge Density, Patch Size and Shape Index).

To assess the influence of the surrounding landscape and local prey and natural enemy abundance on biological control we used partial least squares regression analysis (PLS) (Davis et al., 2007; Carrascal et al., 2009; Rusch et al., 2012). PLS allows for analysis of models with (1) multiple response variables, (2) a large number of predictors which may be collinear, and (3) small sample sizes relative to the number of possible predictor variables that may influence responses (Carrascal et al., 2009). PLS reduces sets of predictor and response variables into a smaller set of latent factors (also called latent vectors or components).

We examined both the effect of landscape composition and heterogeneity on biological control at 7 or 14 d for each region and scale (250, 500 or 1000 m) separately. For landscape heterogeneity, variables were Landscape Diversity, Edge Density, Patch Size and Shape Index). For composition, variables were the proportions of

the following covers: Annual Crops, Alfalfa, Fruit Crops (orchards + vineyards), Abandoned Fields, Woodlots (woodlots + hedgerows), Matorral, and Urban (semi-urban + urban + roads) habitats.

To examine the influence of local prey and natural enemy abundance on biological control at 7 and 14 d we conducted PLS regression analyses also. Variables included were: Abundance of Aphids, All Generalist Predators, Araneae, Coccinellidae, Exotic Coccinellidae, Native Coccinellidae, and Syrphidae.

All predictor and response variables were centered to a mean of zero and scaled to a standard deviation of 1, to give all variables equal weight (Wold et al., 2001). The number of factors to be extracted was determined by cross validation using a minimum predicted residual sum of squares (PRESS) as the stop condition. Explanatory variables with a Variable Importance in Projection (VIP) > 0.8 for a given component were considered significant predictors for that component. For each analysis we interpreted up to the first two components (t_1 and t_2) and only those with a Q^2 value of >0.097 (Johansson and Nilsson, 2002). Correlation loading plots were used to explore the relationship between the predictor and response variables, as manifested through the latent factors. These analyses were conducted using the PLS Module of XLSTAT (Addinsoft).

3. Results

3.1. Predators and aphid abundance in alfalfa fields

In total, we collected a greater abundance of aphid predators in Pirque ($n = 1681$) than in Calera de Tango ($n = 1092$). The predator community found consisted of Anthocoridae, Araneae, Carabidae, Chrysopidae, Coccinellidae, Lygaeidae, Nabidae and Syrphidae. In Pirque and Calera de Tango, the most abundant predators were Coccinellidae (44.5% and 22.16%, respectively), Syrphidae (39.34% and 28.75%) and Araneae (13.50% and 43.50%), with the rest of the community accounting for less than 5.6% (Fig. 1).

A total of eight coccinellid species were found; four exotics (*H. axyridis* (Pallas), *Hippodamia variegata* (Goeze), *Hippodamia convergens* Guérin-Ménéville and *Scymnus loewii* Mulsant)) and four natives (*C. sanguinea* (L.), *Eriopis connexa* (Germar), *Eriopis eschscholtzi* Mulsant and *Hyperaspis sphaeridioides* (Mulsant)). In both regions, exotic coccinellids were more abundant than natives (considering the sum of individuals collected in both weeks, Pirque: 56.9 ± 14.5 versus 17.9 ± 5.8 individuals per alfalfa field; Calera de Tango: 19.8 ± 3.9 versus 4.4 ± 0.9 individuals). In Calera de Tango, coccinellids were less abundant than in Pirque (Fig. 1), and natives were particularly scarce.

Syrphidae consisted solely of adults and larvae of *Allograpta exotica* Weidenmann, being more abundant in Pirque, and Araneae were composed of Anyphaenidae and Lynphiidae (mainly *Neomaso articeps* Millidge), being more abundant in Calera de Tango (Fig. 1).

The abundance of aphids in alfalfa fields was lower in Pirque (83.4 ± 44.3 and 33.7 ± 16.6 aphids per five stems at 7 and 14 d, respectively) than in Calera de Tango (219.2 ± 36.9 and 221.4 ± 34.7 aphids per five stems at 7 and 14 d, respectively). Three aphid species were collected within alfalfa fields: the pea aphid *A. pisum* (Harris), the cowpea aphid *Aphis craccivora* Koch and the spotted alfalfa aphid *Therioaphis trifolii* (Monell), with the first two species being more abundant in both regions, and *A. pisum* representing between 30% and 40% of total aphids.

3.2. Biological control service

We found that predators significantly suppressed aphid populations in both Pirque and Calera de Tango alfalfa fields, illustrated

by lower aphid counts in the Open versus Exclusion Cage treatments at both 7 and 14 d. For Pirque, both Treatment ($F_{2,180} = 37.97$, $P < 0.001$), and Time ($F_{1,180} = 6.13$, $P = 0.014$) were significant predictors of aphid abundance, with no significant Treatment \times Time interaction ($F_{2,180} = 0.23$, $P = 0.791$). Aphids were more abundant within the Exclusion Cage treatment than the Sham Cage or Open Plant treatments at both 7 and 14 d. Populations did not increase or decrease significantly within a treatment across sampling weeks, interestingly even for the Exclusion Cage treatment (Fig. 2). For Calera de Tango, both Treatment ($F_{2,185} = 15.10$, $P < 0.001$), and Time ($F_{1,185} = 4.92$, $P = 0.028$) were significant predictors of aphid abundance, with no significant Treatment \times Time interaction ($F_{2,185} = 2.17$, $P = 0.118$). Aphid abundance in the Exclusion Cage treatment was significantly greater than the Sham Cage or Open Plant treatment at 7 d. The Exclusion Cage treatment supported a significantly higher aphid population than the Open Plant treatment at 14 d, with the Sham Cage treatment not significantly different from either (Fig. 2). These data support a lack of significant cage effects, with the Sham Cage not differing in aphid abundance from the Open Plant for either region. In addition, alate aphids were very scarce (<2.5 alates in 5 stems) and similarly abundant in the Exclusion Cage, Sham Cage, and Open Plant treatments at both 7 and 14 d, discarding significant potential dispersal limitation due to caging.

Using the Exclusion Cage and Open Plant treatment aphid counts, BSI values were calculated for each site. At day 7, on average the BSI was 0.71 ± 0.09 (range: 0.29–1) in Pirque and 0.57 ± 0.07 (0.25–0.90) in Calera de Tango. At day 14, an average BSI of 0.79 ± 0.08 (range of 0.25–1) was found in Pirque and 0.36 ± 0.08 (range of 0–0.71) in Calera de Tango.

3.3. Landscape composition and configuration

For most of the variables measured there was not a significant difference in the abundance of habitats among the two study regions, including Alfalfa ($F_{1,18} = 0.02$, $P = 0.901$), Annual Crops ($F_{1,18} = 0.74$, $P = 0.400$), Fruit Crops and Vineyards ($F_{1,18} = 0.18$, $P = 0.676$), Woodlands and Hedgerows ($F_{1,18} = 0.10$, $P = 0.753$), Matorral ($F_{1,18} = 0.10$, $P = 0.912$) and Semi-Urban areas ($F_{1,18} = 0.82$, $P = 0.377$). The abundance of abandoned fields in Pirque landscapes was marginally significantly higher than Calera de Tango ($F_{1,18} = 3.91$, $P = 0.063$) with means of 19.44 ± 4.16 ha and 10.00 ± 2.33 ha within the two regions. Calera de Tango also had a significantly greater abundance of roads ($F_{1,18} = 10.80$, $P = 0.004$) and Urban areas ($F_{1,18} = 7.00$, $P = 0.016$) within its landscapes than Pirque. Roads covered an average of 5.50 ± 1.34 ha in Pirque and 13.80 ± 2.18 ha in Calera de Tango landscapes. Urban areas encompassed 5.56 ± 1.36 ha in Pirque versus 27.87 ± 8.32 in of Calera de Tango.

The regions exhibited a similar Landscape Diversity ($F_{1,18} = 1.17$, $P = 0.294$) and Average Patch Size ($F_{1,18} = 1.25$, $P = 0.278$). Calera de Tango had marginally greater Edge Density than Pirque ($F_{1,18} = 3.68$, $P = 0.071$, means of 270.82 ± 19.66 versus 211.65 ± 23.76) and significantly greater irregularity of patch shape (Shape Index) ($F_{1,18} = 4.12$, $P = 0.057$, means of 2.80 ± 0.28 versus 2.20 ± 0.10).

3.4. Influence of aphid and natural enemy abundance on biological control services

For aphid biological control in Pirque, we found that BSI at 7 and 14 d was significantly related to the predator community composition. At 7 d, t_1 explained 72.1% and t_2 an additional 3.9% of the biological control service measured within a given alfalfa field (Table 1). At 14 d, t_1 explained 92.1% and t_2 an additional 2.8% of

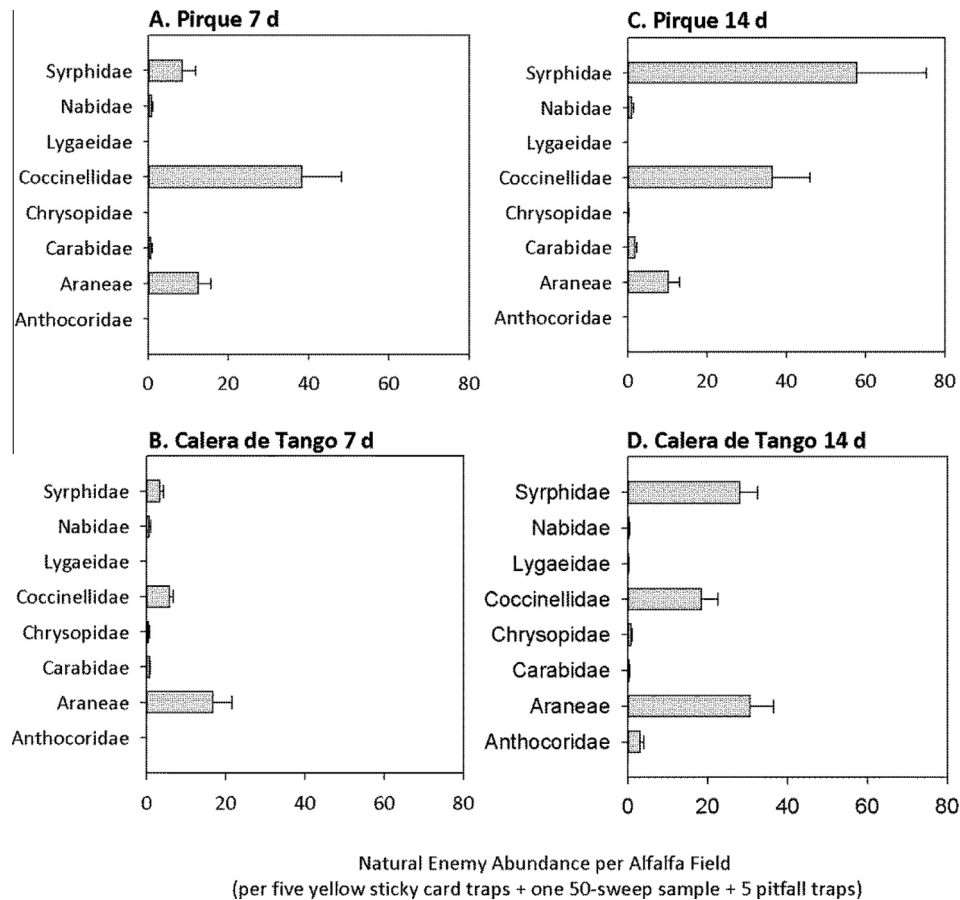


Fig. 1. Abundance of natural enemies (mean \pm SE) captured in 5 yellow sticky traps, 50 sweep-nets and 5 pitfall traps in ten alfalfa fields, in Pirque (A, C) and Calera de Tango (B, D), at 7 and 14 d.

the biological control service measured within a given alfalfa field (Table 1).

For BSI at 7 d, four variables had a VIP score >0.8 for t_1 : Aphididae, Araneae, All Coccinellidae and Native Coccinellidae. BSI was positively related to the abundance of all coccinellids and native coccinellids and was negatively related to Abundance of Aphids and Araneae (Fig. 3a). At 14 d five variables had VIP scores of >0.8 for t_1 : Aphididae, All Coccinellidae, Exotic Coccinellidae, Native Coccinellidae, and Syrphidae. BSI was positively related to the abundance of Native Coccinellidae and Syrphidae and was negatively related to Abundance of Aphids and the abundance of All Coccinellidae and Exotic Coccinellidae (Fig. 3b).

For Calera de Tango, we found that predator abundance models did not explain significant amount of the variance in BSI at either 7 or 14 d as evidenced by all models having a Q^2 score of <0.097 (Table 1).

3.5. Influence of landscape composition and heterogeneity and biological control services

For Pirque, we found that both the landscape composition and landscape heterogeneity (compositional and configurational indexes) models at 250, 500 and 1000 m did not explain a significant amount of the variance in BSI at either 7 or 14 d ($Q^2 < 0.097$, Table 1). For Calera de Tango, landscape heterogeneity models at all spatial scales also did not explain a significant amount of the variance in BSI at either 7 or 14 d (Table 1). However, landscape composition did predict a significant amount of the variance in BSI at 7, but not 14 d. For BSI at 7 d, t_1 of the landscape composition

model at 250 m explained 54.0% the biological control service measured within a given alfalfa field and t_2 was not predictive (Table 1). At 500 m, t_1 of the landscape composition model explained 41.1% of the variation in BSI, with an additional 11.4% explained by t_2 . At 1000 m, t_1 of the landscape composition model explained 52.6% of the variation in BSI measured within alfalfa fields and t_2 an additional 16.6%.

Three variables had a significant VIP score for t_1 of the Calera de Tango landscape composition model at 250 m: Woodlots, Matorral, and Fruit Crops (Fig. 4a). At 500 m four variables had a significant VIP score for t_1 : Woodlots, Alfalfa, Abandoned fields, and Fruit Crops (Fig. 4b). At 1000 m, three variables had a significant VIP score for t_1 : Woodlots, Urban Areas, and Fruit Crops (Fig. 4c). At all scales, biological control was reduced in landscapes dominated by fruit crop production versus those including significant proportions of semi-natural and urban habitats. The cover types most predictive of biological control varied by scale. Woodlots including small forest patches and hedgerows as well as native Matorral habitat within 250 m of an alfalfa field site supported higher BSI. At 500 and 1000 m the proportion of Abandoned Fields, Urban areas and Woodlots were positively related to BSI in alfalfa fields (Fig. 4).

4. Discussion

Our results illustrate that local predator community within a cropland as well as surrounding landscape composition can influence biological control, an important ecological service that can help improve sustainability of crop production. Nevertheless, we found variation in the relative influence of predators and landscape

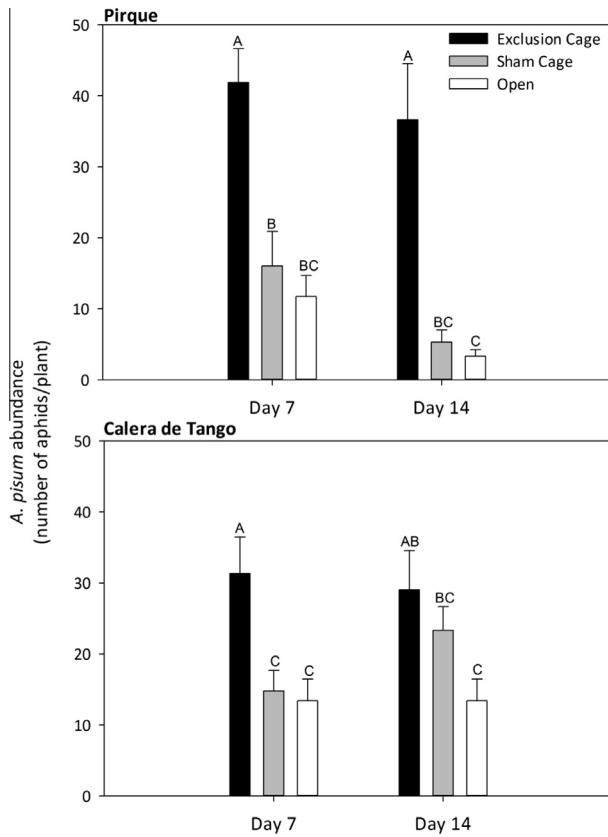


Fig. 2. *Acyrthosiphon pisum* population (mean \pm SE) under three predator manipulation treatments, in Pirque and Calera de Tango at 7 and 14 d. Exclusion Cage: no access of predators, Sham Cage: allowed predator access and measurement of cage effects, and Open Plant: un-caged plant allowing predator access.

in predicting this service within alfalfa fields sampled within two regions of central Chile: Pirque and Calera de Tango.

4.1. Variation in predator communities among study regions

In our study, both the abundance and composition of aphid predators varied between regions. In Pirque, predators were more abundant, with coccinellids and syrphids accounting for more than 70% of the assemblage, whereas in Calera de Tango spiders were the most abundant predator group representing \sim 50% of collected individuals. The higher abundance of coccinellids in Pirque than Calera de Tango is a pattern previously observed in alfalfa and other habitats (Grez et al., 2013). Also, native coccinellids were more abundant and represented a higher proportion of total coccinellids in Pirque than in Calera de Tango, both in this study and in Grez et al. (2013).

The underlying factors and mechanisms that explain this consistent differential abundance between both regions is unknown. Cultivated habitats dominate the landscape of both regions, and there was not an overall difference in the area cultivated with alfalfa, annual crops, or fruit crops and vineyards among regions. However, Calera de Tango contained five times as much urban area and twice the area of roadway running through the landscape than Pirque. The configuration of the Calera de Tango landscapes also varied from Pirque. They had similar landscape diversity, but Calera de Tango had marginally greater edge density and more irregular patches, as indicated by a higher average shape index than Pirque. It is possible that these composition and configuration differences are influencing the region wide species pool able to colonize the alfalfa fields examined in this study.

4.2. Influence of predator communities on aphid biological control

In addition to a greater abundance of predators, aphids were less abundant in Pirque than in Calera de Tango. Over our 14 d study, aphid populations declined in Pirque whereas in Calera de Tango they maintained a consistent higher abundance through time. Aphid abundance within our field sites was negatively related to the Biological Control Service Index values calculated in the cage study. Thus when fewer predators were available to colonize a field and provide control, fields exhibited a lower BSI and higher overall aphid abundance. This is supported by higher BSI values observed in Pirque, both at 7 and 14 d (on average for the 2 weeks: 0.74 in Pirque vs. 0.46 in Calera de Tango).

Further supporting the role of predators in aphid suppression, we found that the BSI values measured in Pirque were significantly related to the predator community. We found that the abundance of native coccinellids was consistently positively related to BSI at 7 and 14 d in Pirque. The consistent positive relation between BSI and the abundance of native coccinellids, but not with the exotics, shows that native species, in spite of not being very abundant, can play an important role in pest suppression (Jansen and Hautier, 2008). For example, Evans (2004) found that native lady beetles responded numerically to changes in prey abundance within alfalfa whereas the exotic *Coccinella septempunctata* did not.

On the other hand, we found a negative association between spider abundance and biological control in Pirque, which was surprising given the fact that spiders have been shown to be effective contributors to biological control (Riechert and Lockley, 1984) with several studies demonstrating significant consumption of aphid pests in the field (e.g., Harwood et al., 2004, 2005; Chapman et al., 2013). Our spider community consisted of the family Anyphaenidae and the dominant linyphiid species *N. articeps*. Both are known aphid predators, with Anyphaenidae foraging both on plants and the soil surface and *N. articeps* catching prey within webs constructed just above ground (Ximenez-Embun et al., 2014). Given the behavior of pea aphids to drop from plants, it is likely that they are one important food resource even for ground hunting and web-building spiders, where significant numbers of aphids can be intercepted (Harwood et al., 2001, 2003; Romero and Harwood, 2010). However, previous observations of aphid consumption in Central Chile have shown that coccinellids and syrphids are the main predators consuming *A. pisum* in spring, with spiders preying on this aphid in alfalfa only in summer and fall (Ximenez-Embun et al., 2014). Thus the diet of spiders within this habitat appears to vary temporally and the timing of our experiments does not coincide with the time at which they contribute to biological control. If fact, we did not see a significant relationship between predator community composition and biological control service in Calera de Tango, where spiders were the dominant natural enemy group. This contrasts to what is observed in humid subtropical agroecosystems in North America, where early-season predation by spiders in winter wheat is an important factor in aphid biological control (Harwood et al., 2004; Chapman et al., 2013). This suggests that temporal synchrony with pest populations is critical for pest control (Welch and Harwood, 2014). Further, antagonistic interactions of spiders with other predators, such as intraguild predation or avoidance, can occur and may have contributed to the negative association we detected between spiders and overall biological control service in Pirque (Finke and Denno, 2002; Denno et al., 2004; Smith and Gardiner, 2013).

4.3. Influence of landscape on aphid biological control

We also found variation in the influence of landscape on biological control among our study regions. In Calera de Tango landscape

Table 1

Results of PLS regression analysis examining the influence of predator abundance, landscape configuration and landscape composition on biological control measured using the Biological Control Services Index at 7 (BSI 7) and 14 (BSI 14) days, in Pirque and Calera de Tango. Landscape configurational and compositional variables were Landscape Diversity, Shape Index, Edge Density, Patch Size, and proportions of: Annual Crops, Alfalfa, Fruit Crops (orchards + vineyards), Abandoned Fields, Woodlots (woodlots + hedgerows), Matorral, and Urban (semi-urban + urban + roads) habitats at 250, 500 or 1000 m. For predator abundance the variables were All Generalist Predators, Araneae, Coccinellidae, Exotic Coccinellidae, Native Coccinellidae, and Syrphidae, and in this model Abundance of Aphids was also included. For each model, we report the Q^2 (the proportion of the variance in the response variable that can be predicted by the model), R^2Y (the proportion of the variance in the response variable that is explained by the model) and R^2X (the proportion of the variance in the matrix of predictor variables that is used in the model) for the first two model components (t_1 and t_2).

Region	PLS model	X variable	t_1			t_2		
			Q^2	R^2Y	R^2X	Q^2	R^2Y	R^2X
Pirque	Predator abundance	BSI 7	0.579	0.721	0.418	0.464	0.760	0.707
		BSI 14	0.605	0.921	0.398	0.505	0.949	0.589
	Landscape configuration 250 m	BSI 7	-0.076	0.072	0.812	-	-	-
		BSI 14	-0.328	0.022	0.813	-1.249	0.031	0.920
	Landscape configuration 500 m	BSI 7	-0.080	0.111	0.675	-0.657	0.152	0.906
		BSI 14	-0.406	0.098	0.349	-0.701	0.136	0.853
	Landscape configuration 1000 m	BSI 7	-0.003	0.149	0.849	-0.310	0.533	0.892
		BSI 14	-0.005	0.116	0.845	-0.411	0.438	0.896
	Landscape composition 250 m	BSI 7	-0.842	0.152	0.230	-2.334	0.183	0.537
		BSI 14	-1.164	0.187	0.192	-2.030	0.257	0.493
	Landscape composition 500 m	BSI 7	-0.046	0.287	0.366	-0.481	0.398	0.631
		BSI 14	-0.418	0.203	0.298	-0.979	0.316	0.573
	Landscape composition 1000 m	BSI 7	-0.204	0.215	0.388	-0.948	0.273	0.643
		BSI 14	-0.475	0.110	0.385	-1.649	0.146	0.653
Calera de Tango	Predator abundance	BSI 7	-0.257	0.210	0.335	-1.437	0.287	0.500
		BSI 14	-0.562	0.634	0.176	-2.517	0.784	0.407
	Landscape configuration 250 m	BSI 7	-0.226	0.231	0.588	-0.026	0.447	0.923
		BSI 14	-0.004	0.103	0.783	-0.121	0.319	0.890
	Landscape configuration 500 m	BSI 7	-0.047	0.134	0.785	-0.191	0.244	0.863
		BSI 14	-0.424	0.258	0.385	-0.653	0.358	0.918
	Landscape configuration 1000 m	BSI 7	0.056	0.270	0.633	-0.538	0.423	0.703
		BSI 14	-1.279	0.032	0.353	-2.630	0.049	0.738
	Landscape composition 250 m	BSI 7	0.145	0.540	0.319	-0.380	0.598	0.571
		BSI 14	-0.633	0.314	0.277	-1.969	0.468	0.484
	Landscape composition 500 m	BSI 7	0.411	0.559	0.482	0.525	0.776	0.660
		BSI 14	-0.419	0.213	0.447	-1.038	0.302	0.679
	Landscape composition 1000 m	BSI 7	0.283	0.526	0.387	0.317	0.692	0.551
		BSI 14	-0.714	0.137	0.364	-1.756	0.412	0.516

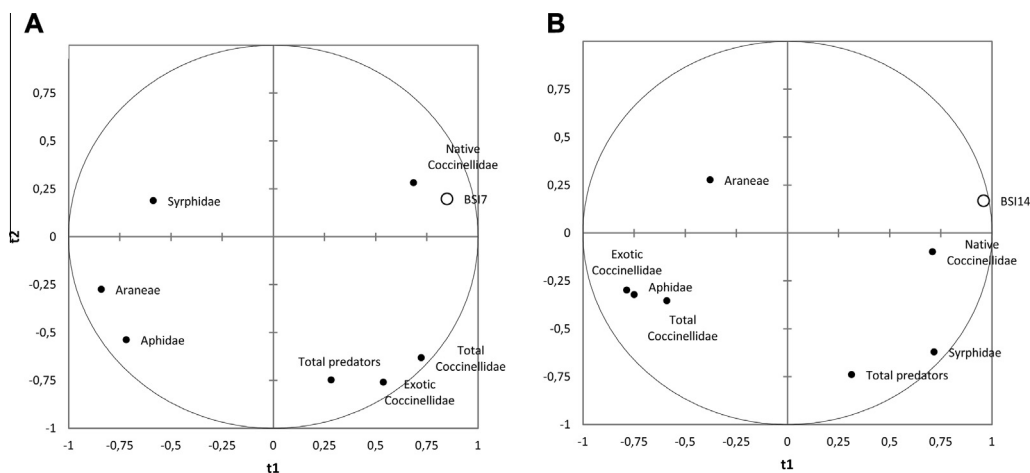


Fig. 3. Correlation maps of the PLS regression of natural enemies and aphids abundance (predictor variables) and Biological Control Service Index (BSI, response variable) for the first two PLS components (t_1 and t_2), in Pirque, at (A) 7 and (B) 14 d. Only variables with $VIP \geq 0.8$ are shown (Tenenhaus et al., 2005).

composition was a significant predictor of biological control service. Independent of the landscape scale examined, biological control was higher in fields surrounded by a high proportion of woodlots and urban habitats and was lower when landscapes were dominated by fruit crops. Although we did not see a direct link between predators and prey suppression in this region, it is likely that the relationship between landscape composition and BSI is indirectly illustrating the differential supply of predatory activity provided to alfalfa fields.

Within the Calera de Tango region, the coccinellid community was dominated by *H. axyridis*, which represented 57% of coccinellids. *H. axyridis* is considered primarily an arboreal species, and Gardiner et al. (2009b) found that its abundance in soybean was positively related to the abundance of woodlots and other forested habitat in the surrounding landscape. Further, it is well known that *H. axyridis* forms overwintering aggregations in buildings (Koch, 2003), thus a spillover of this species from these habitats to alfalfa may have taken place in spring. The negative relationship between

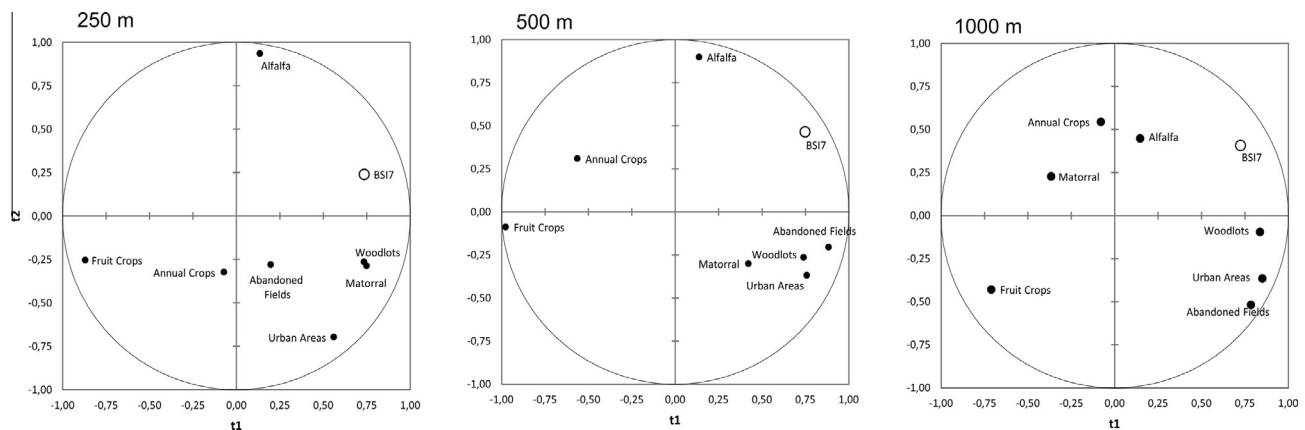


Fig. 4. Correlation maps of the PLS regression of landscape composition at (A) 250, (B) 500 and (C) 1000 m scale (predictor variables) and Biological Control Service Index at 7 d (BSI7, response variable) for the first two PLS components (t_1 and t_2), in Calera de Tango. Only variables with $VIP \geq 0.8$ are shown (Tenenhaus et al., 2005).

BSI and abundance of fruit crops in the landscape could relate to the high pesticide use in these crops, which could negatively impact natural enemies.

These relationships between BSI and landscape composition were observed only at 7 d when BSI was much higher than at 14 d. Contrary to other studies (Gardiner et al., 2009a), we did not find a relation between landscape heterogeneity and BSI in any of the regions.

4.4. Conclusions and Implications

Our study aimed to understand the value of predators in suppressing aphid populations in alfalfa and relate the abundance of key groups, such as exotic and native coccinellids, syrphids and spiders to the biological control service. We found that the predator community present in central Chile varied among our study regions, and in Pirque, where native coccinellids were more common, they consistently exerted a negative impact on aphid populations, whereas neither in Pirque nor in Calera de Tango exotics were not associated with biological control. The recent invasion and population increase of *H. axyridis* has the potential to alter both predator community composition and its ability to suppress aphid pests. This species has become a dominant predator and our research suggests that its value, along with other exotic coccinellids, may vary from that of native species.

Our study also aimed to understand the influence of landscape on biological control. We found landscape to be a more important predictor of biological control in Calera de Tango, where key spring aphid predators were far less abundant. Therefore, landscape effects on biological control service may be weaker than local factors, and only become important when local predator abundance is low.

We found that biological control was reduced in Calera de Tango, the more urbanized of our two regions, yet within the Calera de Tango landscapes the amount of urban habitat within the landscape was positively related to biological control service, along with forested habitats (woodlots). This may be because the biological control service is being provided by predator communities that vary in their habitat use. In Calera de Tango biological control might have been more reliant on exotic coccinellids (i.e. *H. axyridis*), which may be more likely to utilize urban green spaces as foraging habitats.

The invasion of exotic species mediated by changes in land use can exert negative impacts on native species (Didham et al., 2007). Increasing urbanization and the introduction of exotic coccinellids are likely to continue to alter the biological control provided to

alfalfa crops in central Chile. Therefore, within this region, it is critical to put a greater emphasis on habitat management to conserve and promote native biodiversity and the ecosystem services it provides to Chilean agriculture.

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