

Effects of habitat loss and fragmentation on the abundance and species richness of aphidophagous beetles and aphids in experimental alfalfa landscapes

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Abstract. In agro-ecosystems, habitat loss and fragmentation may alter the assemblage of aphidophagous insects, such as foliar-foraging (coccinellids) and ground-foraging predators (carabids), potentially affecting intraguild interactions. We evaluated how habitat loss (0, 55 and 84%), fragmentation (1, 4 and 16 fragments) and their combination affected the abundance and species richness of coccinellids and carabids, and aphid abundance, both in the short-term (summer: December to February) and over a longer time span (autumn: March to May), when different demographic mechanisms may participate. We created four types of 30 × 30 m patches (landscapes) in which alfalfa was grown: Control (1F – 0%, 30 × 30 m patch of alfalfa with no fragmentation or habitat loss), 4F – 55% (4 alfalfa fragments, with 55% total habitat loss), 4F – 84% (4 alfalfa fragments, with 84% total habitat loss), and 16F – 84% (16 alfalfa fragments, with 84% total habitat loss). Each landscape type was replicated five times. Insects were sampled by sweep-netting and pitfall traps, from December (summer) to May (autumn). Total abundance and species richness of carabids, in the short-term, was highest in the 16F – 84% landscapes. Total abundance of adult coccinellids was similar among landscapes, but at the species level *Hyperaspis sphaeridioides*, in the short-term, and *Adalia bipunctata*, in the long-term, had their highest densities in fragments within landscapes with high habitat loss (84%), independently of habitat fragmentation. Species richness in the long-term was higher in the landscapes with 84% habitat loss. Among aphids, in the long term *Aphis craccivora* was less abundant in landscapes with high habitat loss and fragmentation (16–84%), while *Therioaphis trifolii* showed the opposite trend. These results suggest that habitat loss and fragmentation may increase the density and diversity of aphidophagous insects, while their effects on aphids are more variable.

INTRODUCTION

Habitat loss and fragmentation may have large effects on population and community structure of insects, even at small spatial scales (Kareiva, 1987; Hunter, 2002). Habitat fragmentation per se is the subdivision of an originally continuous habitat into more, smaller patches, and habitat loss is the removal of habitat, which might occur without fragmentation (Fahrig, 2003). The two processes usually occur simultaneously in nature. For that reason, their effects have been confounded frequently in the literature (McGarigal & Cushman, 2002).

It has been usually assumed that habitat fragmentation has negative effects on the abundance and diversity of organisms. Nevertheless, recent empirical and theoretical studies that have isolated the effects of habitat fragmentation and habitat loss, suggest that the negative effects of habitat fragmentation are mainly due to the loss of habitat that occurs along with fragmentation, and that often fragmentation per se has no effect, or even may have positive effects on population abundance and species richness (Fahrig, 2003; Grez et al., 2004a, b).

Although habitat loss and fragmentation have been considered of great importance in conservation biology, these processes are also relevant for pest management in agro-ecosystems because of their potential effects on predatory-prey dynamics (Kruess & Tscharrntke, 1994; Thies & Tscharrntke, 1999; Tscharrntke & Kruess, 1999; Hunter,

2002; With et al., 2002). It has been shown that those species belonging to higher trophic levels, such as parasitoids and predators, are more affected by habitat loss and fragmentation than are their prey, the herbivores (Hunter, 2002; Braschler et al., 2003; van Nouhuys, 2005; Ewers & Didham, 2006). Habitat fragmentation may adversely affect the ability of natural enemies to control pest outbreaks in agricultural landscapes by interfering with their searching behaviour and their aggregative numerical response to prey (Kareiva, 1987; With et al., 2002). Therefore, from the perspective of biological control, it is important to study whether changes in the agricultural landscape due to fragmentation and/or habitat loss, can affect the abundance of natural enemies, resulting in a failure to maintain pests at low populations levels.

Coccinellids and Carabids are among the most important natural enemies of aphids in numerous crops, including alfalfa (*Medicago sativa* Linnaeus). In central Chile, approximately ten species of coccinellids are commonly found in alfalfa crops. Among them, the indigenous *Eriopis connexa* (Germ), and the exotic *Adalia bipunctata* (Linnaeus) and *Hippodamia variegata* (Goeze), are most abundant (Zaviezo et al., 2004, 2006). Carabids are also present throughout the growing season, especially those of the genera *Incagonum*, *Notiobia*, *Tetraponoderus*, *Trirammatus* and *Metius* (Zaviezo et al., 2004). Carabids and some species of coccinellids are

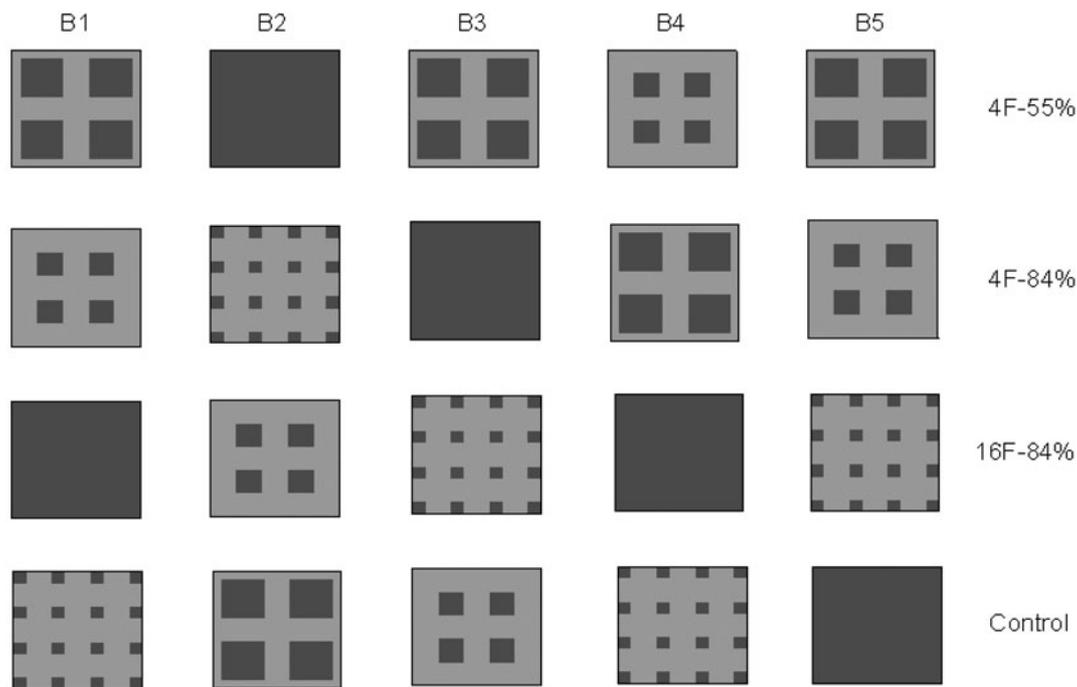


Fig. 1. Spatial distribution of experimental landscapes following a complete randomized block design. Each manipulated 30×30 m plot represents a landscape with alfalfa (black areas) at two fragmentation levels (16 or 4 fragments) and two habitat loss levels (55 or 84%). Unmanipulated 30×30 m plots served as controls. The four resulting landscapes were 4F – 55% (4 fragments, 55% habitat loss), 4F – 84% (4 fragments, 84% habitat loss), 16F – 84% (16 fragments, 84% habitat loss) and Control (no fragmentation, no habitat loss). Bare ground (grey areas) comprised the matrix, both within and between landscapes plots. The four types of landscapes were replicated five times in the field (B = block), for a total of 20 landscapes, with a 20 m buffer zone between landsc

affected by habitat loss or fragmentation in alfalfa crops (Gre \acute{z} et al., 2004a, b; Gre \acute{z} & Zaviezo, 2006), but it is unknown how both processes simultaneously affect these predator populations, and their prey abundance.

In this paper, we studied the effects of habitat loss and fragmentation per se (i.e., number of fragments) on the abundance and species richness of coccinellids and carabids and on the abundance of their prey, the aphids, in experimentally created alfalfa micro-landscapes. Based on previous theoretical and empirical evidence, we predicted that: (1) An increase in habitat loss will reduce insect abundance and richness, particularly of predators. (2) An increase in habitat fragmentation will either have nil effect or will increase insect abundance and richness, particularly of predators. (3) The effects of an increase in both habitat loss and fragmentation will depend on the effect of habitat fragmentation in particular: If habitat fragmentation has nil effect, the effect of both habitat loss and fragmentation will be similar to the effect of habitat loss alone. But if habitat fragmentation has a positive effect, the negative effect of both habitat loss and fragmentation will be less than that of habitat loss alone, because of the compensatory effect of fragmentation.

MATERIAL AND METHODS

Experimental landscapes

The study was conducted at Antumapu Experimental Research Station, University of Chile, Santiago, Chile ($33^{\circ}34'S$, $70^{\circ}37'W$), during the 2003–2004 growing season. Between 22 and 25 August 2003, we sowed alfalfa (Pioneer 5683) in each of

twenty 30×30 -m plots, separated by at least 20 m and distributed as groups of 4 plots in each of 5 blocks (complete randomized block design). The size of the experimental plots (landscapes) was selected based on previous studies of similar questions and organisms (Kareiva, 1987; Banks, 1999; With et al., 2002; Gre \acute{z} et al., 2004a, b; 2005; Zaviezo et al., 2006). Previous theoretical and empirical studies suggest that fragmentation effects on population abundance and searching efficiency by natural enemies should be apparent only at high levels of habitat loss (i.e., over 70–80%, Andr n, 1994; Fahrig, 1997; With & King, 1999; Thies & Tschamtkke, 1999; Flather & Bevers, 2002; With et al., 2002). Therefore, in our experiments we used percentages of habitat loss both above and below this threshold.

On December 20th, three randomly selected landscapes (i.e., 30×30 m plots) from each block were fragmented to yield 4 or 16 fragments, by removing 55 or 84% of the alfalfa by ploughing. In the remaining landscape of each block no alfalfa was removed. Thus, four types of landscapes were created: unfragmented control landscapes or 1F – 0% (0% habitat loss, one fragment of alfalfa), 4F – 55% (four 10×10 m fragments, 55% habitat loss), 4F – 84% (four 6×6 m fragments, 84% habitat loss), and 16F – 84% (sixteen 3×3 m fragments, 84% habitat loss). Fragments were separated by 6 m, because this distance reduces the inter-fragment movement of coccinellids within a landscape, and instead enhances emigration from the landscape (i.e., the coccinellids perceive the landscape as more fragmented than landscapes with closer fragments; Gre \acute{z} et al., 2004a; Gre \acute{z} et al., 2005). Such information on dispersal responses does not exist for carabids or aphids. The areas within and between the experimental landscapes were maintained free of alfalfa and other vegetation throughout the experiment by herbicide application and ploughing as needed (Fig. 1). The remaining alfalfa

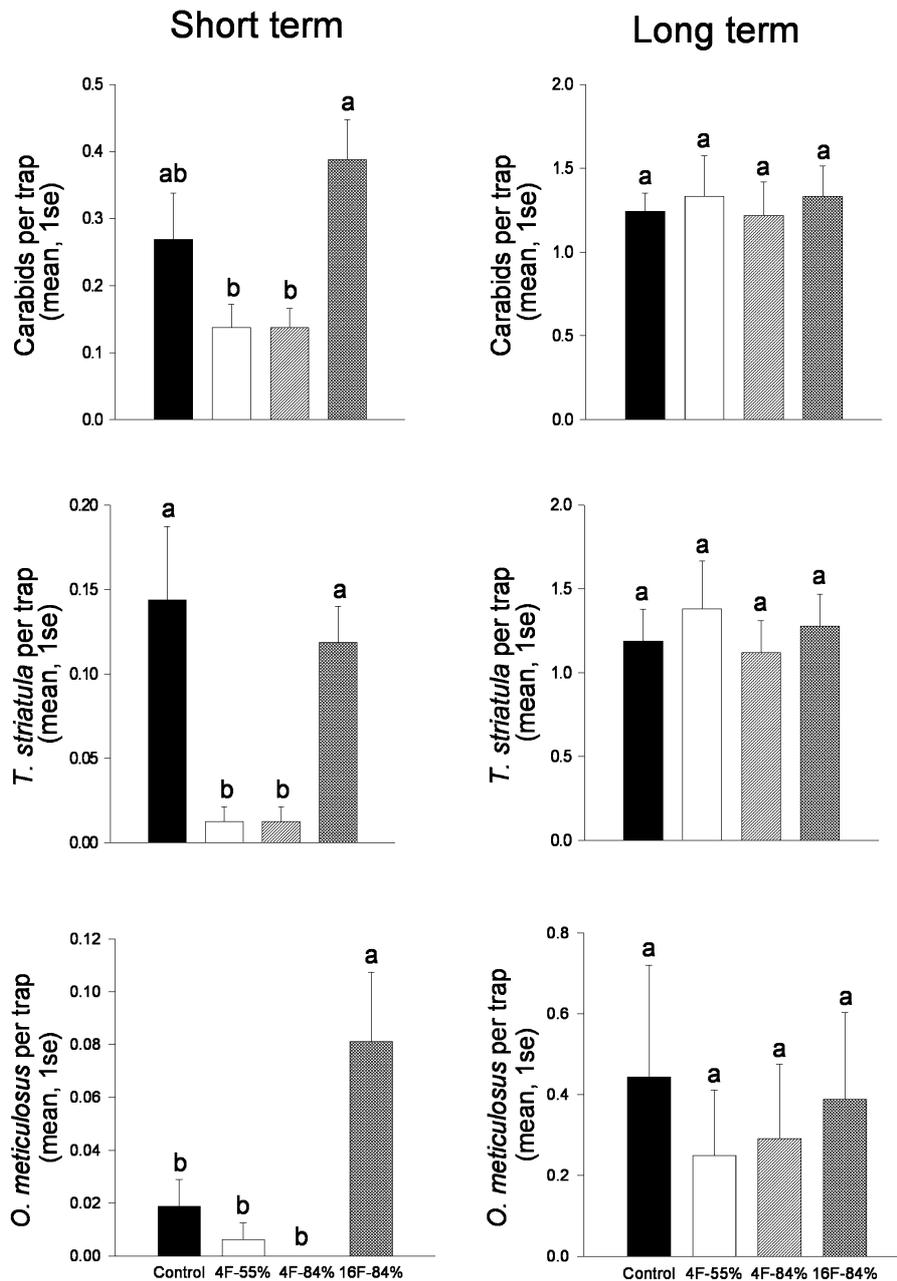


Fig. 2. Total abundance (individuals per trap) and abundance of two species (*Tirammatus striatula* and *Ogmopleura meticulosus*) of carabids within four experimental landscapes (see Fig. 1), during the early sampling period (summer [short term]: weeks 1, 3, 5, and 7 after alfalfa removal, left) and the late sampling period (autumn [long term]: weeks 13, 15 and 17, right). Standard error bars are based on five data points, i.e., five replicates for each landscape type. Different letters on the bars indicate significant differences after planned comparisons and Bonferroni correction.

was irrigated every 2 weeks and harvested on three occasions during the experiment: 17 January, 23 February and 10 May. Between cuttings, the alfalfa was allowed to regrow. No insecticides were applied.

Insect sampling

Carabids were sampled with pitfall traps on seven occasions after removing alfalfa initially to create fragments. Sampling occurred in summer: 1, 3, 5 and 7 weeks after removing alfalfa (2 January, 16 January, 30 January, 14 February); and in autumn: 13, 15 and 17 weeks after removing alfalfa (25 March, 6 April and 20 April). Pitfall trapping is the usual method for sampling carabids, which spend most of the time walking on the ground. Although this method is not the most appropriate for

direct estimation of absolute density, it is useful to compare population size in space and time (Dent & Walton, 1997; Duelli et al., 1990; Perner & Schöler, 2004). The traps consisted of a transparent plastic container, 6 cm diameter and 8 cm depth (259 mL), half-filled with a solution of water, formalin (10%), and detergent. We placed eight traps in each experimental landscape (one or two per fragment, and throughout the landscape in the control). The traps were kept open during four days on each sampling occasion.

Adult coccinellids were sampled by sweep-netting on eight occasions after fragmentation, both in summer: 1, 3, 5 and 7 weeks after removing alfalfa (30 December, 13 January, 28 January, 9 February); and in autumn: 13, 15, 17 and 19 weeks

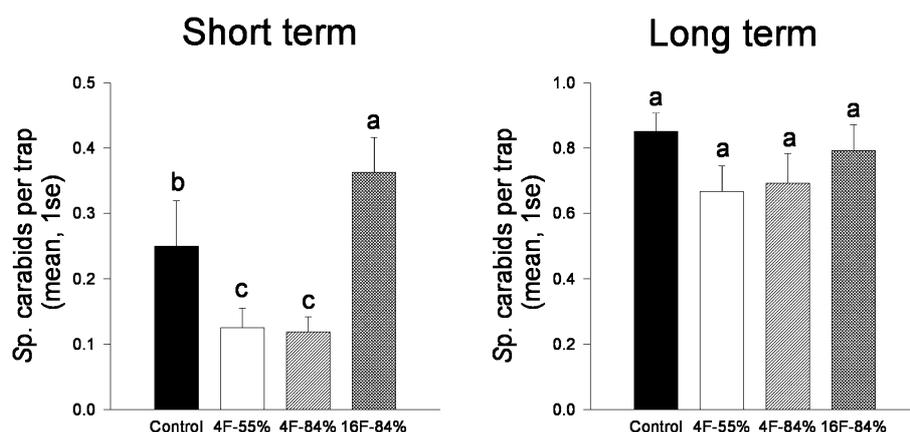


Fig. 3. Species richness (species per trap) of carabids within four experimental landscapes (see Fig. 1), during the early sampling period (summer [short term]: weeks 1, 3, 5, and 7 after alfalfa removal, left) and the late sampling period (autumn [long term]: weeks 13, 15 and 17, right). Standard error bars are based on five data points, i.e., five replicates for each landscape type. Different letters on the bars indicate significant differences after planned comparisons and Bonferroni correction.

after removing alfalfa (24 March, 7 April, 20 April and 5 May). At eight points in each experimental landscape, we took four sweeps with a 30 cm diameter net, covering a total area of approximately 4 m² of alfalfa. Aphids were also sampled by sweep-netting, at the same sampling dates plus one more in autumn: 19 May (21 weeks after removing alfalfa).

Data analyses

The effect of habitat loss and fragmentation on the density and richness of coccinellids and carabids, and on the population abundance of aphids, was analyzed for two periods: summer and autumn. At these two periods, different demographic mechanisms may influence insect densities in our experimental landscapes. During the summer, insects colonize the crop from nearby hibernation refuges. Therefore, insect population changes shortly after habitat loss and fragmentation should be determined mainly by immigration (Greze et al., 2004a). But during autumn, reproduction, survival, and emigration (to hibernate or seek out more suitable patches) may become the most important demographic mechanisms determining insect densities. Therefore, considering the population dynamics and biology of the aphidophagous insects in our system, summer

and autumn represent short and long-term time spans after habitat disturbance, and may be characterized by different responses and mechanisms.

The effects of habitat loss and fragmentation over the short and long-term were studied through analyses of covariance (ANCOVA), with time (sampling dates within each season) as a co-variable, using Statistica 6.0 (Statsoft, 2001). For the analyses, we used the mean density of insects per landscape (averaging the sub-samples) to avoid pseudoreplication (Hurlbert, 1984). We tested our hypotheses with planned paired comparisons between the different types of landscapes:

- (a) 4F – 55% vs. 4F – 84%, to evaluate the effect of habitat loss, with a constant low level of habitat fragmentation.
- (b) 4F – 84% vs. 16F – 84%, to evaluate the effect of habitat fragmentation, with a constant high level of habitat loss.
- (c) 4F – 55% vs. 16F – 84%, to evaluate the effect of increasing habitat loss and fragmentation
- (d) Control landscape v/s all, to evaluate the effects of low and high levels of habitat loss and fragmentation, compared with an undisturbed landscape.

TABLE 1. Results of the ANCOVAs for the short-term (summer) and long-term (autumn) effects of the type of landscape (control, or with varying fragmentation and habitat loss) on the density and species richness of insects.

	Summer		Autumn	
Carabids	$F_{(3,71)} = 6.28$	$P = 0.001$	$F_{(3,51)} = 0.12$	$P = 0.95$
<i>Trirammatus striatula</i>	$F_{(3,59)} = 32.07$	$P < 0.001$	$F_{(3,39)} = 0.84$	$P = 0.48$
<i>Ogmopleura meticulosus</i>	$F_{(3,59)} = 7.32$	$P < 0.001$	$F_{(3,39)} = 0.45$	$P = 0.72$
Species richness	$F_{(3,59)} = 21.05$	$P < 0.001$	$F_{(3,39)} = 1.86$	$P = 0.15$
Coccinellids	$F_{(3,59)} = 0.27$	$P = 0.83$	$F_{(3,70)} = 1.54$	$P = 0.21$
<i>Adalia bipunctata</i>	$F_{(3,71)} = 0.67$	$P = 0.57$	$F_{(3,71)} = 4.30$	$P = 0.005$
<i>Eriopis connexa</i>	$F_{(3,70)} = 0.71$	$P = 0.54$	$F_{(3,70)} = 1.45$	$P = 0.23$
<i>Hippodamia convergens</i>	$F_{(3,71)} = 2.96$	$P = 0.03$	$F_{(3,70)} = 0.62$	$P = 0.60$
<i>Hippodamia variegata</i>	$F_{(3,70)} = 2.85$	$P = 0.04$	$F_{(3,70)} = 0.72$	$P = 0.54$
<i>Hyperapis sphaeridioides</i>	$F_{(3,71)} = 4.72$	$P = 0.004$	$F_{(3,71)} = 2.74$	$P = 0.04$
Species richness	$F_{(3,59)} = 1.21$	$P = 0.31$	$F_{(3,59)} = 5.92$	$P = 0.001$
Aphids	$F_{(3,59)} = 0.33$	$P = 0.80$	$F_{(3,79)} = 1.39$	$P = 0.25$
<i>Aphis craccivora</i>	$F_{(3,69)} = 2.04$	$P = 0.11$	$F_{(3,89)} = 3.17$	$P = 0.03$
<i>Therioaphis trifolii</i>	$F_{(3,69)} = 0.65$	$P = 0.58$	$F_{(3,89)} = 7.71$	$P < 0.001$

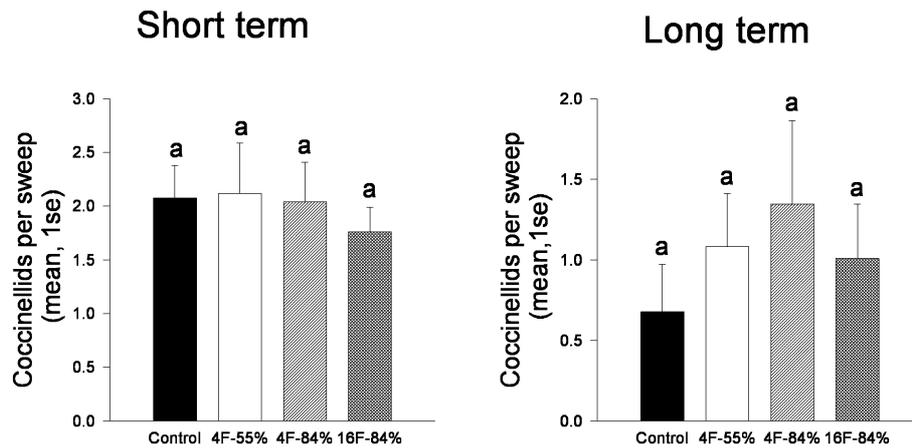


Fig. 4. Total abundance (individuals per 4 m²) of coccinellids within four experimental landscapes (see Fig. 1), during the early sampling period (summer [short term]: weeks 1, 3, 5, and 7 after alfalfa removal, left) and the late sampling period (autumn [long term]: weeks 13, 15, 17 and 19, right). Standard error bars are based on five data points, i.e., five replicates for each landscape type. Different letters on the bars indicate significant differences after planned comparisons and Bonferroni correction.

Bonferroni correction was applied to the resulting probabilities $[1-(1-0.05)^{1/k}]$, with k = number of planned comparisons (Sokal & Rohlf, 1995).

RESULTS

Carabids

The most abundant carabid species were *Incagonum ambiguum* (Solier), *Tetragonoderus* sp., *Ogmopleura meticulosus* (Dejean), *Trirammatus* (*Trirammatus*) *unis-triatus* (Dejan) and *Trirammatus* (*Ferionomorpha*) *striatula* (Fabricius). The latter dominated during the whole study, reaching the highest abundances in autumn. The total abundance of carabids, in the short-term, was higher in the 16F – 84% landscapes than in the 4F – 55% and 4F – 84% landscapes, but similar to the control (Fig. 2, Table 1). *Trirammatus striatula* varied in abundance among landscapes, following the same pattern, and *O. meticulosus* was more abundant in the 16F – 84% landscapes than in the other three types of landscapes. In the long-term, all landscapes had a similar abundance of carabids (in total and at the species level) (Fig. 2, Table 1).

Similarly to population abundance, carabid species richness in the short-term was higher in the 16F – 84% landscapes, but in this case it was also higher than in the control landscapes. In the long-term these differences disappeared (Fig. 3, Table 1).

Coccinellids

The most abundant coccinellids species were *E. connexa* and *H. variegata*, with 42.2% and 37% of the total individuals, respectively. Other less abundant species were: *Hyperaspis sphaeridioides* Mulsant, *Hippodamia convergens* Guérin-Menenville, *A. bipunctata*, *Cycloneda sanguinea* (Linnaeus) and *Scymnus* sp. During summer *E. connexa* was the most abundant species, while in autumn *H. variegata* and *A. bipunctata* were the most abundant species. *Hyperaspis sphaeridioides* was more abundant in summer than in autumn.

The total abundance of coccinellids did not vary among landscapes, in either the short or long-term (Fig. 4, Table

1). At the species level, habitat loss and fragmentation did not affect the abundance of most species of coccinellids in either study period. However, in the short-term *H. sphaeridioides*, and in the long-term *A. bipunctata*, were significantly more abundant in the 4F – 84% and 16F – 84% landscapes than in the control (Fig. 5, Table 1).

Coccinellid species richness in the short-term was similar in all landscapes, but in the long-term there were more species in the fragmented landscapes, particularly in those with 84% habitat loss (Fig. 6, Table 1).

Aphids

The two most abundant species of aphids were *Aphis craccivora* Koch and *Therioaphis trifolii* (Monell), which were more abundant in autumn than earlier in the summer. In the short term, the abundance of neither species varied among landscapes. *Aphis craccivora* tended to be less abundant in the landscapes where alfalfa was removed, but this trend was not statistically significant. In the long term, *T. trifolii* was more abundant in all fragmented landscapes, independent of the level of habitat loss and fragmentation, whereas *A. craccivora* was less abundant in the landscape with high habitat loss and fragmentation (16F – 84%) compared to the control (Fig. 7, Table 1).

DISCUSSION AND CONCLUSIONS

In our study, most aphidophagous insects were unaffected by habitat loss and fragmentation. For those species that were sensitive to landscape structure, habitat loss and fragmentation generally resulted in higher densities within habitat patches, either early or late in the season. This is contrary to previous reports for some coccinellid species, such as *Coccinella septempunctata* (Kareiva, 1987) and *Coleomegilla maculata* (Timberlake) (With et al., 2002).

The total abundance and species richness of carabids, in the short term, were higher in the 16F – 84% than in the 4F – 55% and 4F – 84% landscapes, but there were no differences between the control and fragmented land-

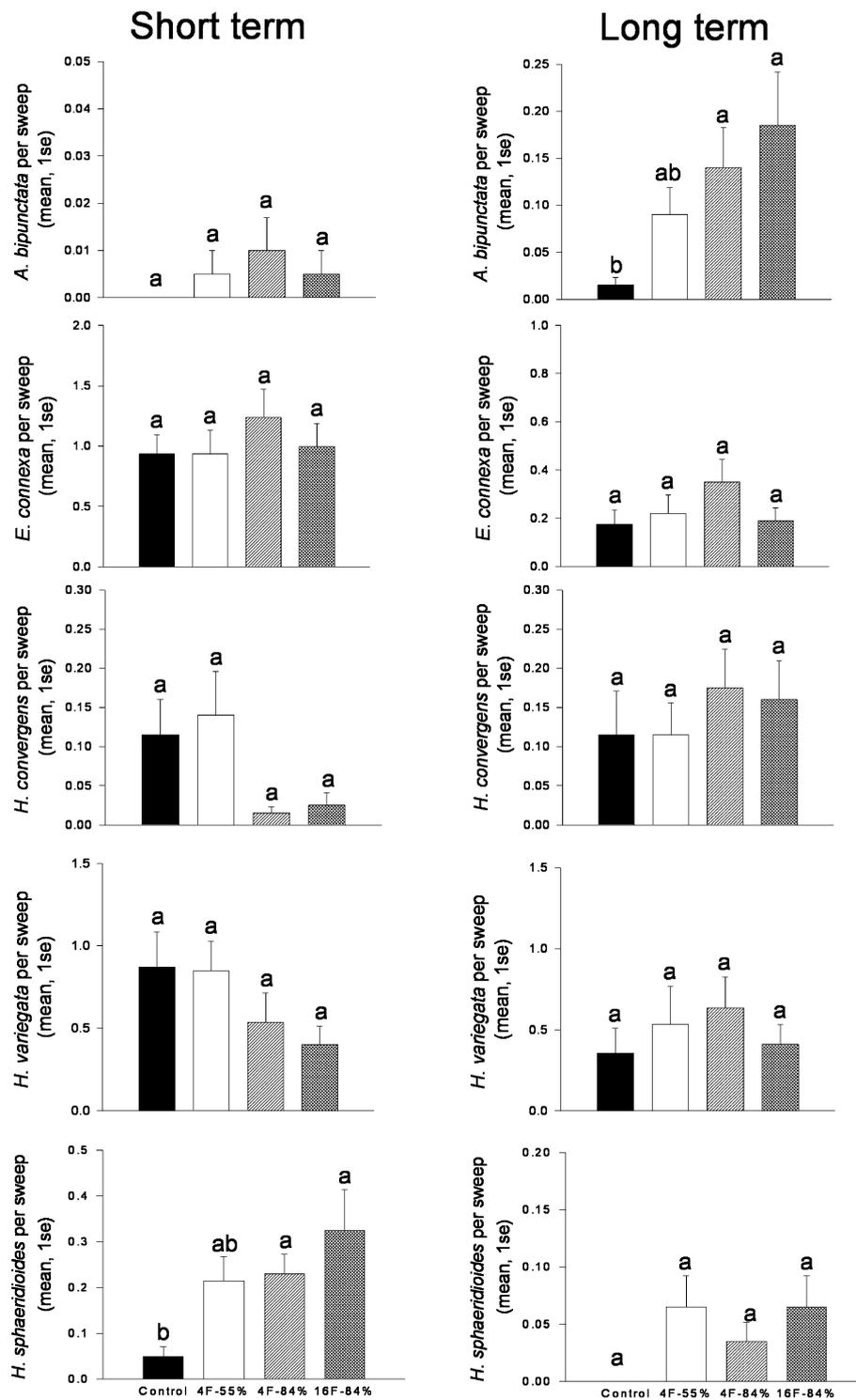


Fig. 5. Abundance (individuals per 4 m²) of five species of coccinellids (*Adalia bipunctata*, *Eriopis connexa*, *Hippodamia convergens*, *Hippodamia variegata*, and *Hyperaspis sphaeridioides*) within four experimental landscapes (see Fig. 1), during the early sampling period (summer [short term]: weeks 1, 3, 5, and 7 after alfalfa removal, left) and the late sampling period (autumn [long term]: weeks 13, 15, 17 and 19, right). Standard error bars are based on five data points, i.e., five replicates for each landscape type. Different letters on the bars indicate significant differences after planned comparisons and Bonferroni correction.

scapes as a whole. At the species level, *T. striatula* followed the same patterns as total carabids, but *O. meticulousus* was less abundant in the control than in the 16F – 84% landscapes. In the long-term, these effects disappeared. These results are similar to those observed in a

previous (independent) study with varying levels of habitat fragmentation and isolation in alfalfa, and a uniformly high level of habitat loss (84%) (Greze et al., 2004b; Greze & Zaviezo, 2006). In that study, the population abundance and species richness of carabids (and

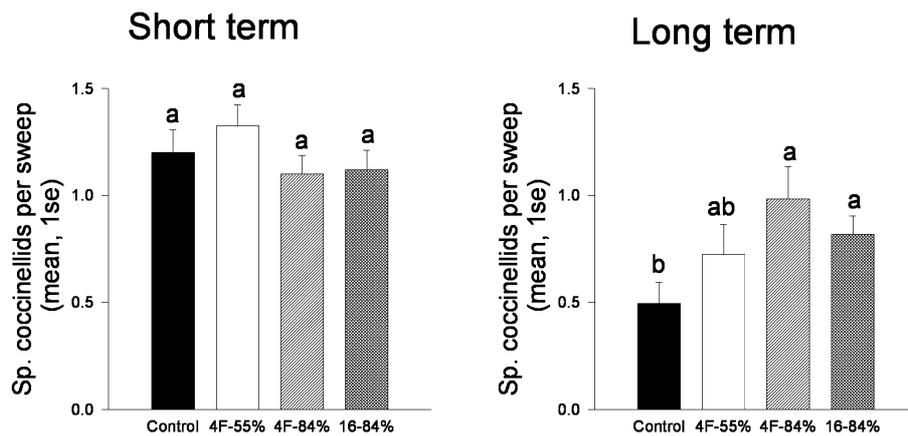


Fig. 6. Species richness (species per 4 m²) of coccinellids within four experimental landscapes (see Fig. 1), during the early sampling period (summer [short term]: weeks 1, 3, 5, and 7 after alfalfa removal, left) and the late sampling period (autumn [long term]: weeks 13, 15 and 17, right). Standard error bars are based on five data points, i.e., five replicates for each landscape type. Different letters on the bars indicate significant differences after planned comparisons and Bonferroni correction.

other beetles) were higher in the more fragmented landscapes, and also this effect disappeared later in the season. The higher abundance of carabids in the 16F – 84% compared to the 4F – 84% landscape in the present study suggests a strong positive effect of habitat fragmentation at high levels of habitat loss, but because results were similar for the 4F – 84% and 4F – 55% landscapes, habitat loss seems insignificant in determining population abundance of carabids. Nevertheless, for one species (*T. striatula*) habitat loss along with low fragmentation level (4 fragments) had a net negative effect, compared with an undisturbed landscape. Increasing the fragmentation level (16 fragments) compensated for any negative effects of habitat loss.

The total abundance of coccinellids was not affected by habitat loss and fragmentation in any period of time, but at the species level some significant effects were observed. *Adalia bipunctata* in the long term and *H. sphaeridioides* in the short-term showed a similar pattern, in which lowest abundances occurred in the control landscapes and highest abundances occurred in the landscapes with highest level of habitat loss, regardless of the fragmentation level (4F – 84% and 16F – 84%). These results suggest that for these two coccinellid species there was a positive effect of habitat loss in landscapes that also had been fragmented. For *H. sphaeridioides* this positive effect of habitat loss in fragmented landscapes has also been reported previously (Zaviezo et al., 2006), and may be explained by a “crowding effect”, where immediately after habitat loss (alfalfa removal), surviving individuals likely moved from the removed habitat to the remaining fragments, increasing their densities there (Collinge & Forman, 1998; Debinski & Holt, 2000). Such an hypothesis is supported when comparing the abundance of *H. sphaeridioides* one week before and one week after alfalfa removal from our experimental landscapes: a significant population increase occurred in the fragmented landscapes but not in the control ($F_{(3,12)} = 3.49$, $P = 0.04$).

Species richness of both carabids and coccinellids increased with fragmentation and habitat loss. Carabids in

the short-term had more species in the 16F – 84% landscapes than in all other landscapes, including the control, while coccinellids in the long-term had more species in all fragmented landscapes compared to the control, particularly in landscapes with higher level of habitat loss. The increase in beetle species richness with increasing fragmentation is not an isolated result. It has been reported also for assemblages of endangered polyphagous butterflies in agricultural landscapes of Germany (Tschardt et al., 2002), insects in grasslands in North America (Collinge & Forman, 1998), and beetles associated with alfalfa landscapes in Chile (Grez et al., 2004b). Furthermore, we have determined that native and exotic species of coccinellids did not segregate in different landscapes. On the contrary, strong positive associations occur more often in landscapes with higher fragmentation and isolation (i.e., distance between fragments) (Zaviezo et al., 2006). These previous results, along with those reported here, suggest that a landscape composed of a set of smaller and isolated fragments may support more species of insects than a larger and continuous landscape, perhaps in part because of dynamics generated at habitat edges (Fagan et al., 1999).

We tested for the effect of habitat loss by comparing fragmented landscapes with the same number of fragments but different amount of habitat loss (4F – 55% vs. 4F – 84%). But to test the effects of habitat loss alone (i.e., without concurrent habitat fragmentation), it is necessary to consider a landscape with habitat loss and no fragmentation (i.e., a landscape with less habitat distributed in only one fragment). We did not do so in this study. Moreover, habitat fragmentation implies an increase in the isolation as well as the number of fragments (Fahrig, 2003). Therefore, fragments separated by 6 m, as in our experimental landscapes, may increase the effects of habitat fragmentation compared with landscapes with closer fragments, which may mimic a landscape with only habitat loss (Zaviezo et al., 2006). Thus, with our experimental design we can not draw conclusions about the effects of habitat loss alone. But, for those coccinellid

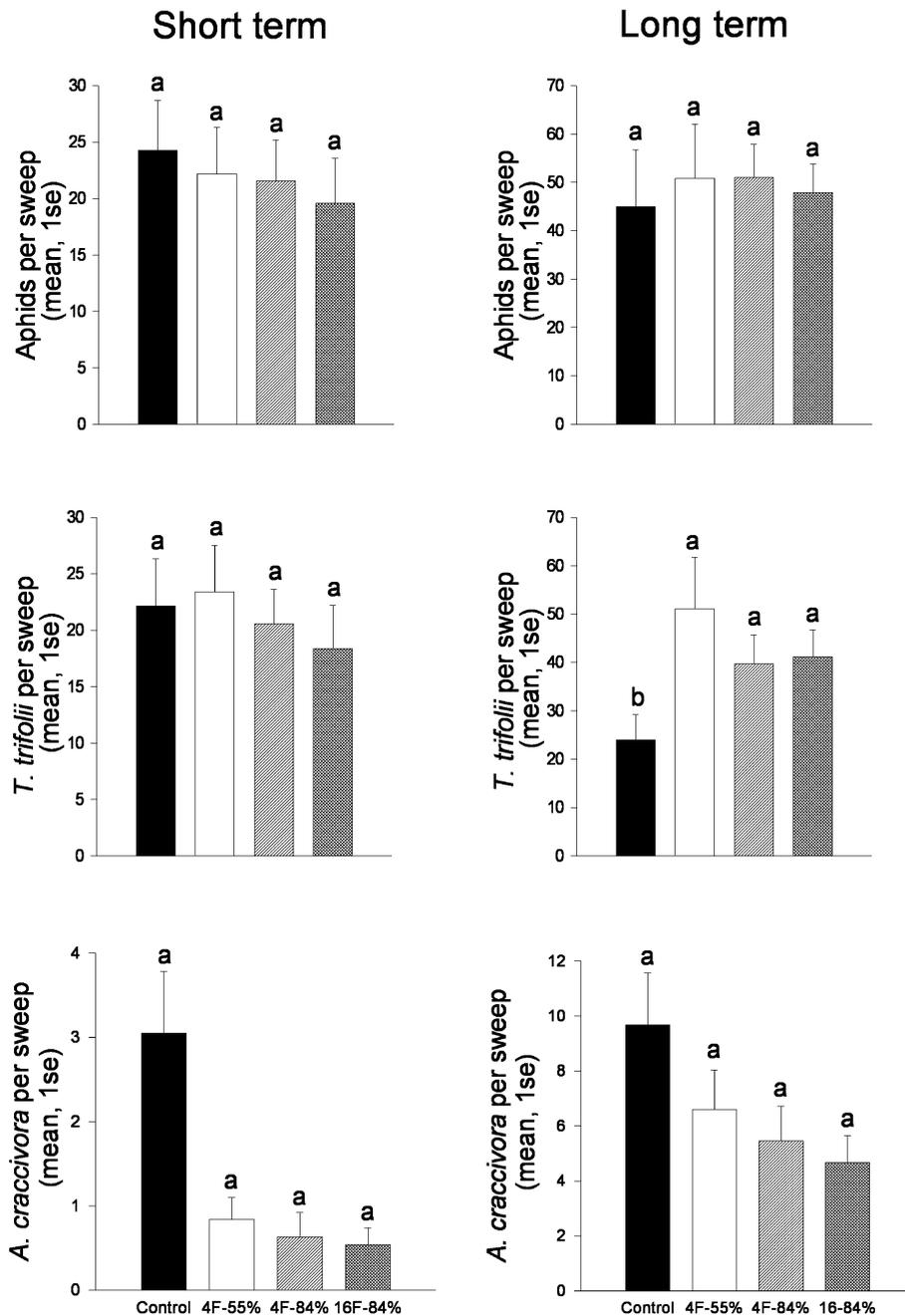


Fig. 7. Total abundance (individuals per 2 m²) of aphids, and abundance of two species of aphids (*Therioaphis trifolii* and *Aphis craccivora*) within four experimental landscapes (see Fig. 1), during the early sampling period (summer [short term]: weeks 1, 3, 5, and 7 after alfalfa removal, left) and the late sampling period (autumn [long term]: weeks 13, 15, 17, 19 and 21, right). Standard error bars are based on five data points, i.e., five replicates for each landscape type. Different letters on the bars indicate significant differences after planned comparisons and Bonferroni correction.

species with similar abundances in the 4F – 84% and 16F – 84% landscapes, which were higher than abundances in the control landscape, we can propose that large habitat loss in fragmented landscapes has a positive effect. Nevertheless, we can not rule out that this positive effect resulted from a compensation of the negative effect of habitat loss by a positive effect of habitat fragmentation.

In this study, many carabid and coccinellid species were unaffected by habitat loss and/or fragmentation, and had similar abundances in all landscapes in the short and long-term periods of time. In previous studies using

similar alfalfa landscapes that varied in fragmentation *per se* and isolation at high levels of habitat loss (84%), there was a weak but positive effect of habitat fragmentation on the abundance of *H. convergens* and *H. variegata*, but only when fragments were 2 m apart and not when they were 6 m apart (i.e., as in the landscapes considered in this study) (Grez et al., 2004a). The variable responses of species to landscape configuration may depend upon species dispersal behaviour and demography (Tischendorf et al., 2005). More mobile species may track more efficiently the landscapes discontinuities than less mobile

species, and their densities should be less affected by habitat fragmentation (Ricketts, 2001; Ewers & Didham, 2006). For example, with greater mobility, *Harmonia axyridis* (Pallas) is more effective than *C. maculata* at tracking fragmented landscapes and prey patches (With et al., 2002). So, species with similar densities among landscapes should be more mobile than species affected by habitat loss and fragmentation. We have some understanding of movement behaviour for *E. connexa* in alfalfa crops (Grez et al., 2005), but not yet for the carabids and the other species of coccinellids associated with alfalfa crops in Chile.

Several mechanisms may account for the higher abundance and diversity of aphidophagous species in landscapes with higher levels of habitat loss and fragmentation. In addition to creating the "crowding effect" as discussed above, fragmented landscapes may increase the immigration of individuals from elsewhere. Because more fragmented landscapes contain more habitat edge *per area* of habitat than less fragmented or continuous habitats, immigrants arriving in the matrix will be more likely to encounter adjacent habitat in the more fragmented landscapes (Bowman et al., 2002; Grez et al., 2004a). Emigration may also be enhanced by increased habitat edge, but this will depend on resource availability, dispersal mode, and boundary crossing probability (Kareiva, 1982; Banks & Yasenak, 2003; Tischendorf et al., 2005). Also, social interactions in some organisms, such as crabs and rodents, may result in high densities or species richness in smaller fragments (Collins & Barret, 1997; Wolff et al., 1997; Caley et al., 2001).

Landscape structure may alter species interactions by changing the nature or abundance of species in the landscape (With, 2002). In our case, the concomitant increase in the abundance of carabids and some species of coccinellids in the landscapes with higher habitat loss and fragmentation may affect intra-guild interactions, potentially affecting the efficiency of biological control of aphids. Laboratory experiments have shown that these coccinellid and carabid species interact in an additive or synergistic way, but never antagonistically (Grez et al., 2007). Therefore, the coexistence of coccinellids and carabids in landscapes with high habitat loss and fragmentation may not interfere with the biological control of aphids, except in resource-limited scenarios.

The total abundance of aphids was not affected by habitat loss and fragmentation. But at the species level in the long-term, the abundance of *A. craccivora* was reduced by habitat loss and fragmentation (i.e., in the 16–84% landscapes compared to the control), while *T. trifolii* was favoured by habitat loss and fragmentation, with higher abundances in all fragmented landscapes, independent of the level of habitat loss and fragmentation. Therefore, the two most abundant species of aphids in alfalfa crops in Chile responded in opposite fashion to landscape structure, late in the season when they were most abundant. The high abundance of several species of carabids and coccinellids in the landscapes with high habitat loss and fragmentation could result in lower abun-

dances of *A. craccivora*, but why this did not occur also with *T. trifolii* remains a puzzle. Assessing the foraging preferences of the individual aphidophagous species may yield a deeper understanding of predator-prey relationships in fragmented landscapes. The dynamics of aphids may also have been affected by other aphidophagous species (e.g., parasitoids), that can also be affected by landscape structure (Thies & Tschamtker, 1999; Marino et al., 2006). In this system, however, the abundance of aphid parasitoids and parasitoidism was similar in all landscapes (Zaviezo et al., in prep).

In conclusion, our results suggest that high levels of habitat loss and fragmentation may increase the density and species richness of aphidophagous insects, although the responses vary over time and are species specific, with some species being more sensitive to landscape configuration than others. Aphids also showed variable responses to habitat loss and fragmentation. These results should be considered when designing agricultural landscapes to enhance biological control.

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