

# Effect of habitat subdivision on the population dynamics of herbivorous and predatory insects in central Chile

Efecto de la subdivisión del hábitat sobre las dinámicas poblacionales de insectos herbívoros y depredadores en Chile central

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## ABSTRACT

Habitat subdivision may facilitate the persistence at low densities of both predator and prey populations. But habitat subdivision may also allow herbivores to escape from predators and therefore reach higher local densities. The outcome will depend on the dispersal behaviour of organisms. The effect of habitat subdivision on populations of aphidophagous coccinellids *Eriopsis connexa* and *Hippodamia variegata* and their prey *Brevicoryne brassicae* was evaluated in crops of *Brassica oleraceae*. In particular, the following responses were analysed: a) density/plant of herbivorous and predatory insects, b) colonisation of herbivorous and predatory insects, c) movement between plant patches and residence time of predators, d) *in situ* recruitment of predators, and e) final weight of plants. Nine continuous and subdivided plots of *B. oleracea* were set up following a 3 x 3 completely randomised block design. The three treatments were: a) continuous, b) subdivided plus weeds, and c) subdivided plus cloth barriers. Density per plant of herbivorous and predatory insects was lower in subdivided plus barriers habitats. Colonisation by herbivores and predators was more rapid in continuous or subdivided plus weeds habitats. Residence time and *in situ* recruitment of predators was greater in continuous habitats. Plant weight was greater in subdivided than continuous habitats. Therefore, habitat subdivision, particularly when patches were more isolated, negatively affected the population densities of both herbivorous and predatory insects. This is likely due to lesser colonisation and *in situ* recruitment, and greater emigration of insects in those subdivided habitats.

**Key words:** *Brevicoryne brassicae*, *Eriopsis connexa*, *Hippodamia variegata*, spatial subdivision, predator-prey relationships.

## RESUMEN

La subdivisión del hábitat puede facilitar la persistencia a bajas densidades de herbívoros y sus depredadores. Pero la subdivisión del hábitat puede también permitir que los herbívoros escapen de sus depredadores, alcanzando altas densidades a nivel local. El resultado dependerá de la conducta de dispersión de los organismos involucrados. En este trabajo se evaluó el efecto de la subdivisión del hábitat sobre las dinámicas poblacionales de los coccinélidos *Eriopsis connexa* e *Hippodamia variegata* y de su presa, el áfido *Brevicoryne brassicae* asociados a *Brassica oleraceae*. En particular se analizaron las siguientes respuestas: a) densidad/planta de insectos herbívoros y depredadores, b) colonización de insectos herbívoros y depredadores, c) movimiento entre parches de plantas y tiempo de residencia de depredadores, d) reclutamiento *in situ* de los depredadores, y e) peso final de las plantas. Se implementaron nueve hábitats continuos y subdivididos siguiendo un diseño de bloques al azar de 3 x 3. Los tres tratamientos fueron: a) continuo, b) subdividido más malezas y c) subdividido más barreras de tela. La densidad/planta de insectos herbívoros y depredadores fue menor en los hábitats subdivididos más barreras. La colonización por herbívoros y depredadores fue más rápida en hábitats continuos o subdivididos más malezas. El tiempo de residencia y el reclutamiento *in situ* de los depredadores fue mayor en hábitats continuos. El peso final de las plantas fue mayor en hábitats subdivididos. La subdivisión del hábitat, particularmente cuando los parches de plantas están más aislados, afecta negativamente las densidades poblacionales de insectos herbívoros y depredadores. Esto se debería a la menor colonización, menor reclutamiento *in situ* y mayor emigración de insectos en aquellos hábitats más subdivididos.

**Palabras clave:** *Brevicoryne brassicae*, *Eriopsis connexa*, *Hippodamia variegata*, subdivisión del hábitat, relación depredador-presa.

## INTRODUCTION

Habitat subdivision, and the consequent increase in environmental heterogeneity may affect population dynamics of the organisms associated to those habitats (Wiens 1976, den Boer 1981, Fahrig & Merriam 1985, Fahrig & Paloheimo 1988a, 1988b, Fahrig & Grez 1996) as well as interactions between species (Huffaker 1958, Hanski 1983, Hanski & Ranta 1983, Kareiva 1986, 1987, 1990a, 1990b, Holyoak & Lawler 1996). In particular, habitat subdivision may have profound effects on predator-prey interactions. Habitat heterogeneity may facilitate the persistence at low densities of both predator and prey populations through the establishment of prey refuges (Huffaker 1958). However, habitat subdivision may also destabilise predator-prey relationships allowing herbivores to escape temporarily from predators and reach higher local densities (Kareiva 1984, 1986, 1987, Kareiva & Andersen 1988, Kareiva 1990a, 1990b).

The dispersal behaviour of the predator and prey populations is crucial for the extent to which habitat subdivision may affect predator-prey dynamics. If habitat subdivision delays but does not hamper the access of predators to prey-rich patches, habitat heterogeneity should lead to stable, low densities, predator and prey populations. But, if habitat subdivision reduces the aggregation of predators in prey-rich patches, herbivore outbreaks may be expected.

The empirical evidence on the consequences of habitat subdivision for predator-prey dynamics is scarce (Kareiva 1987, 1989, 1990a, Bierzychudek 1988). Recently it has been shown that, in fragmented agroecosystems, herbivores suffer a reduced parasitism because of a lower colonisation of natural enemies (Kruess & Tscharntke 1994). This paper evaluates the effect of habitat subdivision on the population dynamics of the herbivore *Brevicoryne brassicae* (Linnaeus) (Homoptera: Aphididae), and the predators *Eriopis connexa* Germar and *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) associated with patches of cabbage, *Brassica oleraceae* var. *capitata* L. In particular, the following

responses to habitat subdivision are analysed: a) density per plant of herbivorous and predatory insects, b) colonisation of plants by herbivorous and predatory insects, c) movement between plant patches and residence time of adult predators, d) *in situ* recruitment of predators, and e) final weight of plants.

*Eriopis connexa* is common throughout Chile (Montes 1970). Its life cycle is completed in one month (Etchégaray & Barrios 1979). Both larvae and adults are predators. Adults are mobile and may disperse at least up to 30 m within one day; larvae, however, have lower dispersal abilities (AA Grez, unpublished data). Immigration to new habitat patches is undertaken mainly by adults. *Hippodamia variegata* was introduced from South Africa to Chile in the 1970's. It is an important biocontrol agent of aphids (Zúñiga et al. 1986a, 1986b). Nothing is known about its ecology in Chile. The cabbage aphid, *B. brassicae*, thrives on annual and biennial crucifers in all temperate crops of the world (Clark et al. 1981). In Chile *B. brassicae* has been present since at least 1953 (Campos 1953, González 1989). It has a high reproductive rate mainly due to its ability to reproduce parthenogenetically (Wellings & Dixon 1987). Immigration to habitat patches results from the aerial dispersal of alates. Once on its host plant, wingless forms are produced, resulting in highly crowded aphid aggregations (Clark et al. 1981, Wellings & Dixon 1987).

## METHODS

Experiments were carried out at the University of Chile Agronomical Station, 40 km SW Santiago, from December 1992 to April 1993. Nine continuous and subdivided experimental plots of *B. oleraceae* var. *capitata* were set up following a 3 x 3 completely randomised block design (Fig. 1). Each plot consisted of seven experimental patches each with nine cabbage plants separated by 1 m. Three treatments with increasing degrees of subdivision were established: a) continuous: patches of cabbage interspersed with more cabbage and no weeds between them, b) subdivided plus

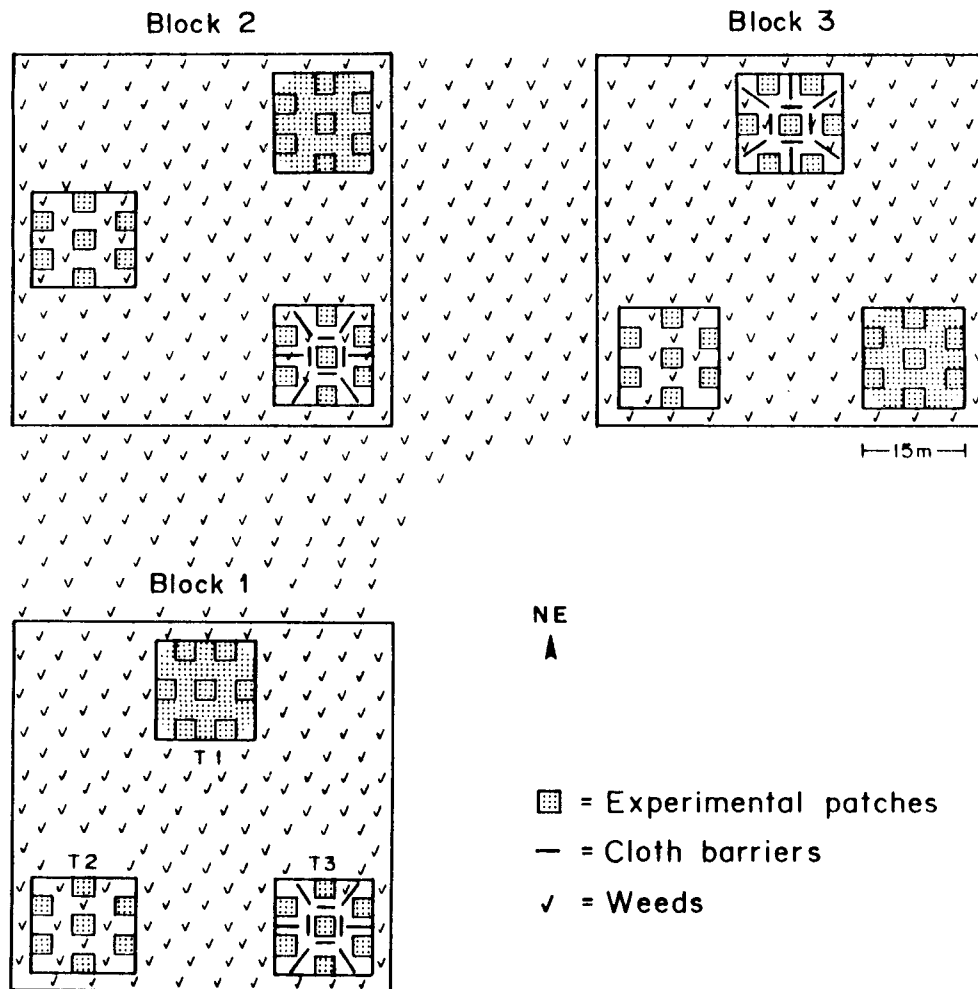


Fig. 1: Experimental design for studying the effect of habitat subdivision on the density of herbivorous and predatory insects. T1: continuous treatment, T2: subdivided plus weeds treatment, T3: subdivided plus barriers treatment.

Diseño experimental para evaluar el efecto de la subdivisión del hábitat sobre la densidad de insectos herbívoros y depredadores. T1: tratamiento continuo, T2: tratamiento subdividido más malezas, T3: tratamiento subdividido más barreras.

weeds: patches of cabbage interspersed with weeds, and c) subdivided plus barriers: patches of cabbage interspersed with mowed weeds and with the addition of 1.5 m high cloth barriers between patches, thus further isolating them (Kareiva 1987). The spatial scale used in this experiment is larger than the majority of the experiments in community ecology (Kareiva and Andersen 1988). The relatively large dispersal ability of the coccinellids species of this study indicated that this spatial scale was adequate to evaluate their response to habitat subdivision. In fact, population response of coc-

cinellids to spatial variation in aphid density is better observed at larger spatial scales (Ives et al. 1993).

The density of larvae and adults of *E. connexa* and *H. variegata* per plant, and the density of wingless forms of *B. brassicae* per leaf, were assessed by direct counting in the field, every two weeks from 4 December, 1992 to 26 April, 1993. Each date, four randomly selected plants from each patch were sampled.

The effect of habitat subdivision on the density of each species was analysed for each date with a two-way ANOVA, with

treatment and block as sources of variation. To avoid pseudoreplication (Hurlbert 1984), arithmetic mean density of insects per patch was used for statistical analyses. Data were log transformed. Tukey tests were conducted for pairwise comparisons.

Initial colonisation of herbivorous and predatory insects was estimated following Kareiva (1987) by counting the number of plants with at least one insect the first sampling date they appeared in the field (4 December for *B. brassicae* and *E. connexa* and 12 January for *H. variegata*). At the beginning of the experiment plants were free of insects since they were transplanted from a greenhouse and carefully selected. Therefore insects found initially in a plant represent colonisation events. These data were analyzed by a  $\chi^2$  test.

The effect of habitat subdivision on the relative residence time of adult coccinellids in each patch and their movements between experimental patches were determined by a mark-recapture experiment conducted from 18 January to 22 January, 1993. Residence time indirectly evaluates the emigration of predators from continuous and subdivided habitats. A total of 567 adults of *E. connexa* were marked individually with acrylic paint (Testor<sup>R</sup> enamel). Each individual was marked with four dots on the elytra; each dot indicating a digit based on the color and location on the elytra. This marking technique has been used before in ecological studies of insects (Bach 1980, 1984, Turchin 1987, Strauss & Morrow 1988, Lawrence & Bach 1989, Grez & González 1995). Coccinellids were placed in plastic jars and kept overnight in the laboratory at 4 °C. Three individuals were released on every plant in all patches of one block. During the following four days all plants from that block were examined and the location of marked beetles was recorded. Statistical differences between recapture curves were assessed by the Peto and Peto's logrank test (Pyke & Thompson 1986).

To determine the effect of habitat subdivision on the *in situ* recruitment of predators, the densities of coccinellid eggs and larvae were also measured on each sampling date. Data from different dates were pooled and statistical differences were as-

essed by a two-way ANOVA. At the end of the experiment (26 April), the aerial biomass of plants growing in the three treatments was assessed. Two plants from each experimental patch were cut off and weighed in the field.

## RESULTS

### *General insect dynamics*

Pooled data from all treatments indicate that, in the whole system, *B. brassicae* had two clear peaks of abundance, one in early summer (29 December) and the other at the end of the summer (16 February). *Eriopsis connexa* was more abundant in early summer (29 December), while *H. variegata* colonized later (12 January) and never reached densities as high as *E. connexa* (Fig. 2). The mono or bimodal abundance curves for the different species are consistently observed in all treatments (Fig 3).

### *Effects of habitat subdivision on the density per plant of herbivorous and predatory insects*

Habitat subdivision, in general, affected negatively the density of insects per plant. All the species were less abundant in subdivided plus barriers habitats (Fig. 3, Table 1). Moreover, the highest peaks of abundance of both *B. brassicae* (29 December) and *H. variegata* (12 January) were achieved in continuous habitats. *Eriopsis connexa* (29 December) was more abundant in subdivided plus weeds habitats, with no difference between the other two treatments (Fig. 3, Table 1).

### *Colonization*

While *B. brassicae* more readily colonised subdivided plus weeds habitats (Table 2,  $\chi^2 = 14.68$ , d.f. = 2,  $P = 0.00065$ ), *E. connexa* equally colonised all treatments (Table 2,  $\chi^2 = 0.99$ , d.f. = 2,  $P = 0.61$ ). However, *H. variegata* colonised continuous habitats to a greater extent than subdivided habitats (Table 2,  $\chi^2 = 51.51$ , d.f. = 2,  $P < 0.00001$ ).

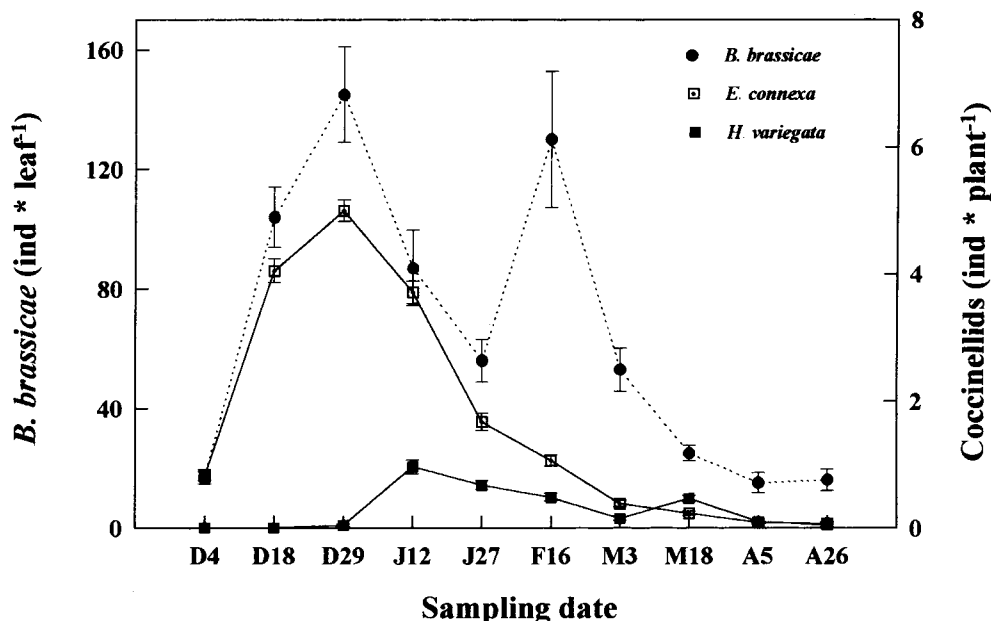


Fig. 2: Population dynamics of *Brevicoryne brassicae*, *Eriopsis connexa* and *Hippodamia variegata* associated to cabbages, independent of habitat subdivision (pooled data), from 4 December 1992 to 26 April 1993.

Dinámica poblacional de *Brevicoryne brassicae*, *Eriopsis connexa* e *Hippodamia variegata* asociados a plantas de repollo, independiente de la subdivisión del hábitat (datos agrupados), entre el 4 de diciembre de 1992 y el 26 de abril de 1993.

#### *Movement of coccinellids between patches and residence time*

Independently of the treatment, most coccinellids stayed on the same plant or moved to adjacent plants within the same patch where they were released. In continuous habitats, 90% of the recaptures were on the same plant and no recaptures occurred in neighbouring patches (Table 3). In subdivided habitats (subdivided plus weeds and subdivided plus barriers habitats), only 68% of the recaptures occurred on the same plant, and only in the subdivided plus weeds treatment, individuals moved to new patches of the same plot, accounting for over 9% of the recaptures (Table 3). The frequency distribution of the distance traveled by *E. connexa* in continuous and subdivided treatments are significantly different  $\chi^2 = 16.62$ , d.f. = 4,  $P = 0.002$ , Table 3).

Percent daily recaptures of adults coccinellids were significantly lower in both subdivided treatments compared with the continuous treatment (Fig. 4, Peto & Peto's logrank test,  $LR > 3.84$ ,  $P < 0.05$ ), indica-

ting a higher residence time in continuous habitats.

#### *In situ recruitment of coccinellids*

The density of egg clumps did not differ among treatments (Fig. 5, two-way ANOVA,  $F_{(2,85)} = 0.83$ ,  $P = 0.44$ ) or blocks ( $F_{(2,85)} = 0.30$ ,  $P = 0.74$ ). However, larval density was significantly higher in the continuous treatment (Fig. 5, two-way ANOVA,  $F_{(2,85)} = 4.06$ ,  $P = 0.02$ ).

#### *Plant weight*

Cabbage plants that grew in the subdivided plus barriers habitats were significantly heavier than those that grew in subdivided plus weeds or continuous habitats (Fig. 6, two-way ANOVA,  $F_{(2,121)} = 9.79$ ,  $P = 0.001$ ).

#### DISCUSSION

Habitat subdivision does not affect the mono or bimodal patterns of abundance of

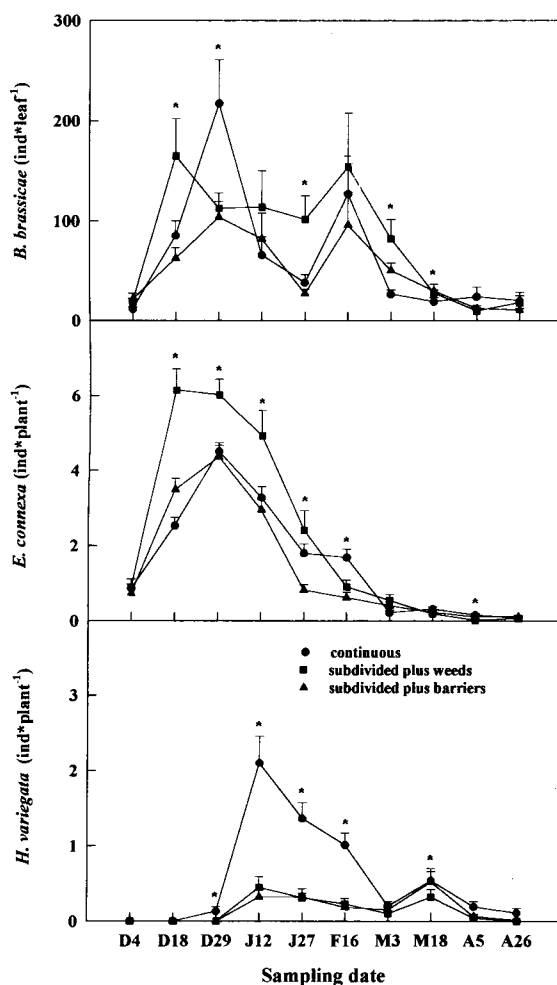


Fig. 3: Population dynamics of *Brevicoryne brassicae*, *Eriopis connexa* and *Hippodamia variegata* associated to continuous, subdivided plus weeds and subdivided plus barriers habitats, from 4 December 1992 to 26 April 1993. Asterisks indicate significant differences.

Dinámica poblacional de *Brevicoryne brassicae*, *Eriopis connexa* e *Hippodamia variegata* asociados a hábitats continuos, subdivididos más malezas y subdivididos más barreras, entre el 4 de diciembre de 1992 y el 26 de abril de 1993. Los asteriscos indican diferencias significativas.

the three species, which were consistently observed in subdivided or continuous habitats. The bimodal pattern of *B. brassicae* may be related to phenological changes of cabbage plants, because both the first and the second peak coincides with the production of new cabbage leaves.

Nevertheless, habitat subdivision does affect the abundance of these species. In general, both predator and prey populations

were less abundant in extremely subdivided habitats which coincides with Huffaker's (1958) report. However, the three species of insects responded differentially to habitat subdivision, particularly when continuous and subdivided plus weeds treatments were analysed.

Although *B. brassicae* achieved their highest peak of density in continuous habitats, they were generally more abundant in subdivided plus weeds habitats. This density pattern may be explained by the higher and continuous colonisation of aphids from surrounding weeds to subdivided patches of cabbages. Weeds surrounding cabbage patches included some wild crucifers which may have been a refuge for cabbage aphids and a source of colonisers.

With regard to predators, *E. connexa* was most abundant in subdivided plus weeds habitats, while *H. variegata* was most abundant in continuous habitats. Differences in patterns of colonisation may partially explain the relative density of these two species. Colonisation of *E. connexa* was not significantly different between treatments, although there was a tendency of a higher colonisation in subdivided plus weeds habitats. Colonisation of *H. variegata* was significantly higher in continuous habitats.

The higher density of *E. connexa* in subdivided plus weeds habitat is more complicated to interpret through emigration patterns since *E. connexa* emigrates more rapidly from these habitats than from continuous ones. But movement pattern of these coccinellids showed that they moved more between patches in subdivided plus weeds habitats, indicating that they can move between weeds. Therefore, although they emigrate more from cabbage patches in subdivided plus weeds habitats, they probably may remain in neighbouring weeds and recolonize cabbage patches, following the abundant aphid population there.

The different density patterns of insects in subdivided plus weeds and subdivided plus barriers habitats indicate that insect dynamics does not depend only on habitat subdivision but also, and more important, on the quality of the matrix. In this study, weeds between cabbage patches were not

TABLE 1

Results from the two-way ANOVAs for the effect of habitat subdivision on population densities of *Brevicoryne brassicae*, *Eriopsis connexa* and *Hippodamia variegata*. ANOVAs were carried out on log of mean values per plant (averaged per patch). Dashes indicate no record.

Resultados de los ANDEVAs de dos vías para el efecto de la subdivisión del hábitat sobre las densidades poblacionales de *Brevicoryne brassicae*, *Eriopsis connexa* e *Hippodamia variegata*. Los ANDEVAs se llevaron a cabo con los logaritmos de los valores promedio por planta (promediados por parche). Los guiones indican ausencia de individuos.

Species	4 Dec	18 Dec	29 Dec	12 Jan	27 Jan	16 Feb	3 Mar	18 Mar	5 Apr	26 Apr
<i>Brevicoryne brassicae</i>										
Habitat subdivision ( $F_{2,58}$ )	3.12	8.63**	3.63*	0.79	5.45*	1.86	4.95*	3.69*	1.58	0.59
Block ( $F_{2,58}$ )	2.08	3.51*	3.02	21.22**	9.57**	12.26**	10.83**	13.45**	3.56*	13.10**
<i>Eriopsis connexa</i>										
Habitat subdivision ( $F_{2,58}$ )	0.38	26.08**	9.11**	5.61*	10.43**	12.18**	0.29	2.46	6.88**	0.22
Block ( $F_{2,58}$ )	8.14**	6.83**	5.23*	20.83**	19.63**	3.85*	12.54**	5.68*	3.73*	0.07
<i>Hippodamia variegata</i>										
Habitat subdivision ( $F_{2,58}$ )	-	-	7.39**	32.18**	26.90**	21.20**	1.60	9.82**	3.00	2.98
Block ( $F_{2,58}$ )	-	-	5.36**	14.10**	17.34**	3.90*	1.01	86.50**	1.50	0.63

\*  $P < 0.05$ , \*\*  $P < 0.005$

TABLE 2

Number of cabbage plants colonized by at least one insect the first sampling date they appeared in the field (4 December for *B. brassicae* and *E. connexa* and 12 January for *H. variegata*). Number of sampled plants from each treatment = 84 (data from all blocks pooled).

Número de plantas colonizadas al menos por un insecto la primera fecha de su aparición en el campo (4 de diciembre para *B. brassicae* y *E. connexa* y 12 de enero para *H. variegata*). Número de plantas muestreadas en cada tratamiento = 84 (los datos de todos los bloques fueron agrupados).

Species	Continuous	Subdivided plus weeds	Subdivided plus barriers
<i>Brevicoryne brassicae</i>	67	81	64
<i>Eriopsis connexa</i>	41	47	42
<i>Hippodamia variegata</i>	59	23	17

strong barriers to insects and therefore subdivided plus weeds habitats were more similar to continuous than to subdivided plus barriers habitats.

Anyway, predators emigrate more from both kinds of subdivided habitats. It has been pointed out that habitat subdivision creates a framework of small patches, each with a small area/perimeter ratio. If these small patches have "soft edges" (*sensu* Stamps et al., 1987), insects may have a high probability of reaching the border and emigrating from the patch. A higher emigration of insects from small patches has

been described mostly for herbivorous insects (Bach 1980, 1984, Risch 1981, Kareiva 1983, Turchin 1986, Grez 1991, Grez & González 1995), but also for predatory insects (Sheehan 1986), which support the patterns observed in the current study.

Besides colonisation and emigration patterns, the higher predator density in continuous habitats may be accounted for by a higher reproductive or survival rate of insects in continuous habitats compared with subdivided habitats (Sheehan 1986). In this study, the density of egg clumps of coccinellids did not differ among treatments, but

TABLE 3

Frequency of distances traveled in 24 h by individuals of *E. connexa*. Data are from recaptures during 4 successive days in January 1993. Numbers in parentheses represent percentages of total recaptures. Distances up to 2.8 m correspond to recaptures within the same experimental patch. When only newly recaptured individuals are considered, the pattern is the same.

Frecuencia de distancias recorridas en 24 h por individuos de *E. connexa*. Los datos provienen de recapturas durante 4 días consecutivos en enero de 1993. Los números entre paréntesis representan el porcentaje del total de recapturas. Las distancias hasta 2.8 m corresponden a recapturas dentro del mismo parche experimental. El patrón es el mismo cuando se consideran sólo los nuevos individuos recapturados.

Distance (m)	Continuous	Subdivided plus weeds	Subdivided plus barriers
0	128 (90.1)	30 (68.2)	24 (68.6)
1	4 (2.8)	5 (11.4)	5 (14.3)
1.4	4 (2.8)	3 (6.8)	1 (2.9)
2	1 (0.7)	1 (2.3)	0 (0)
2.2	2 (1.4)	1 (2.3)	3 (8.6)
2.8	3 (2.1)	0 (0)	2 (5.7)
6	0 (0)	1 (2.3)	0 (0)
7.2	0 (0)	1 (2.3)	0 (0)
8.6	0 (0)	1 (2.3)	0 (0)
12.6	0 (0)	1 (2.3)	0 (0)
Recaptures	142	44	35

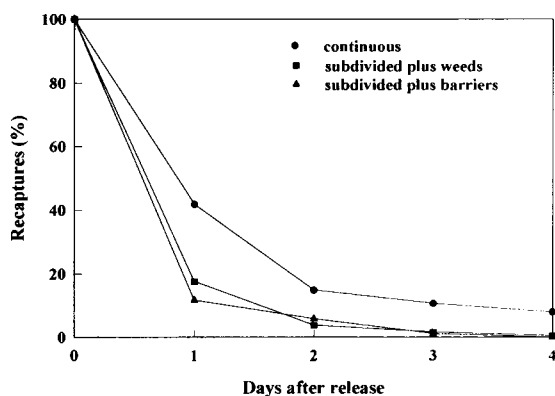


Fig. 4: Percent recaptures of *E. connexa* in continuous, subdivided plus weeds and subdivided plus barriers habitats. Data are from a mark-recapture experiment made in January 1993.

Porcentaje de recaptura de *E. connexa* en hábitats continuos, subdivididos más malezas y subdivididos más barreras. Los datos provienen de un experimento de marcaje-recaptura realizado en enero de 1993.

the density of larvae was higher in continuous habitats. Larval survivorship or their residence time in continuous habitats may have been higher than in subdivided habitats, but this was not evaluated.

The higher biomass of plants growing in subdivided plus barriers habitats may have been the result of the low herbivore load as well as other variables, such as microhabitat changes provided by the inclusion of cloth barriers among patches. It has been noticed that many herbivores respond positively to plant size, but this was not the case here. Instead, herbivores were more abundant in subdivided plus weeds and continuous patches which yielded smaller plants.

The ultimate cause of the lower densities of herbivorous and predatory insects in subdivided plus barriers habitats remains unknown. Were herbivores and predators responding directly or indirectly to habitat subdivision? The resource concentration hypothesis (Root 1973) predicts that herbivorous insects should be more abundant in dense, large and/or monospecific plant patches because they should find these patches more readily, reproduce more there, and stay longer than in less concentrated patches. Subdivided habitats in the current experiment offered less concentrated resources than continuous habitats because of the lower number of cabbage plants (a three-fold

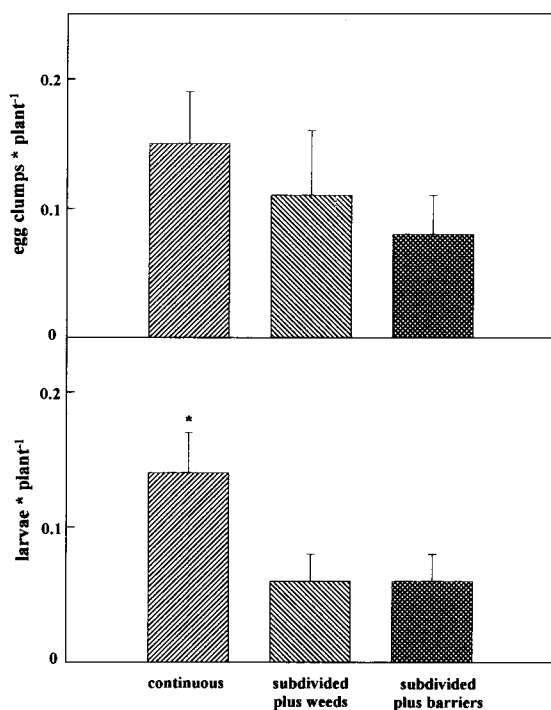


Fig. 5: Egg and larval recruitment of coccinellids in continuous, subdivided plus weeds, and subdivided plus barriers habitats. Figures are mean  $\pm$  1 SE ( $n = 10$  for each treatment, one for each sampling date). Asterisk indicates significant differences.

Reclutamiento de huevos y larvas de coccinélidos en hábitats continuos, subdivididos más malezas y subdivididos más barreras. Las cifras indican la media  $\pm$  1 EE ( $n = 10$  para cada tratamiento, una para cada fecha de muestreo). El asterisco indica diferencias significativas.

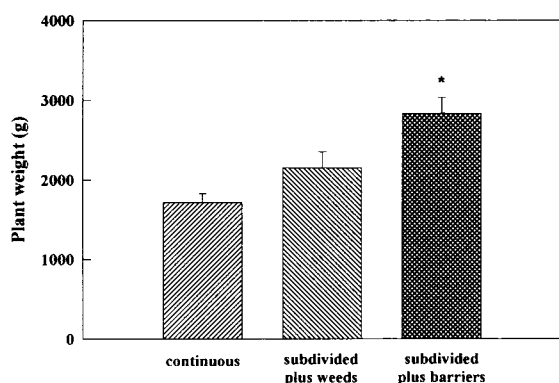


Fig. 6: Final weight of plants from continuous, subdivided plus weeds, and subdivided plus barriers habitats. Data are mean  $\pm$  1 SE ( $n = 42$  for each treatment). Asterisk indicates significant differences.

Peso final de las plantas de hábitats continuos, subdivididos más malezas y subdivididos más barreras. Los datos indican la media  $\pm$  1 EE ( $n = 42$  para cada tratamiento). El asterisco indica diferencias significativas.

difference). Therefore, herbivorous insects may be responding directly to habitat subdivision and habitat loss, immigrating, reproducing, staying longer and achieving higher densities in continuous habitats. Kareiva (1986), however, found that aphids did not respond directly to habitat subdivision.

In summary, herbivorous and predatory insects were less abundant in subdivided plus barriers habitats. This is likely due to lower colonisation, lower *in situ* recruitment and higher emigration of insects in such habitats. Subdivided plus weeds habitats may behave as continuous habitats because weeds offer alternative resources both to herbivorous and predatory insects. In order to reduce the probability of pest outbreaks, it may be profitable to subdivide crops including between patches a matrix not adequate for herbivorous but adequate for predatory insects. This may be achieved through intercropping host and non-host plants.

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