



Land use intensification differentially benefits alien over native predators in agricultural landscape mosaics

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ABSTRACT

Aim Both anthropogenic habitat disturbance and the breadth of habitat use by alien species have been found to facilitate invasion into novel environments, and these factors have been hypothesized to be important within coccinellid communities specifically. In this study, we address two questions: (1) Do alien species benefit more than native species from human-disturbed habitats? (2) Are alien species more generalized in their habitat use than natives within the invaded range or can their abundance patterns be explained by specialization on the most common habitats?

Location Chile.

Methods We quantified the use of different habitat types by native and alien coccinellid beetles by sampling individuals in nine habitat types that spanned a gradient in disturbance intensity, and represented the dominant natural, semi-natural and agricultural habitats in the landscape.

Results Our results provide strong support for the hypotheses that more-disturbed habitats are differentially invaded. Both the proportion of alien individuals and the proportion of alien species increased significantly with increasing disturbance intensity. In contrast, we found no evidence that alien species were more generalized in their habitat use than native species; in fact, the trend was in the opposite direction. The abundance of specialized alien coccinellid species was not correlated with the area of the habitat types in the landscape.

Main conclusion The results suggest that successfully established alien coccinellid species may be ‘disturbance specialists’ that thrive within human-modified habitats. Therefore, less-disturbed agroecosystems are desirable to promote the regional conservation of native species within increasingly human-dominated landscapes.

Keywords

Biodiversity, Coccinellidae, habitat specialization, ladybeetles, specialists and generalists.

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INTRODUCTION

Land use change, resulting from the destruction of natural habitats for human use, and further intensification of management practices on such lands, is a leading driver of global environmental change (Sala *et al.*, 2000; Foley *et al.*, 2005). A reduction in area and fragmentation of the natural habitats upon which native species depend is known to result in increased extinction probabilities and declining biodiversity

(Saunders *et al.*, 1991; Wilcove *et al.*, 1998; MEA, 2005). It is also increasingly recognized that native species are negatively impacted by alien species that benefit from human land uses and/or the accompanying increases in habitat disturbance (Saunders *et al.*, 1991; Gurevitch & Padilla, 2004; Didham *et al.*, 2007). The link between anthropogenic habitat disturbance and invasion (Elton, 1958; Lozon & MacIsaac, 1997; D’Antonio *et al.*, 1999) can result from a number of different underlying mechanisms, including the creation of new

habitats or niches for invasive species, increased productivity, increased propagule pressure and the reduction in biotic resistance of recipient communities (Lozon & MacIsaac, 1997; Byers, 2002). A basic prediction is that alien species differentially benefit from increasing levels of anthropogenic disturbance associated with land use intensification, irrespective of mechanism.

Even if alien species do not directly benefit from disturbance, they may be more tolerant of land use changes if they are generalized in habitat use, that is, able to use and/or thrive in more different habitat types than native species. Species with broader niches, such as habitat generalists, are predicted to be more likely to find the necessary environmental conditions for establishment and spread within a new range compared with habitat specialists. As a consequence, habitat niche breadth should be positively correlated with invasion success, that is, establishment in a new environment, as predicted by the 'niche breadth-invasion success hypothesis' (Vázquez, 2006). Habitat generalists, in turn, should be better able to cope with landscape changes associated with increasing human use, compared with specialists that rely on one or a few habitat types, which may be in decline in human-modified landscapes (Devictor *et al.*, 2008). If indeed generalist species are more successful invaders (i.e. more likely to establish and spread in a new environment), then habitat breadth of alien species within a community should be greater than that of native species in the invaded range (Vázquez, 2006).

However, this pattern may break down for species specializing on widespread resources or habitat types. In such cases, a species may reach high local densities and a broad distribution, despite using a narrow range of habitats or environmental conditions (Brown, 1984; Gaston *et al.*, 1997). This is likely to be particularly important for alien species that thrive in human-dominated ecosystems (Vázquez, 2006). For example, in the case of some insect predators associated with agricultural systems, habitat conversion to crops may actually introduce novel habitat types, and even specific prey species, used by the alien organisms in their native home ranges (Evans *et al.*, 2011a). Under such conditions, extensive cultivation of specific crops might be expected to promote the successful invasion of species that are relatively specialized on, or 'pre-adapted' to, these land use types (Evans *et al.*, 2011a). Thus it is important to consider the relative commonness or rarity of different habitat types when evaluating the importance of habitat niche breadth in invasion dynamics (Vázquez, 2006).

We examined these issues in a guild of predatory lady beetles, the Coccinellidae, an ecologically important group of insects that provide valuable pest control services in agricultural systems (Hodek & Honek, 1996; Landis *et al.*, 2008). As a consequence of their potential utility as biological control agents against aphids, scale insects and a variety of other insect pests, coccinellids have been repeatedly introduced into new geographic regions over the last century (Obrycki & Kring, 1998; Evans *et al.*, 2011b). For example, in North

America alone, at least 179 species of coccinellids have been introduced, and 27 species have become established (Gordon, 1985; Harmon *et al.*, 2007). The increasing abundance and/or dominance by alien coccinellid species has raised concern over potential negative impacts on the often diverse native coccinellid fauna on multiple continents (Dixon, 2000; Harmon *et al.*, 2007; Martins *et al.*, 2009; Grez *et al.*, 2010a, 2011; Brown *et al.*, 2011; Roy *et al.*, 2012).

Habitat attributes and species traits hypothesized to be important in predicting invasion dynamics in general also apply to coccinellids more specifically (Evans *et al.*, 2011b). For example, the common association between habitat disturbance and the establishment and spread of alien species discussed above has also been hypothesized to be important for some invasive alien coccinellids, which have rapidly become dominant in heavily managed agricultural habitats (Elliott *et al.*, 1996; Colunga-García & Gage, 1998). However, most detailed studies of coccinellid invasion to date have focused on relatively disturbed agricultural habitats with less information available from more stable natural or semi-natural systems (Snyder & Evans, 2006; Harmon *et al.*, 2007; Finlayson *et al.*, 2008; Evans *et al.*, 2011b). This has hampered a more general understanding of the extent to which human management and associated disturbance might facilitate invasion by alien species.

Broad and flexible habitat use and the ability to use human-created habitats, such as crops, are also both thought to promote establishment and spread of alien coccinellids (Evans *et al.*, 2011b). Highly successful invasives, such as *Coccinella septempunctata* L. (considered invasive in North America) and *Harmonia axyridis* (Pallas) (invasive in North America and Europe, and recently found in Chile; Grez *et al.*, 2010a), are known to occur in many natural and semi-natural habitats, indicating a high degree of habitat flexibility. However, they tend to be most abundant in agricultural and urban habitats (Evans *et al.*, 2011b). This suggests that while invasive coccinellids can use many different habitat types, their abundance in a landscape may be largely driven by a few dominant and highly suitable human-created habitats.

We used a large-scale cross-habitat sampling approach to evaluate whether there is evidence to suggest that alien coccinellids are differentially benefited by habitat disturbance and/or exhibit higher flexibility in their habitat use compared with native species. In particular, we addressed two specific questions: (1) Do alien species benefit more than native species from human-disturbed habitats? (2) Are alien species more generalized in their habitat use than natives within the invaded range or can their abundance patterns be explained by specialization on the most common habitats?

METHODS

Study system, landscapes and organisms

The study was carried out in two regions near Santiago, Chile, in two consecutive growing seasons. During the

2010–2011 growing season, sampling was carried out in Pirque (33°38'S; 70°33'W), in an area of *c.* 120 km², located 23 km south-east of Santiago, while in 2011–2012, sampling was carried out in Calera de Tango and surrounding districts (33°37'S; 70°46'W), in an area of *c.* 425 km², located 20 km south-west of Santiago (see Figure S1). These regions were separated by a mountain range and were *c.* 10 km apart. Both Pirque and Calera de Tango are composed of a variety of crops (on average less than 3 ha per field, see Table S1), including vineyards, grains, horticultural crops and alfalfa fields, separated from each other by various field boundary structures. To characterize the landcover types present within these regions, we selected 1000-m-radius non-overlapping landscapes, 10 in Pirque and 13 in Calera de Tango. Using GPS receivers, we collected 150 sampling points in Pirque and 254 in Calera de Tango to register the centre coordinates of all different landcover types. These data were used to calibrate and validate the patch delineation in all landscapes on screen using ArcGIS 9.3^{RM} at scale 1:2000, on a SPOT 5 image captured in 2010. Landcover was classified into 13 categories: annual crops, roads, riparian habitats (areas along banks of rivers with a mix of perennial and annual species), urban areas (high densities of houses and public buildings), semi-urban areas (low density rural residential properties), alfalfa fields, woodlands (small planted patches of trees, such as poplar and eucalyptus), orchards, vineyards, wetlands (area saturated with water), sclerophyllous matorral (native shrub land), abandoned fields (annual grasses and weeds) and hedgerows (linear arrangement of trees and shrubs, composed mainly of false acacia and poplar). We then used these data to calculate the area of each landcover type in each landscape, and with this, we estimated the relative abundance of each landcover type within each region.

Quantifying coccinellid densities across habitat types

Coccinellids were sampled in spring (September–October), summer (December–January) and autumn (March–April) in nine of the 13 landcover types present in both regions. The landcover types sampled included four agricultural habitats: alfalfa, wheat, vineyards and orchards (plums and walnuts); three semi-natural habitats: blackberry strips, eucalyptus woodlands and tree hedgerows; and two natural habitats: riparian and sclerophyllous matorral. These represent the dominant natural, semi-natural (anthropogenic unmanaged habitats) and agricultural landcover types in the landscape, or they are habitats known to be important for coccinellids (Gre \acute{z} *et al.*, 2010b). In Calera de Tango, riparian habitats were not sampled because they were very rare in this region. Five different patches of each habitat type (replicates) were sampled within each region. The median distance between sampled patches was 4.76 km, with a range of 0.37–14.55 km for Pirque, and 7.55 km, with a range of 0.70–20.95 km for Calera de Tango. Coccinellids were sampled in each season by placing five unbaited yellow sticky card traps (15 × 25 cm, two-faced) for 2 weeks in each patch.

Yellow sticky traps are commonly used for sampling coccinellids (Parajulee & Slosser, 2003; Stephens & Losey, 2004; Schmidt *et al.*, 2008; Gardiner *et al.*, 2009) and allowed us to sample all habitats in the same way, which could not be done with other techniques (e.g. sweep nets). Traps were placed towards the centre of each patch, 80 cm above ground, and separated by at least 10 m. In the case of hedgerows and blackberries (linear patches), traps were placed at least 1 m from the edge. All adult coccinellids were counted and identified to species (González, 2008), and the number per trap was averaged across all sampling dates. With these data, we estimated species abundance in each habitat type and the relative abundance of native and alien coccinellids. Voucher specimens were deposited in the collection of the Laboratory of Ecology of Fragmented Landscapes, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile.

Generating an index of habitat disturbance intensity

For each of the nine habitat types sampled, we generated two anthropogenic disturbance indices, with high numbers assigned to habitats with greater disturbance (Table 1). The first index considered the sum of the potential effects of: (1) harvesting (number of harvests per year: 0–7), (2) pesticide application (number of applications per year: 0–5), (3) establishment (natural/planted: 0/1), (4) perenniality (number of times a habitat turns over in a 20-year period: 0–7; for annual crops; we took into account the usual rotation with other crops in the area), and (5) dominance of alien vegetation (0: mostly native plant species; and 2: all alien plant species (Donoso, 1982). These values were assigned according to our own experience and expert opinion (G. Montenegro, R. Chorbadian, P. Universidad Católica de Chile, pers. comm.). The second index included the same variables, but they were standardized to a 0–7 scale, such that each factor received equal weighting (Table 1). Finally, we used the disturbance index to rank habitats by disturbance intensity (Table 1). The frequency of pesticide applications and harvesting has similarly been used by Jonsson *et al.* (2012) to generate an index of habitat disturbance.

Quantifying habitat specialization

The degree of habitat specialization for a given species was calculated as the coefficient of variation (CV = standard deviation/mean) in its densities across the different habitat types sampled in a given region/growing season following the approach of Julliard *et al.* (2006) and Devictor *et al.* (2008). This index is not biased by unequal representation of habitats within the sampled area or the number of habitat classes considered (Devictor *et al.*, 2008). We also calculated the Equitability ($J = -\sum(p_i \ln p_i)/\ln H$, where p_i is the proportion of individuals of a species in the habitat i in relation to the total individuals of that species in all habitats, and H is the total number of habitats) and habitat richness (S = the number of habitat types used by each species). Higher CV and/or lower J

Table 1 Estimated values for five disturbance variables in each habitat type: harvest frequency (number per year), pesticide applications (number per year), means of establishment (natural or planted), degree of perenniality (habitat turnover in a 20 year period) and the degree of dominance by alien vegetation (0: mostly native plant species; and 2: all alien plant species). The sum of the values across these disturbance variables generates a cumulative disturbance index. Values for index 1 are raw values, while values for index 2 (in brackets) are standardized to a common scale (1–7) such that each is weighted equally. Disturbance rank categorizes the disturbance index as a ranked variable. See text for a more detailed explanation

Habitat Type	Habitat	Harvest frequency	Pesticide application	Establishment	Perenniality	Dominance of alien vegetation	Disturbance index	Disturbance rank
Natural	Matorral	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1
	Riparian	0 (0)	0 (0)	0 (0)	0 (0)	1 (3.5)	1 (3.5)	2
Semi-natural	Eucalypt wood lot	0 (0)	0 (0)	1 (7)	0 (0)	2 (7)	3 (14.0)	3
	Hedgerow (trees)	0 (0)	0 (0)	1 (7)	0 (0)	2 (7)	3 (14.0)	3
	Blackberry	0 (0)	0 (0)	1 (7)	1 (1)	2 (7)	4 (15.0)	4
Cultivated	Vineyard	1 (1)	3 (4.2)	1 (7)	1 (1)	2 (7)	8 (20.2)	5
	Orchard	1 (1)	5 (7.0)	1 (7)	1 (1)	2 (7)	10 (23.0)	6
	Wheat	1 (1)	1 (1.4)	1 (7)	7 (7)	2 (7)	12 (23.4)	7
	Alfalfa	7 (7)	1 (1.4)	1 (7)	4 (4)	2 (7)	15 (26.4)	8

indicate that a given species is more specialized to certain habitat types. In contrast, a species with relatively even densities across habitats would be considered more generalized in its habitat use (Julliard *et al.*, 2006). *S* has been used as an index of habitat niche breadth in other invasion studies (Vázquez, 2006).

Statistical analyses

One-way ANOVAs were run to compare the abundance (log individuals/trap + 1) of each species across habitat types within each region. Means were separated by Tukey HSD post hoc tests.

To examine the relationship between habitat disturbance and the proportion of alien species, as well as habitat disturbance and the proportion of alien individuals in each region, we used generalized linear models in R (version 2.11.1: R Foundation for Statistical Computing, Vienna, Austria). For Calera de Tango, we did not include orchards in the analysis because very few individuals were captured within this habitat type (only 13 individuals total in the whole season), or riparian habitats because they were very scarce in the region and thus coccinellids were not sampled within this habitat type. Initial analyses indicated that disturbance rank had a better fit to the data than the disturbance indices, and thus, rank was used as the predictor variable in final models and figures reported here. Quasibinomial distributions were specified to account for over- and underdispersion in each model, respectively (Crawley, 2005).

To test whether the alien species exhibited greater habitat generalism than natives ($CV_{\text{aliens}} < CV_{\text{natives}}$; $J_{\text{aliens}} > J_{\text{natives}}$; $S_{\text{aliens}} > S_{\text{natives}}$), we ran one-tailed Mann–Whitney tests comparing the *CV*, *J* and *S* of the alien and native species within each region using Minitab® Statistical Software 16.0 (Minitab Inc., State College, PA, USA).

To test whether specialized alien species were more abundant in the more common habitat types in the landscape, we

ran Spearman rank correlations (Minitab 16.0) between the abundance of coccinellids and the total area of habitat types.

Comparative multispecies analyses of these sorts can be confounded by taxonomic relatedness among species. To address this issue in our data set (see Table S2), we calculated Moran's *I* index, in R, version 2.11.1, to test whether there was any clustering of our trait of interest, origin (alien versus native), at any taxonomic level: genus, tribe and subfamily (Lockwood *et al.*, 2002). We found no taxonomic autocorrelation in this trait at any taxonomic level ($I_{\text{genus}} = 0.28$, $P = 0.35$; $I_{\text{tribe}} = 0.04$, $P = 0.54$; $I_{\text{Subfamily}} = -0.09$, $P = 0.71$). Thus, there was no evidence for any systematic taxonomic bias in our data set.

RESULTS

In both Pirque and Calera de Tango, the cultivated habitats (vineyard, orchards, wheat and alfalfa) dominated the landscape, comprising 60% and 57% of the area, respectively, followed by the natural habitats (matorral and riparian) with 11.5% and 8.6% in each region. The semi-natural habitats (hedgerows, blackberries and eucalypt) made up only 5.5% and 6.1% of each region (Fig. 1, see Table S1). The only notable differences between the regions were that Calera de Tango had relatively more orchards and less wheat than Pirque and that in Calera de Tango riparian habitats were very scarce. The nine habitat types spanned a gradient in disturbance intensity, with the most disturbed habitat being crops, alfalfa and wheat, and the least disturbed native matorral and riparian habitats (Table 1).

Overall, we found 21 predatory coccinellid species, but some were very rare within a region (fewer than five individuals sampled in total); therefore, for the analyses only 16 species were included in Pirque and 15 species in Calera de Tango. In Pirque, eight species were natives and eight aliens, and 55% of the 4837 individuals sampled were natives. The

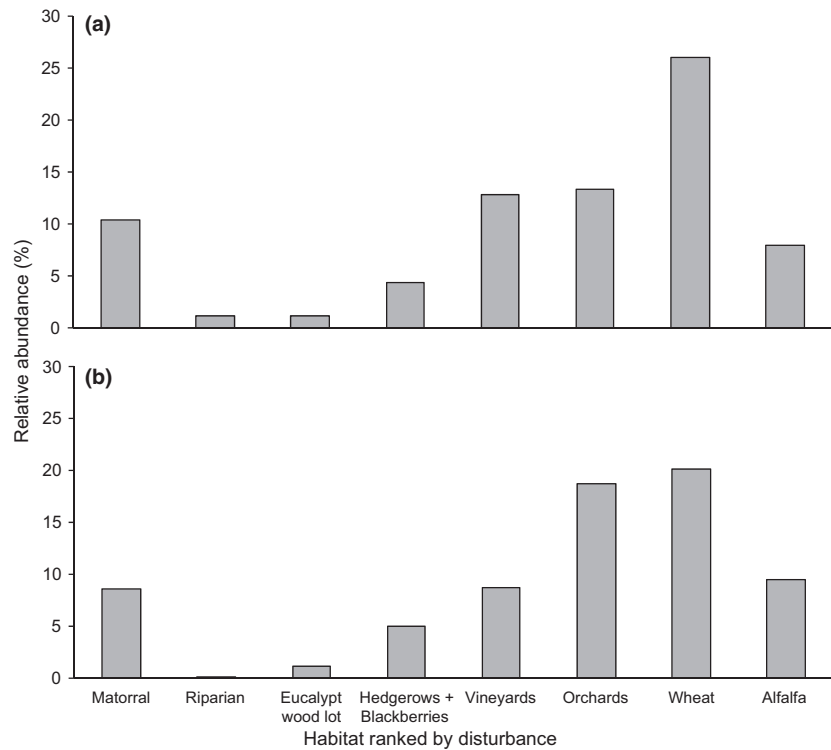


Figure 1 Relative abundance of the different habitats where coccinellids were sampled. (a) Pirque, (b) Calera de Tango. Habitat are ordered by disturbance rank. Hedgerows include blackberries because they were indistinguishable in the satellite images. Percentages are calculated over 3142 ha in Pirque and 4084 ha in Calera de Tango.

dominant species was the alien *Hippodamia variegata* (Goeze), representing 21.6% of all captures, followed by the natives *Scymnus bicolor* (Germain) (13.6%), *Eriopis connexa* (Germar) (8.5%) and *Cycloneda fulvipennis* (Mulsant) (8.0%). In Calera de Tango, nine species were natives and six aliens, but only 45% of the 1793 individuals sampled were natives. The dominant species in this region were the aliens *H. variegata* (33.5%) and *H. axyridis* (8.8%), and the natives *Heterodiomus marchali* (Brèthes) (17.6%) and *S. bicolor* (9.7%).

In Pirque, among alien species, seven of eight varied significantly in their abundances across habitat types (Fig. 3a, Table S3). In general, alien species were more abundant in the more-disturbed habitats. In particular, *H. axyridis* and *Olla v-nigrum* (Mulsant) were much more abundant in alfalfa than in all other habitat types. *Hippodamia convergens* (Guerin-Meneville) was more abundant in alfalfa, wheat and vineyards than in other habitats, and *H. variegata* exhibited a similar pattern, but was also equally abundant in riparian habitats. Only one alien species, *Clistothethus arcuatus* (Rossi), was more abundant in the native matorral habitat and was rarely found in disturbed human-created habitat types. Among native species, half varied significantly in their abundances across habitats (Fig. 3b, Table S3). Of those, *H. marchali* was more abundant in the less-disturbed habitat (matorral) than all other habitats. *Adalia angulifera* Mulsant was also most abundant in the matorral, with intermediate abundances in riparian habitats and orchards, while *S. bicolor* was ubiquitous across habitat types, but also most abundant in the matorral and least abundant in alfalfa. The only native species that exhibited significantly higher densities in the

most disturbed habitats was *E. connexa*, which peaked in abundance in wheat and alfalfa.

In Calera de Tango, among alien species, six varied significantly in their abundances across habitat types, and five of them were more abundant in the more-disturbed habitats, particularly in alfalfa (Fig. 3c, Table S3). Similar to Pirque, these species were *H. axyridis*, *H. convergens*, *H. variegata* and *O. v-nigrum*. In this region, *Adalia bipunctata* (L.) was also more abundant in alfalfa, while *C. arcuatus* was very rare. Among native species, all but *Hyperaspis sphaeridioides* (Mulsant) varied significantly in their abundances across habitats. Even though they were present in several habitats, most of them exhibited higher abundances in the less-disturbed habitats, with the exception of *E. connexa* that was more abundant in alfalfa (Fig. 3d, Table S3). Very few individuals were collected in orchards in this region.

Overall, the proportion of alien to native coccinellid individuals increased strongly and significantly across the gradient in habitat disturbance ($F_{1,43} = 49.24$, $P < 0.0001$, Fig. 2a for Pirque and $F_{1,32} = 223.41$, $P < 0.0001$, Fig. 2b for Calera de Tango), from an average low of *c.* 15% alien in the matorral to an average high of over 80% in alfalfa for Pirque and from less than 10% to over 90% in Calera de Tango. A similar, but less dramatic pattern was observed in the proportion of alien to native species, which again increased significantly with increasing disturbance rank across habitats ($F_{1,43} = 6.71$, $P = 0.013$, Fig. 2c for Pirque and $F_{1,32} = 19.56$, $P = 0.0001$, Fig. 2d for Calera de Tango). Similar results were found when models were run using the two disturbance indices (Table 1) for individuals and species ($P < 0.001$ in all cases).

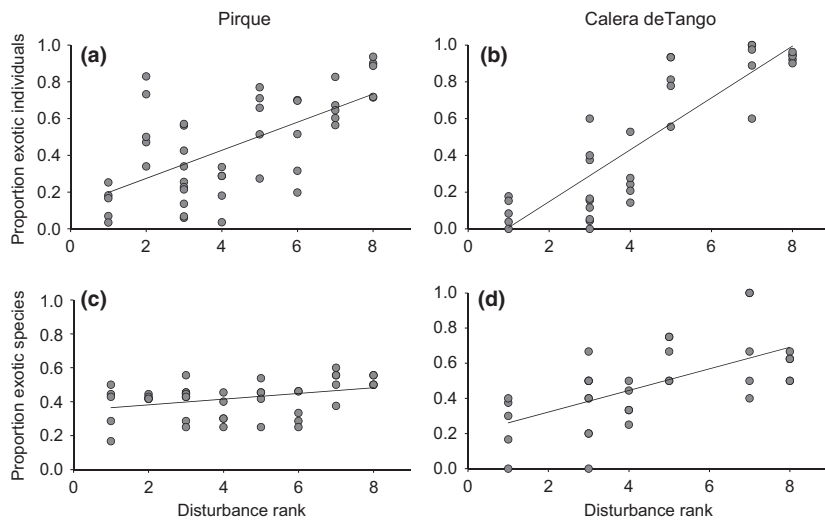


Figure 2 Proportion of alien to native individuals (a and b) and species (c and d) across the gradient in habitat disturbance, in Pirque and Calera de Tango.

Contrary to our predictions, alien species were not more generalized in their habitat use than natives in either region. In fact, although we found no significant differences in median CV and J for alien and native species ($P > 0.05$ for all, Table 2), the trend was in the opposite direction than expected in both Pirque and Calera de Tango. Habitat richness, S , was similar for natives and aliens coccinellids in Pirque, but in Calera de Tango, it was greater for aliens than natives (Table 2). None of indices of specialization (S , J and CV) were correlated with coccinellid species abundance ($P > 0.1$ in all cases), except for S in Calera de Tango, where they were positively correlated. In this case, differences found in S could have been driven by the low densities of natives. Four species were ‘specialized’ (i.e. significantly more abundant in a single habitat type than in all the others) in Pirque and six in Calera de Tango. For Pirque, these included one native, *H. marchali* in matorral, and three aliens, *H. axyridis* and *O. v-nigrum* in alfalfa and *C. arcuatus* in matorral. For Calera de Tango, the specialized species were the natives *E. connexa* in alfalfa and *H. funesta* in matorral, and the aliens *A. bipunctata*, *H. axyridis*, *H. convergens* and *H. variegata*, all in alfalfa (Fig. 3, Table S3).

For the three specialized alien coccinellid species in Pirque and the four in Calera de Tango, abundances across habitat types were not significantly correlated with the area of the habitat types in the landscape ($P > 0.75$ for all species). The habitat types in which these alien species showed the highest abundances in Pirque were matorral and alfalfa, ranked 4th or 5th in terms of area, and in Calera de Tango, it was alfalfa, which ranked 3rd in terms of area in this region (cf. Figs 1 and 3).

DISCUSSION

Overall, our research indicates that alien coccinellid species clearly benefit from habitat disturbance, with both the proportion of alien to native individuals and the proportion of alien to native species increasing significantly with increasing

disturbance across habitat types. In contrast, we found no evidence that alien species are more generalized in their habitat use than native species or that they are specialized on common habitats. The results suggest that successful alien species may be ‘disturbance specialists’ that thrive within human-modified habitats and landscapes.

Alien coccinellids differentially benefit from disturbed habitats

A widely recognized pattern within the ecological literature is that alien species tend to benefit from habitat disturbance (Elton, 1958; Lozon & MacIsaac, 1997; D’Antonio *et al.*, 1999). Most detailed studies of coccinellid invasion have focused on relatively disturbed agricultural habitats with little data available from more natural systems (Snyder & Evans, 2006; Harmon *et al.*, 2007; Finlayson *et al.*, 2008; Evans *et al.*, 2011b). Thus, the extent to which human management and associated disturbance might facilitate invasion by alien species remains poorly understood. In this study, we addressed this knowledge gap by documenting the use of different habitat types by native and alien coccinellid species across a gradient of disturbance intensity in two regions, Pirque and Calera de Tango, and under quite different abundance scenarios.

Our results provide strong support for the hypothesis that more-disturbed habitats are differentially invaded. The percentage of individuals that were alien increased more than fivefold across the gradient in habitat disturbance, from an average low of about 15% in the least disturbed habitat (matorral) to a high of over 80% in the most disturbed habitat (alfalfa) for Pirque and from less than 10% to over 90% in Calera de Tango. The strong preference of some abundant alien coccinellids, such as *H. variegata* and *H. axyridis*, for disturbed agricultural habitats such as alfalfa and wheat may have partly contributed to this pattern. However, the proportion of species that were alien also increased significantly with habitat disturbance, suggesting a more general

Table 2 Coefficient of variance (CV), equitability (J) and habitat richness (S) for alien and native coccinellid species, and Wilcoxon test for Pirque (nine habitats sampled) and Calera de Tango (eight habitats sampled)

Species	Pirque			Calera de Tango		
	CV	J	S	CV	J	S
Aliens						
<i>Adalia bipunctata</i> (L.)	1.16	0.78	8	1.86	0.66	4
<i>Clitostethus arcuatus</i> (Rossi)	2.12	0.59	6	–	–	–
<i>Harmonia axyridis</i> (Pallas)	2.12	0.50	8	1.93	0.52	8
<i>Hippodamia convergens</i> (Guerin-Meneville)	1.39	0.71	8	2.55	0.32	3
<i>Hippodamia variegata</i> (Goeze)	0.68	0.90	9	1.88	0.54	8
<i>Olla v-nigrum</i> (Mulsant)	2.04	0.73	5	1.79	0.81	3
<i>Parastethorus histrio</i>	0.71	0.93	8	–	–	–
Chauzeau						
<i>Scymnus loewii</i> Mulsant	1.13	0.80	9	1.43	0.64	8
Natives						
<i>Adalia angulifera</i>	1.01	0.84	9	1.93	0.66	4
Mulsant						
<i>Adalia deficiens</i>	0.77	0.89	9	1.47	0.70	6
Mulsant						
<i>Cycloneda fulvipennis</i> (Mulsant)	0.78	0.87	9	–	–	–
<i>Cycloneda sanguinea</i> (L.)	0.97	0.85	8	1.62	0.61	6
<i>Eriopis connexa</i> (Germar)	1.01	0.84	8	1.75	0.75	4
<i>Heterodimus marchali</i> (Brèthes)	1.85	0.60	8	1.94	0.47	6
<i>Hyperaspis sphaeridioides</i> (Mulsant)	0.58	0.93	9	1.65	0.85	3
<i>Hyperaspis funesta</i> (Germain)	–	–	–	1.81	0.69	4
<i>Hyperaspis nana</i> Mader	–	–	–	2.32	0.66	2
<i>Scymnus bicolor</i> (Germain)	0.67	0.94	8	1.42	0.72	6
Median aliens	1.27	0.76	8.0	1.87	0.59	6.0
Median natives	0.87	0.86	8.5	1.75	0.69	4.0
Mann–Whitney W	85.0	52.5	56.0	54.5	36.0	54.5
	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P < 0.05$

pattern. Furthermore, especially in Calera de Tango, the increase in proportion alien individuals and species was quite continuous, with habitat types with intermediate disturbance showing degrees of invasion intermediate between the two extremes. These patterns for individuals and species were also found when using the two alternative disturbance indexes, giving even stronger support to this hypothesis.

Habitat disturbance may enhance the dominance of alien species over natives directly or by modifying their ecological interactions (Didham *et al.*, 2007). There is evidence that alien coccinellid species can negatively affect natives through competition for resources or intraguild predation (Snyder & Evans, 2006). Thus, if native habitats are more resistant to invasion by alien species, they could provide important refuges for native coccinellid species (Evans, 2004). In our study, the dominant alien, *H. variegata*, which accounted for 21% and 33% of all captures in Pirque and Calera de Tango,

respectively, had very low abundances in the natural matorral habitat. However, despite a strong and significant overall pattern of increasing alien dominance in more-disturbed agricultural habitats, there were a number of individual exceptions. For example, we found that one alien species, *C. arcuatus*, had higher relative abundances in the less-disturbed matorral habitat in Pirque. At the same time, one native species, *E. connexa*, was most abundant in disturbed agricultural habitats and rarely occurred in more natural habitats such as matorral, in either region.

In contrast to our study and that of Evans (2004), which suggest that less-disturbed natural habitats are generally less invaded, Finlayson *et al.* (2008) found alien coccinellids to be widespread and abundant in both agricultural as well as natural habitats, while native species were relatively rare everywhere. Gardiner *et al.* (2009) found that native species within soybean fields tended to increase with landscape scale

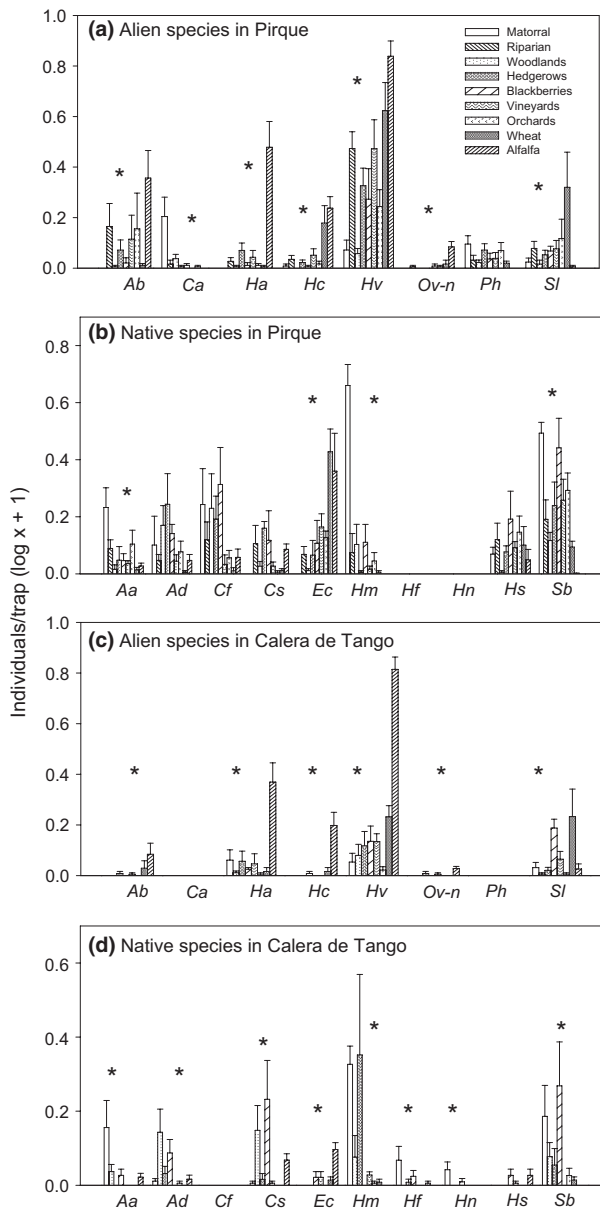


Figure 3 Coccinellid species abundance (mean + SE) in each habitat type: (a) aliens in Pirque, (b) natives in Pirque, (c) aliens in Calera de Tango and (d) natives in Calera de Tango. Habitats are ordered by disturbance rank along the x-axis, and species names are abbreviated by the first letter of genus and species. Results of ANOVAs and Tukey HSD tests are reported in Table S3.

abundance of natural grasslands, while alien species (primarily *H. axyridis*) increased with increasing forest cover (mostly native deciduous forest), suggesting that neither natives nor aliens benefited from disturbed agricultural habitats per se at landscape scales. Thus, the association between habitat disturbance and invasion may depend to some extent on the dominant alien species or system examined.

Our study was unique in that the richness of alien and native coccinellid species was relatively high compared with other studies and latitudes (e.g. Gardiner *et al.*, 2009), and we

sampled across replicate habitat types that spanned a gradient in disturbance. Thus, we were able to test for a more general relationship between habitat disturbance and coccinellid invasion, which to our knowledge has not been previously directly assessed. Our results reinforce conclusions from the broader invasion literature that habitat disturbance facilitates invasion by alien species and further indicate that this effect is not simply due to neutral probabilistic effects of habitat availability.

Alien coccinellids are not habitat generalists

Overall, we found no evidence that alien coccinellid species are more generalized in their habitat use than natives within our study system, as predicted by the niche breadth-invasion success hypothesis (Vázquez, 2006). In fact, the trend was in the opposite direction, with native species tending to be more generalized in their habitat use (lower CV and higher J) than aliens and with fewer native species specialized in one habitat type (one native versus three alien species in Pirque and two natives versus four aliens in Calera de Tango exhibited significantly higher densities in a single habitat type). Although sample sizes were quite low for some species in some years, this is unlikely to have biased our conclusions, given that there was generally no significant relationship between number of individuals sampled and our generality indices, and species with low abundances were present for both native and alien categories. In general, our findings re-enforce results from studies of invasive alien coccinellids, such as *C. septempunctata* and *H. axyridis*, which show that although these species can use many natural and semi-natural habitats, indicating a degree of habitat flexibility, they tend to thrive in more-disturbed agricultural and urban habitats (Hesler & Kieckhefer, 2008; Evans *et al.*, 2011b).

In a review of studies examining the niche breadth-invasion success hypothesis, Vázquez (2006) found only one study comparing the breadth of habitat use by native and alien species. In this study of plant species in Hawaii, Kitayama & Mueller-Dombois (1995) found that the ecological range of native species was generally greater than that of alien species, a pattern consistent with our results. However, studies comparing niche breadth in the native range of successful versus failed invaders or comparing the niche breadth of invaders in their native versus introduced ranges have found evidence for a positive relationship between niche breadth and invasion success across a variety of taxa (Vázquez, 2006). A number of factors may underlie the lack of a positive relationship observed in our study. First, we cannot rule out the possibility that highly specialized native species may have already gone extinct within this assemblage in response to human-mediated environmental changes, which might increase the apparent ‘generalism’ of the native assemblage. Indeed, declines in specialist species, in response to habitat and climate changes, have been observed across many taxa worldwide (Clavel *et al.*, 2011). Second, the potential habitat breadth of recently arrived alien species may be underestimated in a system if they have not yet reached their distributional equilibrium (Kitayama & Mueller-

Dombois, 1995). Some of the more recently introduced coccinellids have been in Chile for a relatively short time (e.g. natural populations of *H. axyridis* were first recorded in 2008; Grez *et al.*, 2010a). Thus, habitat use disequilibrium may play a role. However, this seems unlikely given the presence of all habitat types within relatively close proximity to one another in the invaded range, the relatively high dispersal abilities of these insects and reports of habitat use from other regions (Hesler & Kieckhefer, 2008; Evans *et al.*, 2011b). Nevertheless, to really understand the long-term pattern for this particular species, further years of sampling would be needed.

Habitat specialists may be successful invaders if they are specialized on widespread or abundant habitat types, and this can obscure the expected relationship between habitat generalism and invasion success (Vázquez, 2006). However, in our study, relative abundance across habitat types was not significantly correlated with the area of that habitat type in the landscape for any of the more specialized species examined. In fact, the most abundant habitat (wheat) was preferentially used by only one alien species (*H. convergens*) and only in one of the regions. The other abundant habitats, such as orchards and vineyards, had no species specialized on them. Therefore, the relative commonness of habitat types in our system does not appear to determine the relative success of alien coccinellid species.

CONCLUSION

The worldwide trend towards simplification of agricultural landscapes, caused by planting extensive annual crops and eliminating edges of less-disturbed natural or semi-natural habitats, can alter the structure of the guild of natural enemies, favouring alien species over natives, as shown in this study. This, in turn, could result in a reduction in biological control services due to the loss of species with different functional roles in the agroecosystems (Didham *et al.*, 2007; Tylianakis *et al.*, 2008; Gardiner *et al.*, 2009). The ultimate effects of shifts in the balance between alien and native coccinellids on biological control services in our system remain to be investigated and will depend in part on the relative functional efficiency of native compared with alien species and the extent to which communities exhibit density compensation following invasion (Rand & Louda, 2012). Either way, our results strongly suggest that the adoption of less-disturbed agricultural systems and practices, as well the conservation of non-productive habitats, within agricultural landscape mosaics, could help to promote the regional conservation of native coccinellid species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Sampling locations within both regions.

Table S1 Metrics for landcover types.

Table S2 List of coccinellid species.

Table S3 Results of ANOVAs.

BIOSKETCH

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