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ORIGINAL CONTRIBUTION

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Potential spatial interaction of the invasive species *Harmonia axyridis* (Pallas) with native and endemic coccinellids

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Abstract

Biological invasions represent a serious menace to local species assemblages, mainly due to interspecific relationships such as competition and predation. One important invasive species worldwide is *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), which has invaded many regions of the world, threatening the native and endemic coccinellid assemblages due to negative interspecific interactions. These interactions have been widely studied at a local scale, but have been less studied at regional scales. Our aim was to estimate and analyse the potential spatial interaction associated with the co-occurrence of *H. axyridis* with native and endemic species in Chile, considering bioclimatic and land cover variables. First, we created species distribution models (SDM) for *H. axyridis*, native and endemic coccinellids and six representative coccinellid species using maximum entropy technique. Then, we overlapped each SDM with land cover types to estimate the bioclimatic suitability within each land cover type. Finally, we identified the co-occurrences of organisms according to the SDM and the land cover types, estimating in what land covers *H. axyridis* and the other coccinellids are more likely to co-occur. Our results show that the suitable area for *H. axyridis* occurs from 30° to 42°S in Chile, while for native and endemic species this area is greater. The six selected species are mainly concentrated in central Chile, but differ in their potential suitable areas; *Adalia angulifera* Mulsant and *Scymnus bicolor* (Germain) have the largest range, and *Mimoscymnus macula* (Germain) has the most restricted one. The highest level of potential spatial interactions with *H. axyridis* occurs in central Chile, specifically in croplands and scrublands, and the lowest in primary native forest for all the species. Our results provide a spatially explicit baseline for coccinellid conservation and management of this invasive species.

KEYWORDS
bioclimatic suitability, biological invasions, harlequin ladybird, native and endemic coccinellids, potential spatial interaction, species distribution models

1 | INTRODUCTION

Biological invasions are of fundamental concern in conservation biology (Manchester & Bullock, 2000). The accidental or intentional introduction of species may generate many adverse effects on the native and endemic biota; invasive species interaction has been associated with predation, competition, parasitism and the arrival of new pathogens, among others (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016; Lymbery, Morine, Kanani, Beatty, & Morgan, 2014; Manchester & Bullock, 2000; Vilcinskas, 2015). These interactions among native and invasive species may be inferred from the estimation of the geographic co-occurrences (simultaneous occurrence of organisms in a determined space) of the interacting organisms. However, it is necessary to consider that effective interactions may be determined by other factors such as biotic interactions, dispersal ability (accessibility), site habitat preferences and scale issues (Araújo & Rozenfeld, 2014; Barve et al., 2011; Soberón, 2007; Soberón & Nakamura, 2009). The realized niche and potential niche of invasive species are likely to be similar in colonized zones, because these species are scarcely limited by biotic interaction due to their generalist behaviour, and also can spread to all the suitable areas due to the unstable state of recent biological invasions (Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012; Mestre et al., 2013). Species distribution models (SDM) (Elith, 2016; Elith & Leathwick, 2009; Elith et al., 2011) allow estimation of the ecological or environmental niche hypervolume of an organism based on its specific abiotic requirements, projecting them onto geographic space through the principle of niche–biotope duality (Colwell & Rangel, 2009; Hirzel & Le Lay, 2008; Hutchinson, 1957). SDM have been widely used for biological conservation purposes, to guide wildlife monitoring and management (Elith, Kearney, & Phillips, 2010; Pyke, Andelman, & Midgley, 2005; Zhang et al., 2012). Recently, SDM have been applied to study complex ecological dynamics, such as the effects of climate change on species range, biological invasions and disease vector dynamics (Alaniz, Bacigalupo, & Cattan, 2017; Elith et al., 2010; Porfirio et al., 2014). SDM allow identification of zones where the niche requirements of different species match or overlap and therefore where spatial interactions could develop if the species manage to access these sites and the biotic conditions are favourable (Barve et al., 2011; Soberón & Nakamura, 2009). Previous studies have identified niche similarities using ENMtools or co-occurrence in binary models; however, no model has determined the spatial interaction considering levels of expected interactions in a spatially explicit way applied to invasive species (Pellissier et al., 2010; Polce et al., 2013; Silva et al., 2014; Warren, Glor, & Turelli, 2010).

The invasive species *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), native to Asia, is a generalist predator that was introduced to many countries in North America, Europe and South America for the biological control of aphids in crops, but then spread accidentally to several other regions in these and other continents. Now, it is distributed worldwide (Camacho-Cervantes, Ortega-Iturriaga, & del-Val, 2017; Roy et al., 2016). The introduction of this insect has caused negative impacts because it affects humans by overwintering inside houses and other buildings, causing cosmetic damage and allergic reactions by bites, and also causes problems to agriculture by damaging soft fruits such as grapes, thus potentially affecting the wine industry (Brown et al., 2011; Grez, Zaviezo, Gonzalez, & Rothman, 2010; Koch & Galvan, 2008; Linder, Lorenzini, & Kehrli, 2009). But the greatest concern relates to its negative impact on native coccinellids, through competition for prey or space or intraguild predation of eggs, larvae and pupae, among other causes (Brown & Roy, 2017; Brown et al., 2011; Roy et al., 2012). In fact, in USA, Europe and Chile, local native coccinellid populations have declined after the arrival and spread of *H. axyridis* (Bahlai, Colunga-Garcia, Gage, & Landis, 2015; Brown et al., 2011; Grez, Zaviezo, Roy, Brown, & Bizama, 2016; Losey et al., 2014; Roy et al., 2012, 2016).

Harmonia axyridis was first introduced to Chile intentionally in 1998 from France for biological control of aphids. Then, in 2003, new populations arrived and probably experienced a latent period until 2010, when populations started to be very abundant in central Chile (Grez et al., 2010; Lombaert et al., 2014). Now, it is widely and continuously distributed along 1283 km in the country (Grez et al., 2016), from 29° to 41°S approximately.

A total of 115 native and alien coccinellid species have been reported in Chile (González, 2014), with ~50% being endemic to the country and ~35% native to southern South America. The biogeography of this family in Chile is poorly known; however, coccinellids have patterns of endemism and richness similar to other organisms (e.g., plants), concentrating the highest values in the central part of the country (González, 2014; Samaniego & Marquet, 2009; Scherson, Albornoz, Moreira-Muñoz, & Urbina-Casanova, 2014; Segovia, Hinojosa, Pérez, & Hawkins, 2013). These distribution patterns suggest that, in central Chile, *H. axyridis* should frequently co-occur with native and endemic coccinellids, with high level of interaction. Nevertheless, these interactions may be modulated by the differential use by *H. axyridis* and endemic and native species of land cover types present in an area. It has been reported that in Chile *H. axyridis* is more abundant in ornamental, urban and agricultural land covers, but more recently it has also invaded natural habitats such as native scrubland. In contrast, most native species are associated with more natural habitats, although some native species also thrive in disturbed habitats like crops (Grez, Rand, Zaviezo, & Castillo-Serey, 2013, Grez et al., 2016).

Species distribution models (SDM) have been used to identify the areas in different continents and countries, including South America, where *H. axyridis* may invade successfully (Bidinger, Lotters, Rodder, & Veith, 2012; Poutsma, Loomans, Aukema, & Heijerman, 2008; Veran et al., 2016), but these models have not been used to assess its potential spatial interaction with other species in areas where it has been already introduced and has invaded. In this study, we propose an approach to estimate spatial interactions between invasive and native species using SDM. Specifically, through this approach, we studied the spatial interactions between *H. axyridis* and native and endemic coccinellids in Chile. For this, we first generated SDM for *H. axyridis*, native and endemic coccinellids and for six coccinellid species, and then, we identified and analysed the sites of co-occurrence of organisms according to bioclimatic suitability and land cover types. We expected that: (i) because *H. axyridis* initially colonized central Chile, and given that most native and endemic species also inhabit this area, this would be the area with the highest level of spatial interactions; (ii) even though *H. axyridis* in Chile prefers croplands, and native and endemic coccinellids are more associated with natural land cover, there will be some land cover types where they will have high levels of potential interaction.

2 | MATERIALS AND METHODS

We aimed to estimate the potential co-occurrence or potential spatial interaction of *H. axyridis* with native and endemic coccinellids as

TABLE 1 Statistical parameters for each species distribution model

Model	Initial occurrences	Occurrences after rarefy (used in the model)	AUC	SD	Number of variables	Contribution of variable 1 (%)	Contribution of variable 2 (%)	Contribution of variable 3 (%)	Contribution of the three most important variables
Harmonia axyridis	2715	783	0.951	±0.015	6	29.6 (BIO8)	24.8 (BIO9)	22.3 (BIO19)	76.7
Natives (N)	721	667	0.938	±0.033	9	24.0 (BIO18)	20.7 (BIO19)	20.0 (BIO5)	64.7
Endemics (E)	600	423	0.949	±0.049	6	32.4 (BIO19)	26.9 (BIO15)	18.4 (BIO 8)	77.7
Adalia deficiens (N)	106	76	0.977	±0.001	5	42.9 (BIO19)	29.0 (BIO 18)	23.2 (BIO 8)	75.1
Cycloneda eryngii (N)	44	38	0.988	±0.003	6	51.4 (BIO18)	21.2 (BIO19)	13.6 (BIO15)	86.2
Adalia angulifera (N)	72	61	0.973	±0.004	5	29.2 (BIO8)	29.0 (BIO5)	21.0 (BIO19)	79.2
Psyllobora picta (E)	45	38	0.989	±0.001	5	45.5 (BIO19)	35.3 (BIO18)	7.4 (BIO 5)	88.2
Mimoscymnus macula (E)	52	38	0.993	±0.001	6	53.4 (BIO19)	41.5 (BIO18)	4.2 (BIO6)	99.1
Scymnus bicolor (E)	47	43	0.983	±0.002	5	55.0 (BIO18)	22.8 (BIO9)	15.6 (BIO8)	93.4

groups and with six individual species of coccinellids. We considered native coccinellids as the species present both in Chile and in other countries of South America, while endemic coccinellids were species present only in Chile, based on the distributions reported by González (2006, 2014). Thus, we considered them as two distinct groups in the analyses (native and endemic), generating one model for each group. For this, we assumed a generalization of the specific requirements of all included species (Bolnick et al., 2010; Pianka, 2011) (Figure S1). Additionally, we selected three native species and three endemics and estimated their potential spatial co-occurrence with *H. axyridis*. These species were selected considering data availability (enough occurrences for modelling based on van Proosdij, Sosef, Wieringa, & Raes, 2016) and habitat similar to *H. axyridis*: the natives *Adalia deficiens* Mulsant, *Cycloneda eryngii* (Mulsant) and *Adalia angulifera* Mulsant and the endemics *Psyllobora picta* (Germain), *Mimoscymnus macula* (Germain) and *Scymnus bicolor* (Germain).

2.1 | Spatial distribution of organisms

2.1.1 | Occurrences dataset

Occurrences of *H. axyridis* were taken from our website of citizen science (www.chinita-arlequin.uchile.cl) and from government data of the Chilean Phytosanitary Service (SAG), with a total of 2715 records. The occurrences of native and endemic coccinellids were compiled from 17 entomological collections distributed throughout Chile, including 721 records for modelling natives and 600 for endemics. The occurrences for the selected species are in Tables 1, S1 and Figure S2.

2.1.2 | Environmental dataset

We used as predictor variables the 19 environmental variables of Pliscoff, Luebert, Hilger, and Guisan (2014) at 2.5 arc minutes of spatial resolution. This is a regional bioclimatic model more accurate than WorldClim that integrates a greater number of climate stations for Chile, demonstrating good performance for modelling species in the country by reducing the uncertainties in background point generation for species distributed in Chile (Pliscoff et al., 2014). The layers of Pliscoff et al. (2014) model correspond to tiles 33 and 43 of WorldClim. We decided to use only bioclimatic variables in the modelling process because at regional scale the distribution of organisms is highly explained by bioclimatic factors (Pearson & Dawson, 2003). Also, considering that insects are ectotherms, they are highly influenced by climatic and environmental factors (Paaijmans et al., 2013).

Land cover types were not included in the modelling process because in Chile land covers have changed frequently through time and space in the last 50 years (Miranda, Altamirano, Cayuela, Lara, & González, 2017), and thus, the land cover at the time of collection might be different than the current one. Additionally, some types of land covers can have disproportionally high or low number of occurrences due to sampling efforts, which could generate biases in the model outcomes.

2.1.3 | Model parametrization

Species distribution models for *H. axyridis*, native and endemic coccinellids and the six selected species were generated using the maximum entropy technique with MaxEnt V3.3.3k (Phillips, Anderson, & Schapire, 2006). The process for developing each model was as follows: first an exploratory model was generated using all bioclimatic variables (19), calculating the relative contribution (i.e., per cent contribution and permutation importance) of the bioclimatic variables in the model. We determined the normality of each variable using the Shapiro–Wilk test. Then, to avoid the statistical collinearity of variables, we performed a correlation analysis between pairs of bioclimatic variables, using a multiple correlation matrix—expressed in correlograms—using the absolute correlation coefficient (Bradley, 1985). The objective of this process was to select the predictor variables with higher importance and lower correlation index (less than ± 0.7), aiming to reduce the overfitting in the model (Figure S3). The spatial autocorrelation of occurrence points was reduced by applying a spatial rarefy function (Brown, 2014) which deletes the higher autocorrelated occurrences, maintaining the non-autocorrelated ones randomly (considering more than 5 km distance between each locality) (Phillips et al., 2009). The biases in recording effort were reduced by considering many entomological collections distributed along the whole country.

Then, we generated a final model in MaxEnt using a cross-validation technique for *H. axyridis* and the modelled species groups (natives and endemics), and bootstrap for the six selected species (due to the low number of occurrences). As parameters in MaxEnt, we used logistic output format, default auto features option on and 95% confidence interval in suitability estimation. The input data included only the selected bioclimatic variables from the exploratory model and the non-autocorrelated occurrence datasets. Cross-validation uses a proportion of the occurrence dataset to generate an independent validation of the model and another proportion to evaluate it (train and test sets). The MaxEnt outcome considers the specificity *vs.* sensitivity of the model prediction expressed by the area under the curve (AUC) of the receiver operating characteristic (ROC) as a measure of model quality. AUC compares true presences with pseudo-absences (based on background points) to estimate the accuracy of the model prediction in relation to a random model (Phillips et al., 2006; ¸ Elith et al., 2010, 2011). (Figure S4). We considered as a threshold to define suitability/unsuitability on the SDM the 10th percentile of suitability estimation from the MaxEnt outcome (from 0 to 1). Finally, we analysed the importance and patterns of bioclimatic variables to estimate their suitability for *H. axyridis* and the six selected species by the generation of response curves and the interpretation of spatial patterns of distribution of the predicted suitable areas.

2.2 | Estimating spatial interactions

We adapted the protocol proposed by Alaniz et al. (2017), which uses SDM to estimate the potential interaction between a mosquito species and human populations in a spatially explicit way. This method estimates the potential co-occurrence of different species by considering suitability predicted by an SDM. The method aims to identify the pixels where both organisms have high expected suitability and hence where the probability of spatial interaction increases.

Using a geographic information system (GIS), we reclassified the suitability of the SDM outcome of *H. axyridis*, natives and endemics and each of the six selected species to convert the continuous raster into discrete levels of suitability (null = 0; low = 1; medium = 2; high = 3) (Figure 1), following Alaniz et al. (2017). These levels were assigned by sorting the histogram of suitability prediction into four equal intervals. The null level corresponds to the probabilities under the 10th percentile MaxEnt prediction.

Then, we multiplied the discrete grids of suitability for the interacting organisms (e.g., *H. axyridis* with native coccinellids) using the raster calculator tool in GIS, obtaining a new grid with six levels of spatial interaction as a product of the multiplication process (null, very low, low, medium, high, very high, see Figure 1). With this information, we generated the corresponding maps of expected spatial interactions, considering the different levels of spatial interaction. Finally, we calculated the area of potential spatial interactions, by level, between coccinellids and *H. axyridis* and also the percentage of the suitable area of coccinellids where they may be interacting, at different levels, with *H. axyridis*.

2.3 | Characterization of spatial interaction areas according to land cover type

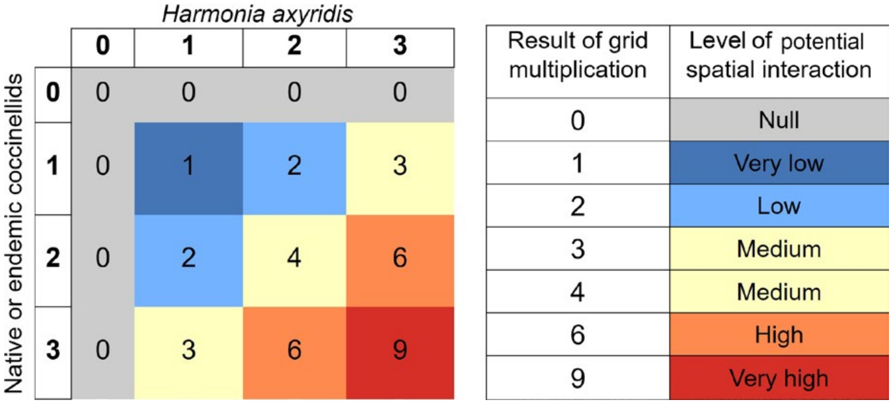
We overlapped the interaction maps with the reclassified land cover map of Zhao et al. (2016, Figure S5) to characterize the levels of potential spatial interactions between *H. axyridis* and natives, endemics and the six selected species, in relation to land cover classes. Finally, we calculated the percentage of contribution of each land cover class to each level of spatial interaction.

3 | RESULTS

3.1 | Spatial distribution of coccinellids

All the models reached an AUC above 0.9, which corresponds to a good fit of the SDM suitability prediction (see Figure S4).

The distribution of *H. axyridis* in Chile ranges from 30° to 42°S, mainly in the coastal area and central valley; bioclimatic suitability south of this range is extremely low. The northern limit of its distribution is the Atacama Desert. The species currently is distributed in an area of 244,142 km^2, representing 32.3% of continental Chile (Figure 2). The bioclimatic variables with the highest contribution for the *H. axyridis* model were the mean temperature of the wettest quarter (BIO8), the mean temperature of the driest quarter (BIO9) and the precipitation of the coldest quarter (BIO19) (Table 1). The bioclimatic suitability decreased with the increase in temperature in the wettest quarter, reaching a peak between 8 and 15°C, while the highest suitability occurred where temperatures of the driest quarter are greater than 15°C, but decreased drastically at 21°C. The suitability increased asymptotically with the precipitation of the coldest quarter, reaching a peak at 200 mm (Figure S6).



Native or endemic coccinellids \ *Harmonia axyridis*	0	1	2	3
0	0	0	0	0
1	0	1	2	3
2	0	2	4	6
3	0	3	6	9

Result of grid multiplication	Level of potential spatial interaction
0	Null
1	Very low
2	Low
3	Medium
4	Medium
6	High
9	Very high

FIGURE 1 Diagram of the raster multiplication and resulting potential spatial interaction levels. Left: Double entry matrix generating a linkage grid between the suitability of the invasive species *Harmonia axyridis* and the native or endemic coccinellids. The values 0–3 represent the four reclassified levels of each variable. Right: Categories level of potential spatial interaction (co-occurrence) according to the grid multiplication (modified from Alaniz et al., 2017) [Colour figure can be viewed at wileyonlinelibrary.com]

Native coccinellids are concentrated in central Chile from 27° to 43°S, but also with suitability in extreme zones in northern and southern Chile. Suitability decreased in the zone between 43° and 50°S and was very low in the Atacama Desert (Figure 2). The most important variables were the precipitation of the warmest quarter (BIO18), precipitation of coldest quarter (BIO19) and the maximum temperature of the warmest month (BIO5) (Table 1).

Endemic coccinellids are mainly distributed in the central zone of the country between 27° and 45°S, with a high bioclimatic suitability in the Andes and in the Coast Range. Another area with high suitability is the northern coastal zone between 19° and 22°S (Figures 2 and S7). The most important variables were the precipitation of the coldest quarter (BIO19), precipitation seasonality (BIO15) and the mean temperature of the wettest quarter (BIO8) (Table 1).

The six species of coccinellids are distributed mainly in the central zone of Chile, between 30° and 40°S. *Adalia angulifera* and *S. bicolor* have the widest distribution, with 375,024 km^2 and 302,235 km^2, respectively, while *M. macula* has the most restricted distribution, with 129,387 km^2. The most important variables in the model for the six species were precipitation of the coldest quarter (BIO19) and precipitation of the warmest quarter (BIO18) (Table 1; Figure S6). These species occur more associated with Mediterranean climate, with high suitability with low precipitation in the warmest quarter (summer) and high precipitation in the coldest quarter (winter), reaching a peak of suitability at 0 and 1,200–1,400 mm, respectively. However, additional variables are also important for *A. angulifera* and *S. bicolor*. There is high suitability for *A. angulifera* at low temperatures of the wettest quarter (BIO8) and high maximum temperatures of warmest month (BIO5), conditions that are present in the semiarid zone of northern Chile. For *S. bicolor*, there is high suitability at high mean temperatures of the driest quarter (BIO9) and low precipitation of the warmest quarter (BIO18), coinciding with conditions present in the coastal desert of northern Chile (Figures 3 and S2).

3.2 | Potential spatial interactions

The areas of potential spatial interactions due to co-occurrence between *H. axyridis* and native and endemic coccinellids are very similar. However, considering only the "very high" level of interaction, the area for endemics was twice as large as that for natives, while the area of "high" level of interactions was larger for natives than for endemics (Figures 3, 4a and Table S3). The lowest interaction levels were towards the south of the country, south of 40°S, as a consequence of the abrupt decrease in the suitability for *H. axyridis* in this zone (Figure 4a). The endemic coccinellids have a larger proportion of their suitable distribution area potentially co-occurring with *H. axyridis* compared to native coccinellids (55.8% and 37.1%, respectively, Figure 4b, Tables S3 and S4).

The spatial configuration of the different levels of potential spatial interaction with *H. axyridis* differs for the six selected species (Figure 3). The species with the largest area of co-occurrence with *H. axyridis* are *A. angulifera* and *A. deficiens*, with 264,279 and 237,128 km^2, respectively, while the species with the lowest area of co-occurrence is *C. eryngii*, with 89,964 km^2 (Figure 4a, Table S3). Nevertheless, considering the total suitable area for each species, those that have the largest proportion of their area co-occurring with *H. axyridis* are *P. picta* and *M. macula*, with 89.1% and 87.3%, respectively. The species with the lowest proportion of their suitable area co-occurring with *H. axyridis* are *C. eryngii* and *S. bicolor*, with 41.9% and 42.5%, respectively (Figure 4b). Among these species, *A. angulifera* is the one with the largest area, total and relative, of very high level of potential spatial interaction with *H. axyridis* (Figure 4a and b).

3.3 | Potential spatial interaction areas according to land cover type

For native and endemic coccinellids, very low levels of potential spatial interaction with *H. axyridis* occur in less disturbed cover types (i.e., secondary and primary forests and grasslands), while very high levels of potential interaction occur in scrublands and also in more disturbed

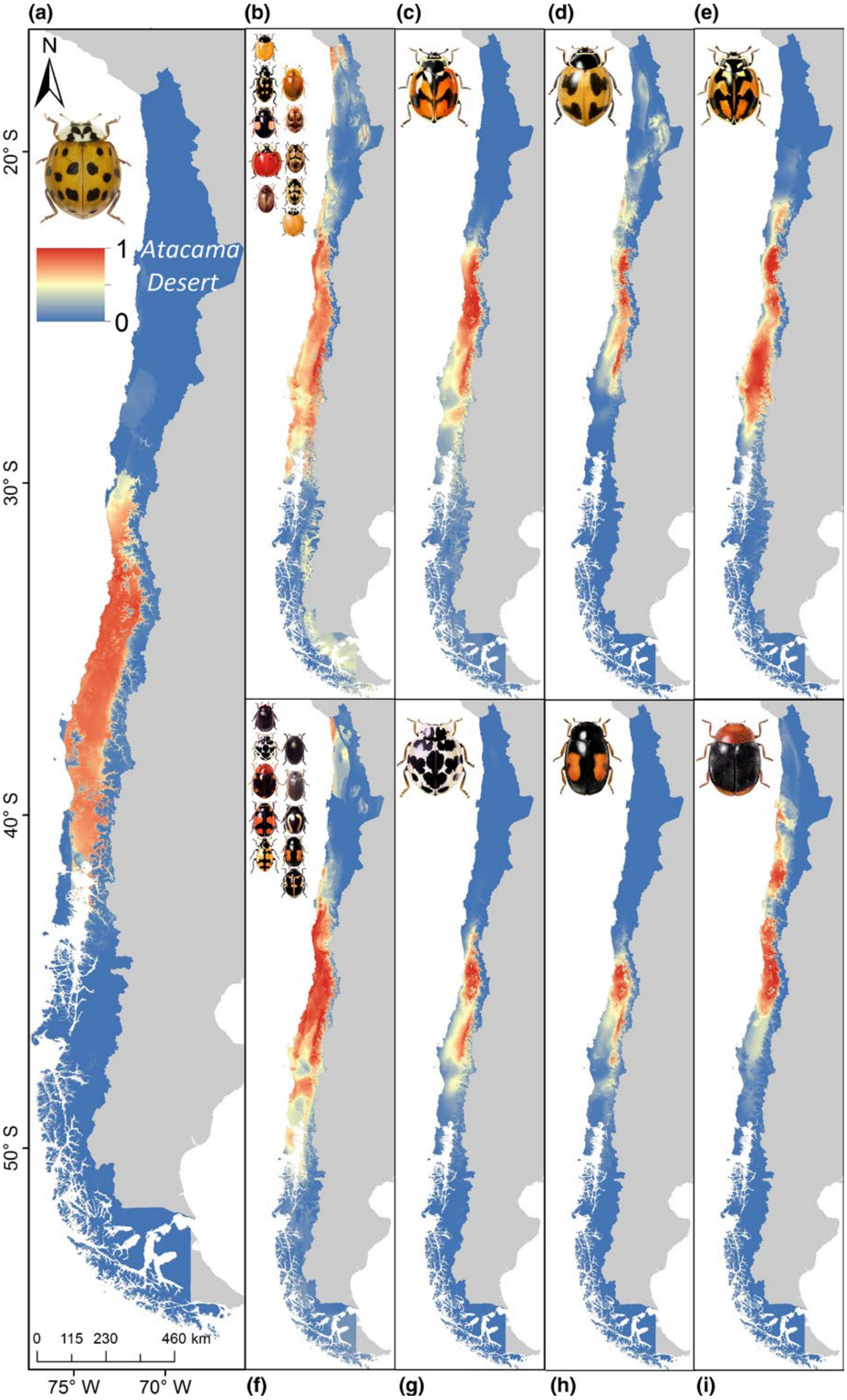


FIGURE 2 Species distribution models (SDM) of the coccinellids. Maps of bioclimatic suitability from 0 to 1 (blue to red colours) of (a) *Harmonia axyridis* (b) native coccinellids of Chile, (c) *Adalia deficiens*, (d) *Cycloneda eryngii*, (e) *Adalia angulifera*, (f) endemic coccinellids of Chile, (g) *Psyllobora picta*, (h) *Mimoscymnus macula* and (i) *Scymnus bicolor*. Illustrations of coccinellids of González (2006) [Colour figure can be viewed at wileyonlinelibrary.com]

cover types (i.e., croplands and exotic plantations) (Figure 5). *Adalia deficiens* and *A. angulifera* follow the same patterns as total natives and endemics, at both levels of potential spatial interaction. For the three endemic species and *C. eryngii*, scrubland is the cover type with a higher proportion of the area where both very low and very high levels of potential spatial interaction occur. For all species, croplands represent a cover type with a very high level of potential spatial interaction with *H. axyridis* (Figure 5). For the contribution of the land covers in the intermediate levels of potential spatial interactions, see Figure S8.

4 | DISCUSSION

4.1 | Distribution and interactions between *H. axyridis* and native and endemic coccinellids in Chile

One of the main issues associated with the invasion of *H. axyridis* is the negative effect on native coccinellids, due to antagonistic ecological interactions such as intraguild predation, exploitative competition and pathogen transmission (Roy et al., 2016). These

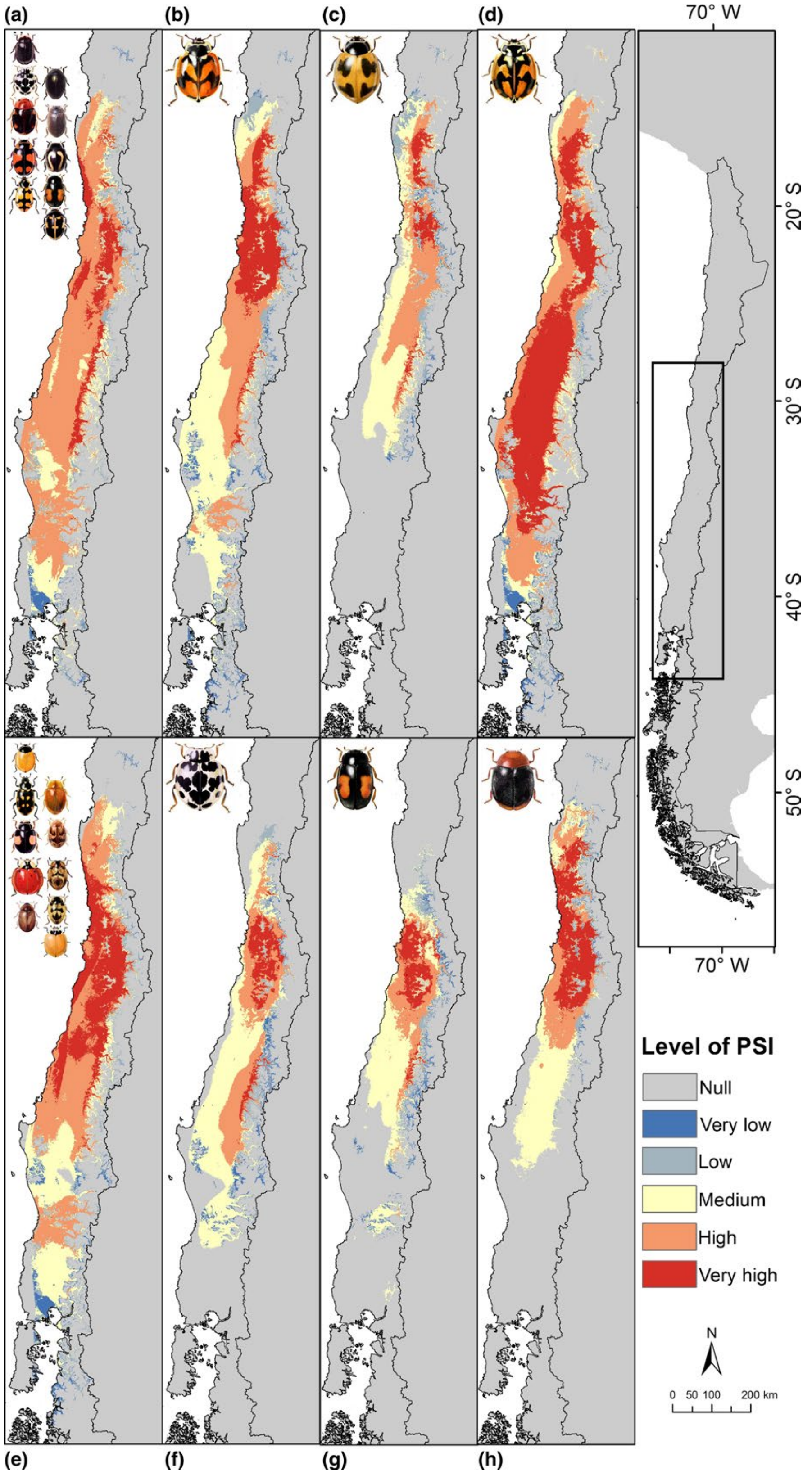


FIGURE 3 Maps of potential spatial interaction due to co-occurrence. Maps of co-occurrence by level between *Harmonia axyridis* and (a) native coccinellids of Chile, (b) *Adalia deficiens*, (c) *Cycloneda eryngii*, (d) *Adalia angulifera*, (e) endemic coccinellids of Chile, (f) *Psyllobora picta*, (g) *Mimoscymnus macula* and (h) *Scymnus bicolor*. Different colours represent the levels of potential spatial interactions according to according to Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

interactions require the co-occurrence of the interacting species in space, which will depend in part on the species sharing environmental requirements. Our results based on SDM show that effectively *H. axyridis* potentially may potentially co-occur with native and endemic coccinellids as groups in large areas of central Chile, as well as with several endemic and native coccinellid species where all these species are more frequent. Bioclimatic restrictions identified by the models would preclude *H. axyridis* colonization towards the

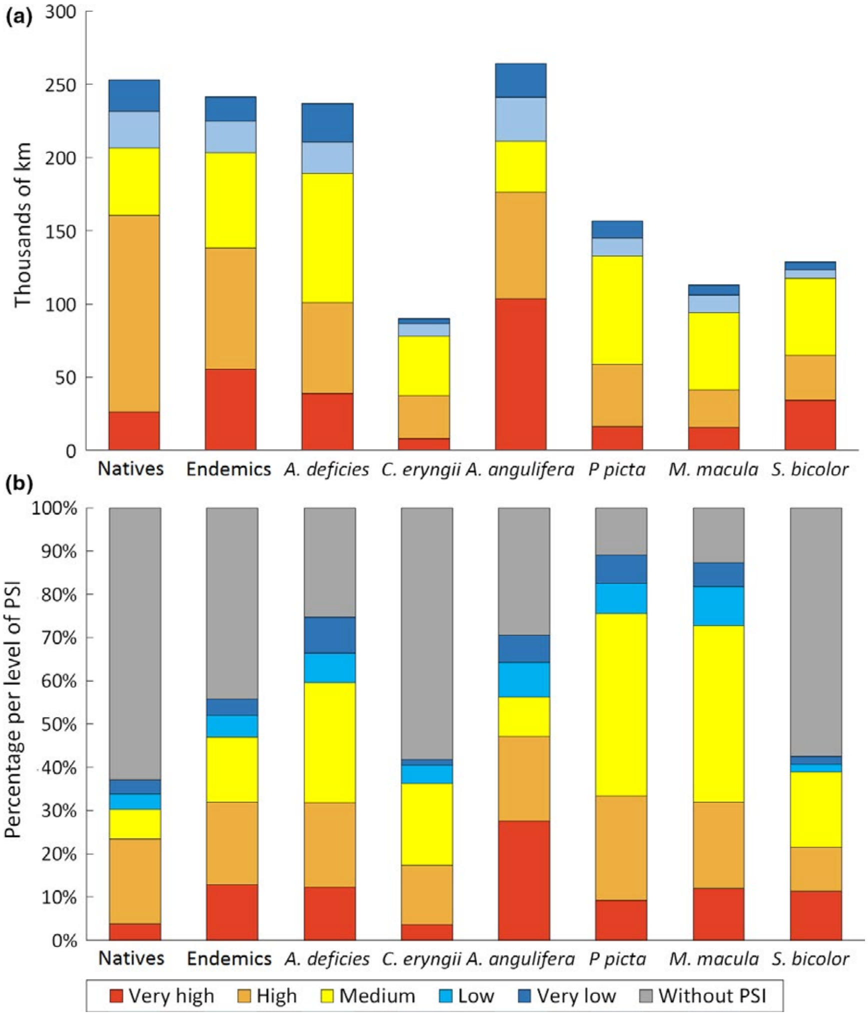


FIGURE 4 Area of potential co-occurrence by level and percentage of are exposed to co-occurrence with *Harmonia axyridis*. (a) Area of co-occurrence with *H. axyridis* by level of potential spatial interaction (PSI) in thousands of km^2 (b) percentage of area by level of potential spatial interaction, the zones in grey colour show the proportion of suitable area without co-occurrence with *H. axyridis* (total amounts in km^2 and percentages are detailed in Tables S3 and S4) [Colour figure can be viewed at wileyonlinelibrary.com]

north and south regions of Chile, keeping the invasion restricted to the central region of the country. These results agree with the current distribution of *H. axyridis* reported by Grez et al. (2016) between 30°S and 42°S, but not with the southern limit proposed by Bidinger et al. (2012), who predicted *H. axyridis* to be present up to 55°S. Furthermore, our results add some particular areas where this species could still invade and propose suitable areas where antagonistic interactions with native and endemic species may occur. Also, here we describe for the first time the current and potential distribution of several native and endemic coccinellid species, providing useful information for conservation and management strategies and to guide biodiversity surveys.

The distribution of *H. axyridis* and native and endemic coccinellids could be explained by biogeographic barriers, similar to other taxa in Chile. In the northern region of the country, around 25°S, the Atacama Desert, part of the arid diagonal of South America, is considered an important barrier for the dispersal and establishment of many taxa, such as butterflies, mammals and native trees (Samaniego & Marquet, 2009; Scherson et al., 2014; Segovia et al., 2013; Villagran & Hinojosa, 1997). In the south, from 40°S to 55°S, the presence of westerly winds determines the occurrence of extremely high precipitation events (>6,000 mm/year) which may hinder the dispersal and establishment of species (Segovia et al., 2013; Villagran & Hinojosa, 1997).

These geographical patterns for *H. axyridis* and native and endemic coccinellid species are supported by the most important bioclimatic variables estimated by SDM (BIO19 and BIO18), with high suitability of Mediterranean and temperate climates present in central Chile (Di Castri & Hajek, 1976). However, for some native and endemic coccinellids, there are also other suitable areas in the north and south of the country, which could represent a refuge from potentially negative interactions with *H. axyridis*.

Within central Chile, the areas of coccinellid co-occurrence, and therefore potential spatial interactions of natives and endemics with *H. axyridis*, are not spatially homogeneous, with certain places where levels of spatial interaction are higher and others very low (Figure 3), allowing us to identify where efforts and actions of control and management of this invasive species should be prioritized. Lumped species models show that the areas for the two highest levels of potential spatial interactions with *H. axyridis* include those areas predicted by the models at species levels. Therefore, our model lumping species provides a conservative baseline to identify where potential spatial co-occurrence of *H. axyridis* with these coccinellids may occur. The lumped model underestimates a large area

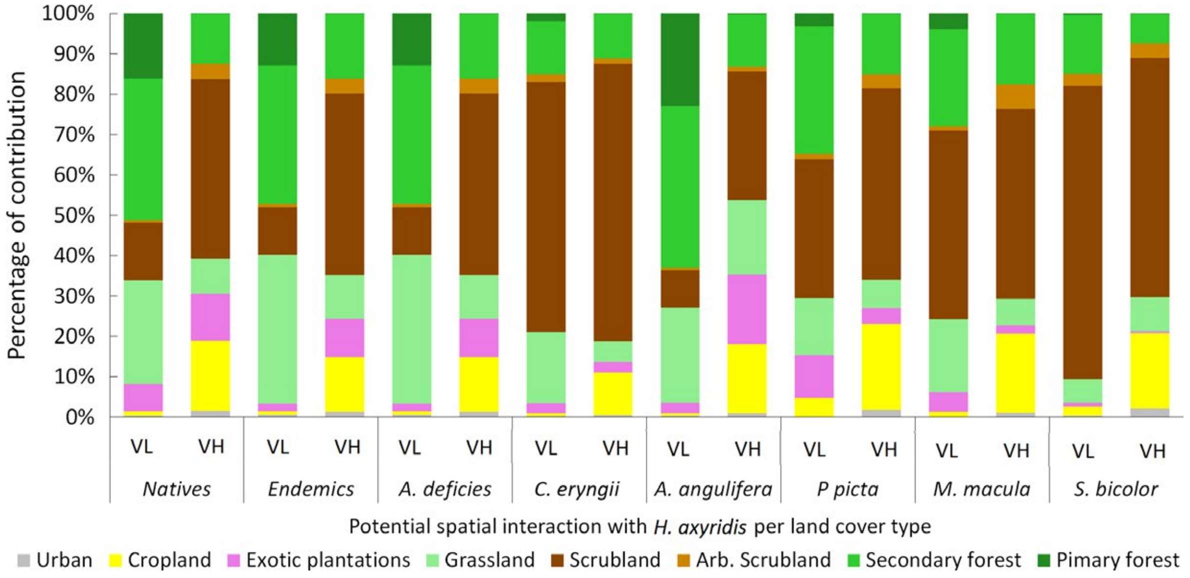


FIGURE 5 Percentage of contribution of land covers by categories of spatial interaction of *Harmonia axyridis*. Contribution of each land cover by level of potential spatial interaction (PSI) (Very Low = VL and Very High = VH) between *H. axyridis* with each modelled species or group [Colour figure can be viewed at wileyonlinelibrary.com]

where a very high level of potential spatial interactions may occur only for *A. angulifera*.

In relation to land covers, we found that those with very low levels of potential spatial interaction generally differ from those with very high levels of potential spatial interaction. As expected for this invasive species, this has been described to be associated more frequently with anthropogenic habitats (Grez et al., 2016; Roy et al., 2016). Our results predict that very high levels of potential interaction with native and endemic coccinellids in Chile would occur in more disturbed cover types (i.e., croplands and exotic plantations). More precisely, high and very high levels of potential spatial interactions may occur in 80% of the area occupied by croplands in Chile. Coccinellids are important natural enemies of crop pests, with native species playing an important role in biological control (Brown et al., 2011; Grez, Zaviezo, & Gardiner, 2014; Obrycki & Kring, 1998). The insurance hypothesis of biodiversity proposes that a higher enemy biodiversity strengthens herbivore suppression (Straub & Snyder, 2006, 2008). Hence, the co-occurrence of *H. axyridis* with native coccinellids in croplands in Chile may affect biological control negatively, because in many regions of the world its invasion has resulted in impoverishment of coccinellid assemblages and a reduction in the abundance of native species (Brown & Roy, 2017; Grez et al., 2014; Mizell, 2007). Interestingly, scrublands, a less disturbed cover type where native coccinellids dominate (Grez et al., 2014), represent the highest proportion of area where very high levels of potential spatial interactions with *H. axyridis* would occur, becoming a concern for the conservation of coccinellids in these habitats. Among the negative interactions that can arise in places where these species spatially co-occur, we could expect competition with the aphidophagous species such as *A. deficiens*, *C. eryngii* and *A. angulifera* (González, 2006, 2014), and asymmetric intraguild predation upon all native and endemic coccinellids in favour of *H. axyridis* (Gardiner & Landis, 2007; Roy et al., 2012, 2016).

4.2 | Potentialities and assumptions of the methodological approach

SDM can be useful to estimate the levels of ecological interactions such as predation, pollination or competition in a spatially explicit way based on co-occurrence of species. Most approaches have estimated ecological interactions only based on overlapping binary models (i.e., presence/absence) that identify the spatial co-occurrence of organisms (Broennimann et al., 2012; Pellissier et al., 2010; Polce et al., 2013; Silva et al., 2014), or by calculating a niche similitude index using ENMtools methodology, without a spatial prediction (Warren et al., 2010). Unlike niche overlap analyses, which are based in comparing the niches on an n-dimensional environmental space (Hutchinson niche) using statistical analysis (principal components analysis, Schoener's D index, multidimensional scaling, etc.) (Broennimann et al., 2012), our approach estimates the potential spatial interaction in a geographic biotope (Grinnellian niche) using spatially explicit processing of data in GIS. Thus, this approach compliments previous methods for the estimation of interactions by adding a spatially explicit estimation of the expected level of the potential interactions (Pellissier et al., 2010; Polce et al., 2013; Silva et al., 2014; Warren et al., 2010).

Nevertheless, our approach has some constraints in predicting actual interactions between species. First, species occurrence in a given area is influenced by biotic (B), abiotic (A) and movement-related (M) factors (BAM framework; Soberón & Peterson, 2005). But for invasive species like *H. axyridis* we assumed that there is no dispersal limitation and that the influence of biotic factors is lower (Mestre et al., 2013). Therefore, the occurrence in a given area should be mostly limited by abiotic factors, and thus, climate-based SDM are a good tool for this kind of species, but necessarily so for native and endemic species. On the other hand, we used only local occurrences to predict the current occupied area, which in the case of *H. axyridis* avoids the overestimation of areas of occurrence in the present. Nevertheless, due to its recent arrival this species is probably in a non-equilibrium invasion state, and its real potential area of occurrence could still expand (Elith, 2016; Gallien et al., 2012; Hill, Gallardo, & Terblanche, 2017). As described above, in SDM for lumped endemic and native species we assumed a generalization of the niche of all included species and a loss of specific niche requirements. However, this is similar to the loss of information of individual phenotypic traits (or populations) within a given species when estimating a species distribution through SDM (Bolnick et al., 2010; Pianka, 2011) (Figure S1). Finally, species co-occurrence does not necessarily imply that interaction will always take place, because at a local scale species could differ in microhabitats, food preferences or phenology.

In summary, this study shows that there is a high level of potential spatial interaction between native and endemic coccinellids with *H. axyridis* in central Chile, one of the 35 worldwide biodiversity hotspots (Mittermeier, Robles Gil, Hoffman, & Robles, 2004), where native and endemic coccinellids concentrate. Thus, this study provides a spatially explicit baseline for coccinellid conservation and management of this invasive species and proposes a useful tool to explore other potential spatial ecological interactions.

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AUTHOR CONTRIBUTION

Author 1 generate the idea, compile the data, process the information and write the article; author 2 and author 3 contributed with the redaction, correction and review of the article, and with the discussion of the results obtained on the processing step.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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