UNIVERSIDAD DE CHILE

Facultad de Ciencias Forestales y de la Conservación de la Naturaleza

Magíster en Áreas Silvestres y Conservación de la Naturaleza

INTERACCIÓN ESPACIAL ACTUAL ENTRE LA ESPECIE INVASORA *Harmonia axyridis* (COLEOPTERA: COCCINELLIDAE) Y LOS COCCINÉLIDOS NATIVOS Y ENDÉMICOS DE CHILE

Tesis para optar al Grado Académico

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Resumen

Harmonia axyridis ha invadido muchas regiones del mundo, reduciendo la diversidad y abundancia de los coccinélidos residentes. Muchos estudios de interacciones se han realizado a escala local, sin embargo, las interacciones a escala regional han sido menos estudiadas. El objetivo de este estudio fue estimar y analizar la potencial interacción espacial de *H. axyridis* con especies nativas y endémicas en Chile, considerando variables bioclimáticas y de coberturas de suelo. Para ello, se usaron modelos de distribución de especies (MDE) con MaxEnt. En primer lugar, se crearon MDEs para *H. axyridis*, coccinélidos nativos y endémicos, luego se estimó la idoneidad bioclimática de cada grupo en cada tipo de cubierta de suelo. Por último, se identificaron y analizaron los sitios de co-ocurrencias de los organismos de acuerdo a la idoneidad bioclimática y los tipos de cobertura del suelo. *Harmonia axyridis* ocurre continuamente de 30 ° a 42 ° S en Chile, mientras que las especies nativas y endémicas tienen mayores áreas de distribución, desde el norte al sur del país. *Harmonia axyridis* tiene alta idoneidad en todos los tipos de cobertura de suelo, excepto bosque nativo, mientras que coccinélidos nativos y endémicos ocurren con más frecuencia en cultivos, matorral arborescente y matorrales. Las mayores probabilidades de interacción espacial entre estos grupos están en Chile central, específicamente en cultivos y matorrales, mientras que las más bajas en el bosque nativo primario. Este trabajo muestra que *H. axyridis* puede estar presente no sólo en cultivos sino también en coberturas de suelo naturales y que en ambos tipos de cobertura podría representar una amenaza para las especies nativas y

endémicas. Nuestro enfoque metodológico podría ser útil para estimar la interacción espacial entre esta especie invasora de todo el mundo, y también otras interacciones ecológicas, representando una herramienta útil para el manejo y la conservación.

Abstract

Harmonia axyridis has invaded many regions of the world, reducing the diversity and abundance of resident coccinellid assemblages. Many studies of interactions have been performed at a local scale, but the interactions at regional scales have been less studied. The aim of this study was to estimate and analyze the spatial interaction of *H. axyridis* with native and endemic species in Chile, considering bioclimate and land cover variables. For this, we used Species Distribution Models (SDMs) with MaxEnt. First, we created SDMs for *H. axyridis*, native and endemic coccinellids, then we estimated the bioclimatic suitability of each coccinellid group in each land cover type. Finally, we identified and analyzed the sites of co-occurrences of organisms according to bioclimatic suitability and land cover types. *Harmonia axyridis* occurs from 30° to 42° S in Chile, while native and endemic species have larger distribution areas. *Harmonia axyridis* has high suitability in all land cover types except native forest, whereas native and endemic coccinellids occur more frequently in croplands, arborescent scrubland and scrublands. The highest probabilities of spatial interactions among these groups occur in central Chile, specifically in croplands and scrublands, and the lowest in primary native forest. *Harmonia axyridis* may be present in crops and natural land cover types, where it could represent a

threat to native and endemic species. Our methodological approach could be useful to estimate spatial interaction between this worldwide invasive species around the globe, and also other ecological interactions, representing a tool for management and conservation.

Introducción

Las invasiones biológicas representan una temática fundamental para la conservación biológica (Vásclavik y Meentemeyer, 2009; Bidinger et al. 2012). La introducción de especies de manera accidental o intencionada trae muchas veces efectos adversos para la biota nativa, la cual interactúa con estos nuevos integrantes del ensamble ecológico (Carlton, 2001; Lim *et al.,* 2011). Estas interacciones entre especies nativas e invasoras pueden ser inferidas a partir de la estimación potencial de la distribución de los organismos interactuantes. Los modelos de distribución de especie (MDE) (Hirzel et al. 2006; Elith y Leathwick 2009; Elith et al. 2011; Elith 2016) permiten estimar el área de potencial presencia de un organismo basado en la teoría de nicho (Hutchinson 1957; Hirzel y Le Lay 2008). El nicho ecológico de las especies puede ser estimado a través de la modelación de sus requerimientos de recursos (Schurr et al. 2012). MDE han sido ampliamente utilizados para propósitos de conservación biológica, permitiendo guiar los esfuerzos de monitoreo y manejo de la vida silvestre (Pyke et al. 2005; Elith et al. 2010; Ferraz et al. 2012; Zhang et al. 2012). Recientemente, los MDE han sido aplicados al estudio de dinámicas ecológicas complejas, tales como el efecto del cambio climático en la modificación del rango de las especies, invasiones biológicas

y dinámicas de enfermedades infecciosas vectoriales (Elith et al. 2010; Porfirio et al. 2014; Alaniz et al. 2017). Los MDE permiten la identificación de zonas donde los requerimientos de diferentes especies coinciden o se traslapan, y por lo tanto donde la interacción espacial es altamente probable. Estudios previos han estimado la similitud de nichos utilizando ENMtools o la co-ocurrencia en modelos binarios, sin embargo ningún modelo ha determinado la interacción espacial considerando probabilidades de la interacción esperada (Warren et al. 2010; Pellissier et al. 2010; Illoldi-Rangel et al. 2012; Polce et al. 2013; Silva et al. 2014).

La especie invasora *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), nativa de Asia, es un depredador generalista que ha sido introducido en muchos países para el control biológico de áfidos en cultivos, pero que también se ha propagado accidentalmente hacia muchas otras regiones (Roy et al. 2016). La introducción de este insecto ha generado efectos adversos como plaga doméstica y agrícola (Koch 2003; Koch and Galvan 2008; Linder et al. 2009; Grez et al. 2010; Brown et al. 2011). Sin embargo, la mayor preocupación se relaciona con sus impactos negativos en la biodiversidad, y en particular en los coccinélidos nativos, a través de la competencia indirecta y la depredación intragremio (Gardiner y Landis 2007). De hecho, en Estados Unidos, Europa y Chile las poblaciones locales de coccinélidos nativos han declinado en los lugares colonizados por *H. axyridis* (Brown et al. 2011; Roy et al. 2012; Losey et al. 2014; Bahlai et al. 2015; Roy et al. 2016; Grez et al. 2016).

En Chile, *H. axyridis* fue introducida en 1998 desde Francia, sin embargo tales poblaciones no lograron establecerse. Más tarde, en 2003, la primera población feral

fue encontrada en localidades muy restringida en Chile central, y a partir de 2010 se ha expandido de forma constante y cada vez mayor (Grez et al. 2010). Actualmente se encuentra amplia y continuamente distribuida a lo largo de 1283 kilómetros en el país (Grez et al. 2016), desde 29°S hasta los 41°S, aproximadamente. En Chile han sido reportadas 115 especies de coccinélidos nativos e introducidos (González 2014), siendo ~50% endémicos del país y ~ 35% nativos del sur de Sudamérica. La biogeografía de esta familia en Chile es escasamente conocida, sin embargo los patrones de endemismo y riqueza de los coccinélidos son similares al de otros organismos (e. g plantas), concentrando los valores más altos en la zona central del país (Samaniego y Marquet 2009; Segovia et al. 2013; González 2014; Scherson et al. 2014). Estos patrones de distribución sugieren que en Chile central *H. axyridis* debiera co-ocurrir con coccinélidos nativos y endémicos, generando una alta probabilidad de interacción. No obstante, tales interacciones pueden estar moduladas por el uso diferencial de las coberturas de suelo presentes en el área por parte de *H. axyridis*, endémicos y especies nativas. Se ha reportado que en Chile *H. axyridis* posee mayor abundancia en coberturas ornamentales, agrícolas y urbanas, sin embargo, recientemente también ha invadido hábitats naturales como matorrales nativos. En contraste, la mayoría de las especies nativas están asociadas a coberturas más naturales, aunque algunas especies nativas también prosperan en hábitats perturbados como cultivos (Grez et al. 2013, 2016).

Los MDE han sido usado para identificar las áreas en diferentes continentes y países, incluyendo Sudamérica, donde *H. axyridis* puede invadir con éxito (Poutsma et al. 2008; Bidinger et al. 2012; Veran et al. 2015), sin embargo esos modelos no han sido utilizados para evaluar la potencial interacción espacial con otras especies en las áreas donde se ha introducido y ha invadido. En este estudio proponemos un enfoque novedoso para estimar la interacción espacial entre invasores y especies nativas mediante el uso de MDE. Especialmente, a través de este enfoque estudiamos la interacción espacial entre *H. axyridis* y los coccinélidos nativos y endémicos en Chile. Para ello, generamos MDEs para *H. axyridis*, nativos y endémicos, luego estimamos la probabilidad de presencia de cada grupo de coccinélidos en cada tipo de cobertura, y finalmente identificamos y analizamos los sitios de co-ocurrencia de los organismo de acuerdo a la idoneidad bioclimática y el tipo de cobertura de suelo. Se espera que: 1) Debido a que *H. axyridis* colonizó inicialmente Chile central, y dado que la mayoría de las especies nativas y endémicas también se distribuyen en esta área, esta sería la zona con mayor probabilidad de interacción espacial. 2) A pesar de que *H. axyridis* en Chile prefiere los cultivos agrícolas, y los coccinélidos nativos y endémicos están más asociados a cuberturas de suelo naturales, debieran existir algunos tipos de cobertura que posean alta probabilidad de interacción.

Hipótesis

1. Si la Familia Coccinellidae posee patrones biogeográficos similares a otros organismos en Chile, con mayor abundancia de especies nativas y endémicas en la zona central, entonces la mayor probabilidad de interacción espacial potencial con *H. axyridis* ocurrirá en esta zona.
2. Si *H. axyridis* posee preferencias por coberturas agrícolas, donde también existen especies de coccinélidos nativos, la mayor probabilidad de interacción espacial con estos coccinélidos ocurrirá en este tipo de coberturas. Por otro lado las especies endémicas al estar más asociadas a coberturas naturales tendrán menor probabilidad de interacción espacial potencial.

Objetivos

Objetivo General:

- Identificar y analizar la interacción espacial potencial actual entre *H. axyridis* y los Coccinellidae nativos y endémicos de Chile

Objetivos específicos:

Para responder a la hipótesis 1

1. Determinar la distribución espacial actual de *H. axyridis* y de los coccinélidos nativos y endémicos en Chile.
2. Identificar los sitios de interacción espacial potencial actual entre *H. axyridis* y los coccinélidos nativos y endémicos de Chile

Para responder a la hipótesis 2

1. Identificar las coberturas de suelo potenciales de *H. axyridis* y de los Coccinélidos nativos y endémicos.
2. Asociar el nivel de interacción espacial potencial entre *H. axyridis* y los Coccinélidos nativos y endémicos con las coberturas de suelo.

Artículo

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

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Introduction

Biological invasions are of fundamental concern in conservation biology (Vásclavik and Meentemeyer 2009; Bidinger et al. 2012). The accidental or intentional introduction of species may generate many adverse effects to the native and endemic biota with which invasive species interact (Carlton 2001; Lim et al. 2011). These interactions among native and invasive species may be inferred from the estimation of the potential distribution of the interacting organisms. Species Distribution Models (SDM) (Hirzel et al. 2006; Elith and Leathwick 2009; Elith et al. 2011; Elith 2016) allow estimating the area of potential presence of an organism based on ecological niche theory (Hutchinson 1957; Hirzel and Le Lay 2008). The ecological niche of a species may be approached by modeling its resource requirements (Schurr et al. 2012). SDM have been widely used for biological conservation purposes, to guide wildlife monitoring and management (Pyke et al. 2005; Elith et al. 2010; Ferraz et al. 2012; 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 (Elith et al. 2010; Porfirio et al. 2014; Alaniz et al. in press). SDM allow identification of zones where the niche requirements of different species match or overlap, and therefore where spatial interactions are highly probable. Previous studies have identified niche similarities using ENMtools or co-occurrence in binary models, however no model has determined the spatial interaction considering probabilities of expected

interactions (Warren et al. 2010; Pellissier et al. 2010; Illoldi-Rangel et al. 2012; Polce et al. 2013; Silva et al. 2014).

The invasive species *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), native to Asia, is a generalist predator that has been introduced to many countries for the biological control of aphids in crops, but it also has spread accidentally to several other regions (Roy et al. 2016). The introduction of this insect has generated adverse effects as a household and agricultural pest (Koch 2003; Koch and Galvan 2008; Linder et al. 2009; Grez et al. 2010; Brown et al. 2011). Nevertheless, the greatest concern relates to its negative impact on biodiversity, particularly on native coccinellids, through indirect competition and intra-guild predation (Gardiner and Landis 2007). In fact, in USA, Europe and Chile local native coccinellid populations have declined in places colonized by *H. axyridis* (Brown et al. 2011; Roy et al. 2012; Losey et al. 2014; Bahlai et al. 2015; Roy et al. 2016; Grez et al. 2016).

In Chile, *H. axyridis* was introduced in 1998 from France, however these populations did not establish. Later, in 2003, the first feral populations were found in very restricted locations in central Chile, and from 2010 on they were consistently and increasingly reported (Grez et al. 2010). 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 (Samaniego and Marquet 2009; Segovia et al. 2013; González 2014; Scherson et al. 2014). These distribution patterns suggest that in central Chile *H. axyridis* should frequently co-occur with native and endemic coccinellids, with high probability of interaction. Nevertheless, these interactions may be modulated by the differential use by *H. axyridis*, 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 et al. 2013, 2016).

SDM's have been used to identify the areas in different continents and countries, including South America, where *H. axyridis* may invade successfully (Poutsma et al. 2008; Bidinger et al. 2012; Veran et al. 2015), but these models have not been used to assess its potential spatial interaction with other species in areas where it has been introduced and has invaded. In this study we propose a novel approach to estimate spatial interactions between invasive and native species using SDM. Specifically, through this approach we studied the spatial interactions between *H. axyridis*, native and endemic coccinellids in Chile. For this, we first created SDMs for *H. axyridis*, native and endemic coccinellids, then we estimated the probability of presence of each coccinellid group in each land cover type, and finally we identified and analyzed the sites of co-occurrences of organisms according to bioclimatic

suitability and land cover types. We expected that: 1) Because *H. axyridis* initially colonized central Chile, and given that most native and endemic species are also distributed in this area, this would be the area with the highest probability of spatial interactions, 2) 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 probability of interaction.

Materials and methods

The groups of coccinellids considered in this study were a) the invasive *H. axyridis*, b) Native coccinellids and c) Endemic coccinellids. Native coccinellids were those species present both in Chile and other countries of South America, while endemic coccinellids were species present only in Chile, based on the distributions reported by González (2006, 2014); thus they are two distinct groups in the analyses.

Spatial distribution of organisms

Species distribution models for *H. axyridis*, native and endemic coccinellids were generated using the maximum entropy technique with MaxEnt V3.3.3k (Phillips et al. 2004; Phillips et al. 2006). For this we used the 19 environmental variables of Pliscoff et al. (2014) at 2.5 arc minutes of spatial resolution. This is a regional bioclimatic model more accurate than WorldClim because it integrates a greater number of climatic stations for Chile (Pliscoff et al. 2014). The background of the model corresponds to zones 33 and 43 of Worldclim tiles. 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 natives and 600 for endemics (Available as Supplementary material).

First, preliminary models for *H. axyridis*, natives and endemics were generated using all bioclimatic variables (19) with a 15-fold cross-validation technique, calculating the relative contribution (i.e., percent contribution and permutation importance) of the bioclimatic variables in the model. We determined the normality of each variable using the Shapiro-Wilk test (Roystone 1982, 1983). Then statistical correlations between pairs of bioclimatic variables were determined using a multiple correlation matrix expressed in correlograms, calculated using the absolute correlation coefficient (Bradley 1985). The objective of this process was to select the variables with higher importance and lower correlation index (less than ± 0.7) to reduce the overfitting in the model (Supplementary Material Fig. S1). To avoid biases in the model due to the spatial autocorrelation of occurrence points we applied a spatial rarefy function (Brown 2014) that determined the clusters with higher autocorrelation and selected randomly only points with more than 5 km distance between each locality. The final models run with the 40-fold cross-validation technique included only the selected bioclimatic variables for each group (i.e., *H. axyridis*, natives, endemics) with 95% confidence. The accuracy of models was estimated using the area under the curve metric (AUC) of the Receiver Operating Characteristic (ROC) (Supplementary Material Fig S2).

Finally, we analyzed the importance and patterns of bioclimatic variables to estimate their suitability for *H. axyridis*, natives and endemics, representing their physiological limitations (Gerick et al. 2013; Woodin et al. 2015).

Estimating spatial interactions

We adapted the protocol proposed by Alaniz et al. (in press) to estimate the spatial interaction between species. Using a geographic information system (GIS), we classified the probability of presence of *H. axyridis*, natives and endemics in four levels (null=0; low=1; medium=2; high=3), to convert the continuous grid into discrete levels of probability grid (Fig. 1). These levels were assigned by sorting the probabilities of presence into four equal intervals of probability. These discrete grids were multiplied in pairs using the raster calculator tool, obtaining a grid with six different levels of spatial interaction (null, very low, low, medium, high, very high, see Fig. 1) for *H. axyridis* and natives and another grid for *H. axyridis* and endemics. With this information we generated the corresponding maps of expected spatial interactions, considering the different levels of probability.

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	Probability of 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 interaction levels. Left: Double entry matrix generating a linkage grid between the probability of presence of the invasive species *H. axyridis* and the native or endemic coccinellids. The values 0 to 3 represent the four reclassified levels of each variable. Right: Categories of probability of spatial interaction according to the grid multiplication (modified from Alaniz *et al.* 2017).

Characterization of bioclimatic suitability per land cover type

Each SDM was intersected with a land cover categorical map to identify the probability of presence of coccinellids in each class of land cover. We used R 3.2.2 software to generate a histogram of the bioclimatic suitability per land cover type for *H. axyridis*, natives and endemics. We used the more up-to-date map available for land cover types in Chile (Zhao et al. 2016), with the types grouped into a subset of classes from the 39 original classes of Zhao et al. (2016) (Supplementary Material Table S1 - Fig. S3). We calculated three metrics to identify the suitability in each land cover type: Mean of bioclimatic suitability (X), maximum value of bioclimatic

suitability (Max) and the 25% highest values of bioclimatic suitability within a land cover class (3. Q).

Characterization of spatial interaction areas

We intersected the interaction maps with the reclassified land cover map of Zhao et al. (2016) to characterize the probability of spatial interactions between *H. axyridis* and natives and between *H. axyridis* and endemics in relation to land cover classes (Supplementary Material Fig. S3). Finally, we calculated the percentage of contribution of each land cover class to each level of spatial interaction and the total area of interactions for each level.

Results

Spatial distribution of coccinellids

The distribution of *H. axyridis* in Chile ranges from 30° to 42° S, mainly in the coastal and central depression zone; 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 161.898 km2, representing 21.14% of continental Chile (Fig. 2 and 3). 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 probability of presence decreased with the increase of temperature in the wettest quarter, reaching a peak between 8 and 15 C°, while the highest probability of presence 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 (Supplementary Material Fig. S4A).

Table 1: SDM Parameters

Statistical parameters of each species distribution model.

Model	initial occurrences	Occurrences after rarefy (Used in the model)	AUC	SD	Number of variables	Importance of variable 1 (%)	Importance of variable 2 (%)	Importance of variable 3 (%)	Contribution of most important variables
H. axyridis	2715	783	0.951	±0.015	6	29.6 (BIO8)	24.8 (BIO9)	22.3 (BIO19)	76.7
Natives	721	667	0.938	±0.033	9	24.0 (BIO18)	20.7 (BIO19)	20.0 (BIO5)	64.7
Endemics	600	423	0.949	±0.049	6	32.4 (BIO19)	26.9 (BIO15)	18.4 (BIO8)	77.7

Native coccinellids are concentrated in central Chile from 27° to 43° S, but also with probability of presence in extreme zones in northern and southern Chile. Probabilities of presence decreased in the zone between 43° and 50° S and were very low in the Atacama Desert (Fig. 2 and 3). 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). The suitability had a single peak between 0 and 400 mm precipitation of the warmest quarter; suitability increased gradually with the precipitation of the coldest quarter, reaching a peak at 1200 mm and decreasing above that value. The suitability increased gradually with the maximum temperature of the warmest month, with a

peak at 26 C° and a threshold at 30 C°, above which the suitability becomes zero (Supplementary Material Fig. S4B).

Endemic coccinellids are mainly distributed in the central zone of the country between 27° and 45° S, with a high probability of presence in the Andes and in the Coast Range. Another area with high suitability is the northern coastal zone between 19° and 22° S (Fig. 2 and 3). 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 response of the curve of the precipitation of the coldest quarter was similar to the native coccinellids, increasing gradually; the probability of presence increased asymptotically with precipitation seasonality, but with a peak at low levels of seasonality associated with northern endemic species. The probability of presence had a Gaussian pattern in relation to the mean temperature of the wettest quarter, reaching a peak at 10 C° (Supplementary Material Fig. S4C).

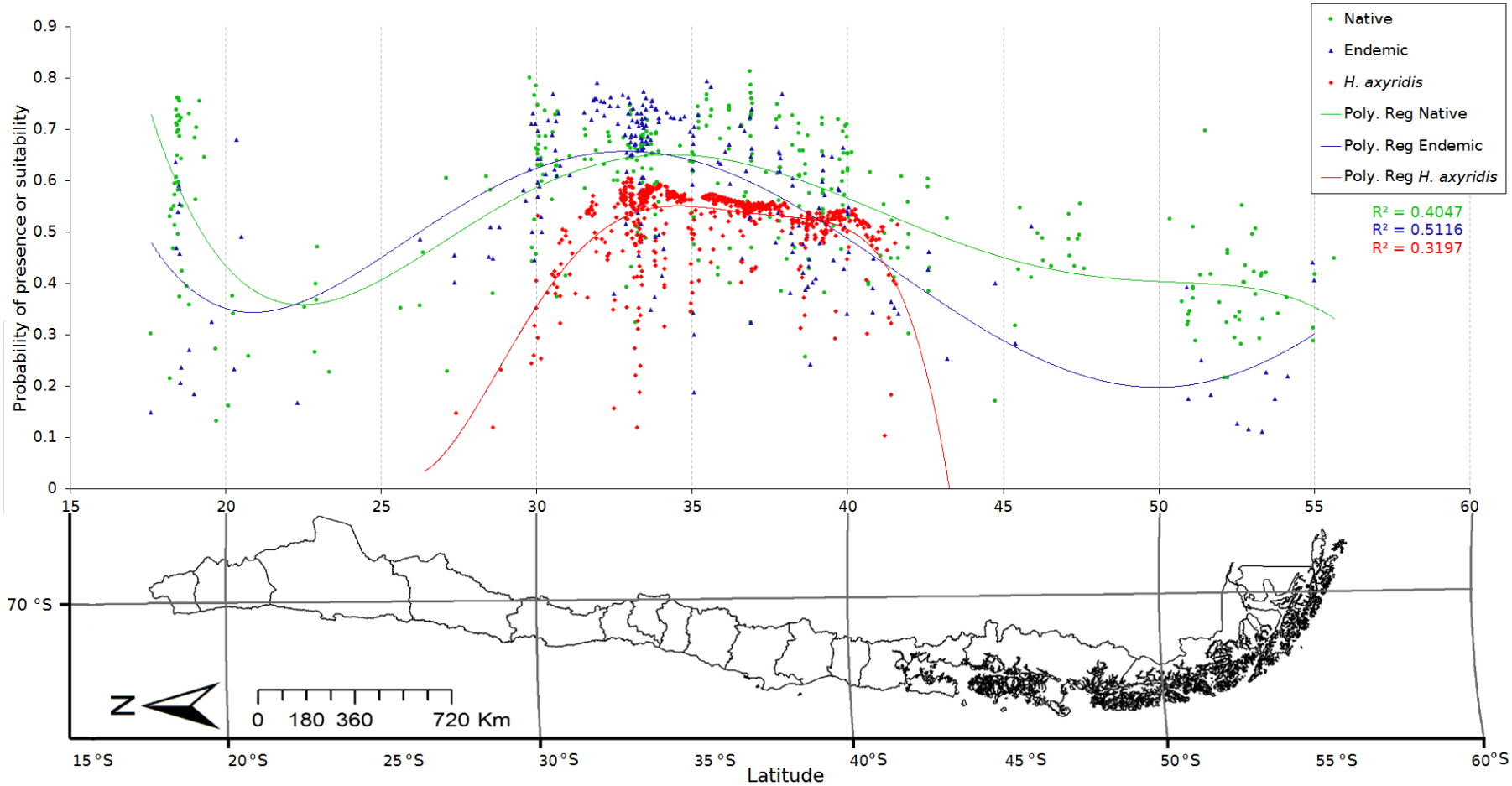

Figure 2: Probability of presence of *H. axyridis*, native and endemic coccinellids in Chile.

Probability of presence or bioclimatic suitability per latitude of *H. axyridis* (red), native (green) and endemic coccinellids (blue). Points represent occurrences. Probabilities correspond to the mean of the 40-fold cross-validation technique. The tendency lines were generated using a 5th order polynomial regression. The lower panel presents a map of Chile.

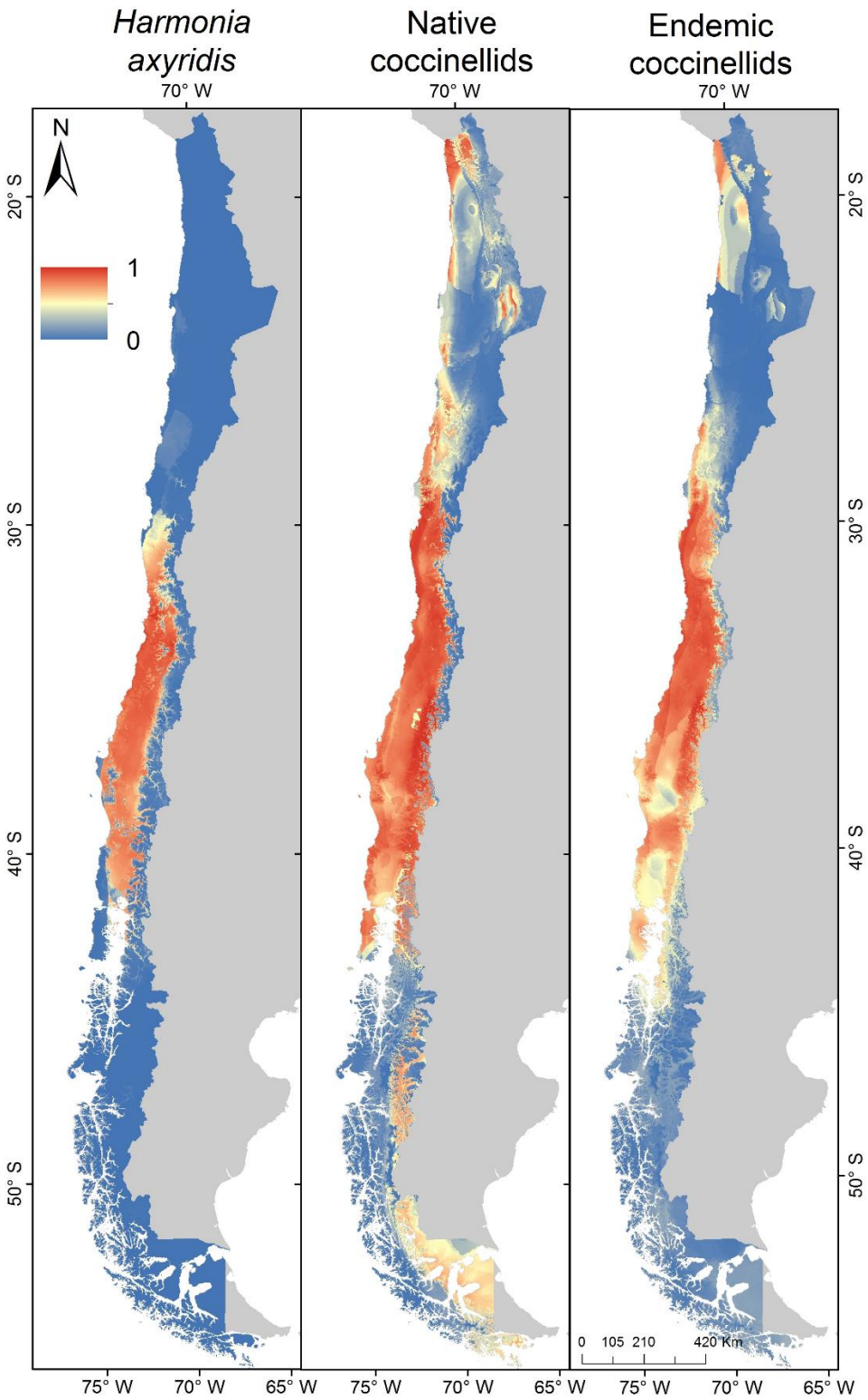

Figure 3: SDM of *H. axyridis*, native and endemic coccinellids of Chile.

Maps of probability of presence or bioclimatic suitability for the coccinellids.

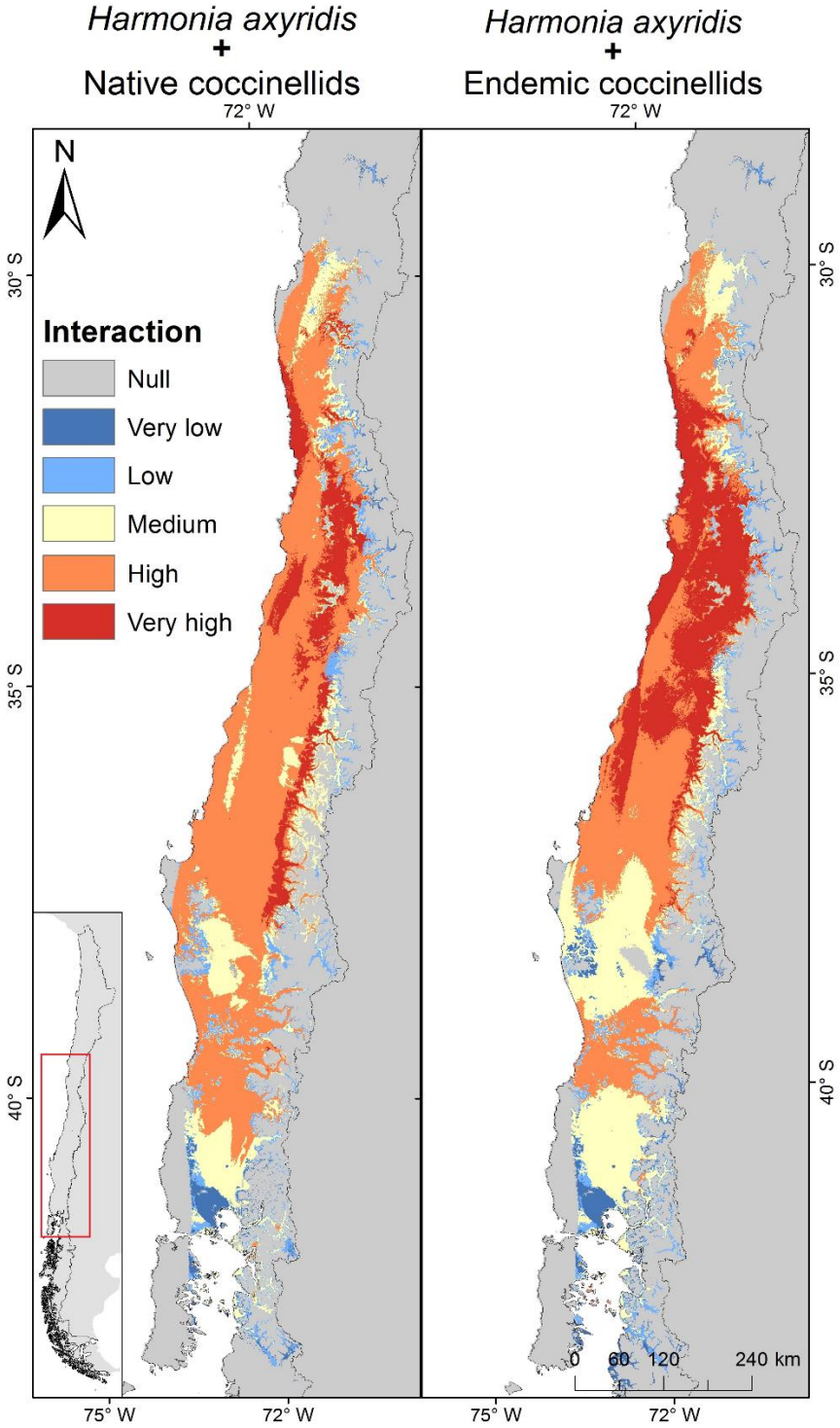

Figure 4: Maps of spatial interaction.

Interaction between *H. axyridis* with native coccinellids (left) and endemic coccinellids (right). Different colors represent the categories of interactions according to according to Fig. 1.

Spatial interactions

The areas of potential spatial interactions with *H. axyridis* are dissimilar between native and endemic coccinellids. The spatial interaction zone of *H. axyridis* with native coccinellids was larger than that with endemics, but considering only the “very high” level of interaction the area was larger for endemics than for natives (Fig. 4). The area of “high” level of interactions was larger for natives than for endemics (Fig. 4). The medium and low probability of spatial interaction was similar for both groups, influenced by the homogeneous probability of presence of *H. axyridis* in all its distribution (Fig. 3 and 4). The levels of interaction were lower towards the south of the country, with low and very low levels of interaction south of 40° S, as a consequence of the abrupt decrease in the probability of presence of *H. axyridis* in this zone (Fig. 3).

Bioclimatic suitability per land cover type

For *H. axyridis*, the maximum bioclimatic suitability was 0.61 and similar for all land cover classes, while for native and endemic coccinellids it was 0.87 in scrubland and 0.88 in cropland and scrubland, respectively (Max, Fig. 5). In the area of higher bioclimatic suitability for *H. axyridis* all land cover classes have a high frequency of occurrence, except for primary native forest (X and 3.Q., Fig. 5). For native coccinellids, arborescent scrubland, cropland, secondary native forest and scrubland had high frequency in the area of higher bioclimatic suitability, and for endemics this applies for arborescent scrubland, cropland and scrubland (highest X and 3.Q., Fig. 5). For these last two groups of coccinellids, in the area of medium

bioclimatic suitability (0.3 - 0.5) primary native forest had the highest frequency (Fig. 5).

Characterization of spatial interaction areas

Higher levels of potential interactions between *H. axyridis* and native and endemic coccinellids generally occurred in scrublands (Fig. 6). As the degree of spatial interaction of *H. axyridis* with both native and endemic coccinellids increased, the percentage of contribution of more disturbed cover types (i.e. croplands and exotic plantations) also increased, while the contribution of less disturbed cover types (primary forest and secondary forest) decreased (Fig. 6).

Most of the area where *H. axyridis* interacts with native and endemic coccinellids had a high degree of spatial interaction, but for the natives this area was almost twice as large as for endemics (92,000 vs 57,000 km2; Fig. 6). In contrast, very low and low level of spatial interactions between these coccinellids were found in a very small area, around 17,000 km2 for natives and 21,000 km2 for endemics (Fig. 6).

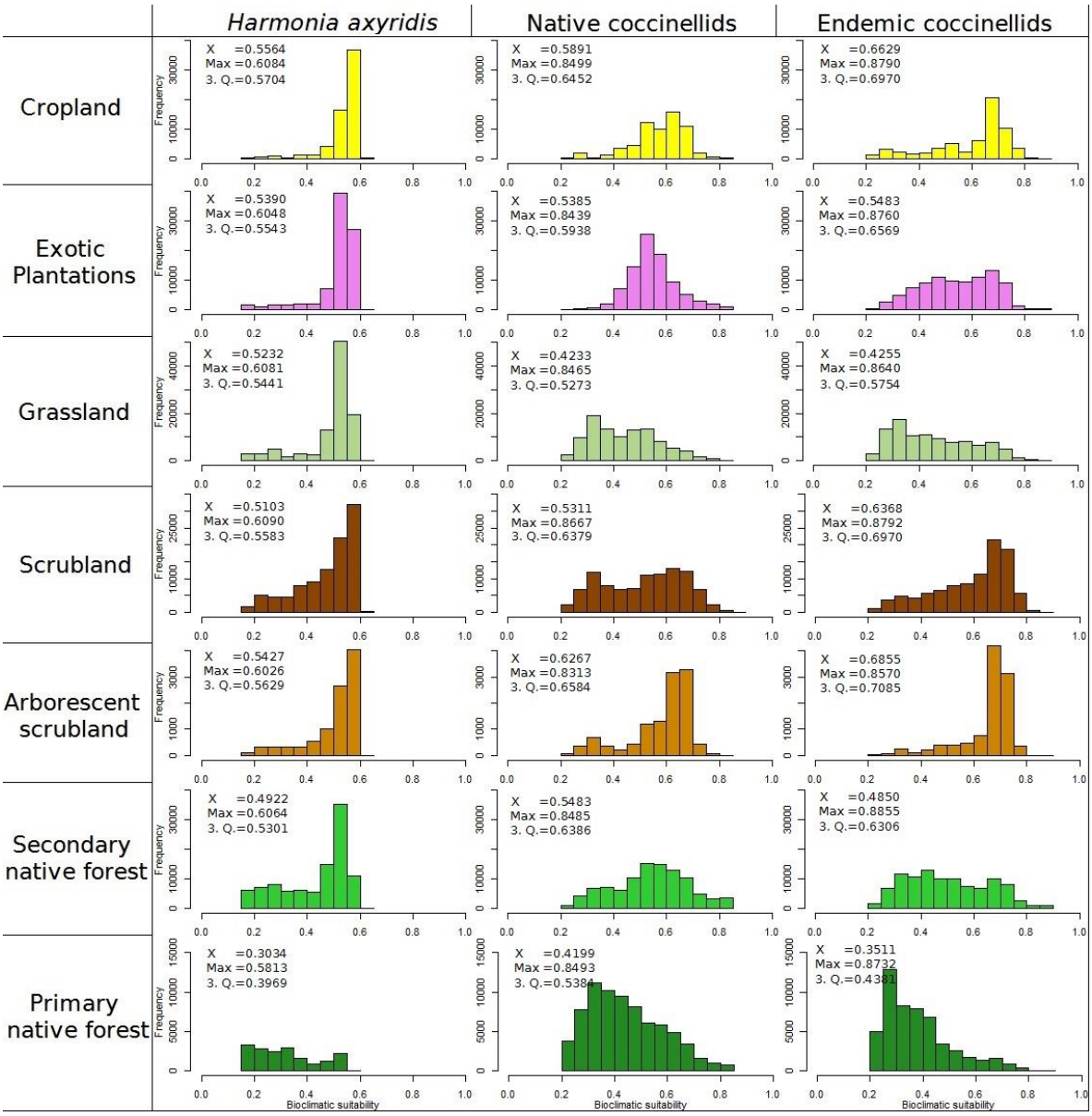

Figure 5: Histograms of bioclimatic suitability per land cover type for *H. axyridis*, native and endemic coccinellids of Chile.

Histograms show the frequency (in pixels) of the value of suitability in each land cover type, based on the Zhao *et al.* (2016) land cover map. Each histogram includes three statistics: X = Mean of bioclimatic suitability; Max = Maximum value of bioclimatic suitability; 3.Q.= 3th quartile of all pixel values of bioclimatic suitability, representing the 25% highest values in the land cover.

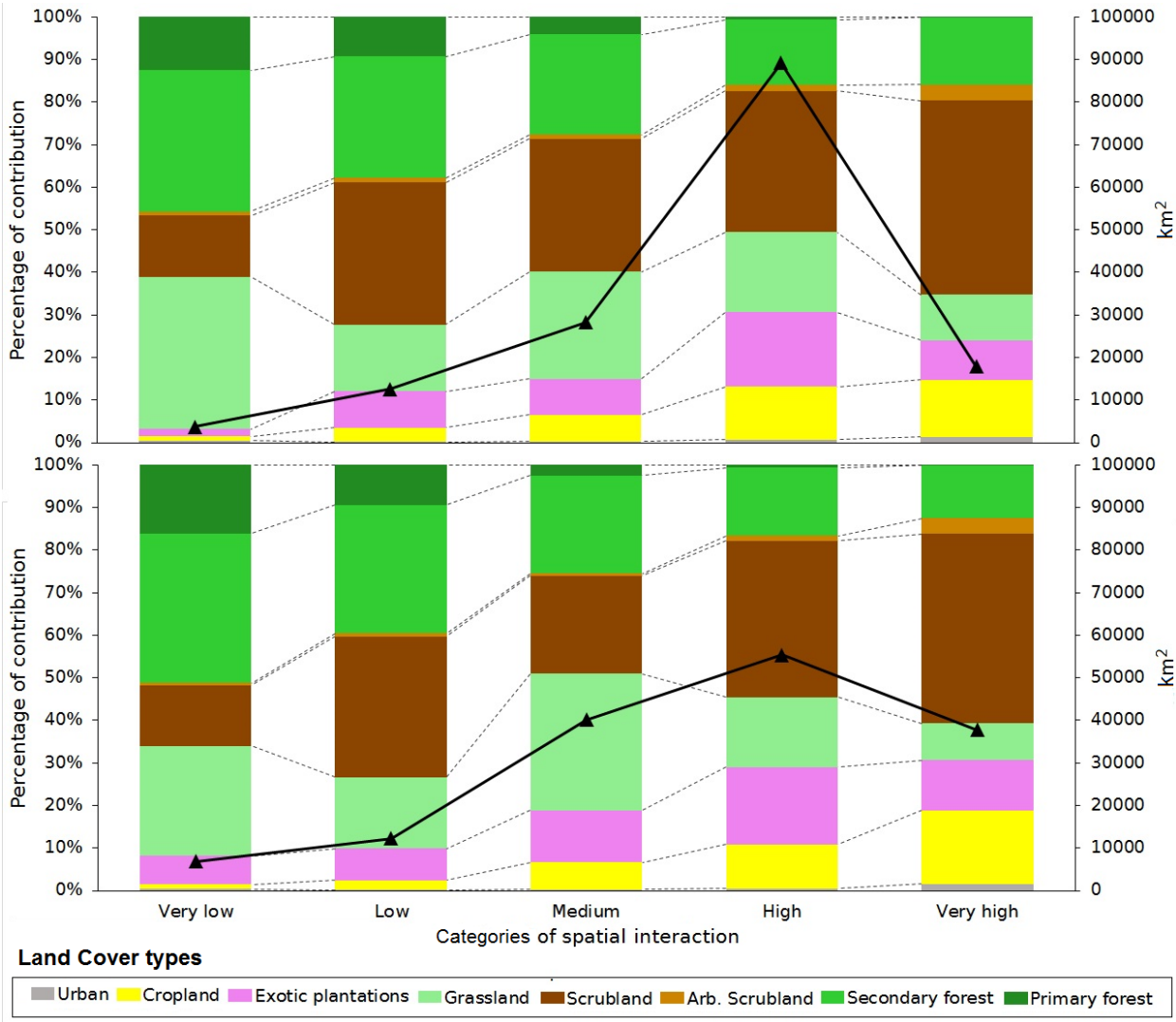

Figure 6: Percentage of contribution of land covers by categories of spatial interaction of *H. axyridis* with native and endemic coccinellids and area of each category.

Bars show the relative area (percentage) of each land cover type within each level of interaction. Land cover types are organized from more (bottom) to less disturbed (top), according to Grez *et al.* (2013). The black line corresponds to the total area (km^2) in the country covered by each category of interaction, excluding the null category. The upper plot is the interaction between *H. axyridis* and native coccinellids, and the bottom plot is the interaction of *H. axyridis* with endemic coccinellids.

Discussion

Potentiality of SDMs to estimate the spatial interaction between species

SDMs have been frequently used to estimate the potential distribution of organisms, like the change in distribution areas of species under different scenarios of climate change (Pyke et al. 2005; Ferraz et al. 2012; Zhang et al. 2012; Porfirio et al. 2014) or to estimate the phases of a biological invasion (Gallien et al. 2012). They can also be useful to estimate, in a spatially explicit way, the probabilities of ecological interactions such as predation, pollination or competition, based on co-occurrence of species. If there is evidence that species are interacting at a local scale, through these models it is possible to estimate other areas where these interactions are more or less likely to occur. This has been done, but most approaches have estimated ecological interactions only based on overlapping binary models (i.e. presence/absence) that identify the spatial co-occurrence of organisms (Pellissier et al. 2010; Illoldi-Rangel et al. 2012; 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). However, these approaches do not allow predicting the strength of interactions. In this study we present a novel approach using SDMs to estimate, with different probabilities, the areas in Chile where interactions between the invasive *H. axyridis* and native and endemic coccinellids are likely to occur, considering bioclimatic variables and land cover types. Given that negative effects of *H. axyridis* on resident coccinellids have been reported in several regions around

the world (Gardiner and Landis 2007; Brown et al. 2011; Grez et al. 2010; Grez et al. 2016; Roy et al. 2016), this methodology has global application.

At a regional scale the distribution of organisms is mainly explained by bioclimatic patterns (Pearson and Dawson 2003), therefore in our study SDMs were generated based only on bioclimatic variables, which also allowed us to estimate the physiological restrictions of the modeled species (Gerick et al. 2013; Woodin et al. 2015). However, to improve the predictions of interaction areas, bioclimatic models should then be associated with other species requirements. In our case we associated the bioclimatic model with land cover types, as a proxy of habitat use by coccinellids, whose species associate differentially with land cover types (Gardiner et al. 2009; Grez et al. 2014a, b). However, including them in the SDMs is not recommended because some land cover types can have disproportionally high or low number of occurrences due to sampling efforts, and are highly dynamic in time and space, and this would create biases in the model.

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

Our models predicted that *H. axyridis*, native and endemic coccinellids are mainly distributed in central Chile. For *H. axyridis*, bioclimatic restrictions to colonization of the north and south of Chile would keep the invasion restricted to the central region of the country. This prediction agrees with the distribution of *H. axyridis* so far reported by Grez et al. (2016), but adds some other areas where this species could still invade. Nevertheless, our predictions differ from the model of Bidinger et al.

(2012) that proposes that *H. axyridis* could also invade southern Chile up to 55°S. The restricted distribution of *H. axyridis*, native and endemic coccinellids could be explained by biogeographic barriers, similar to what happens with 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, represents a fundamental climatic configuration. The formation of the Arid Diagonal during the Miocene generated important evolutionary pressure on many taxa (Villagrán and Hinojosa 1997; Segovia et al. 2013), resulting in low richness and abundance of species in this region. Currently, it is considered an important barrier for the dispersal and establishment of many taxa such as butterflies, mammals and native trees (Villagrán and Hinojosa 1997; Samaniego and Marquet 2009; Segovia et al. 2013; Scherson et al. 2014). Therefore, the Atacama Desert would constitute a historical barrier for the dispersal of native and endemic coccinellids of Central Chile, and a current limitation for the dispersal of *H. axyridis*.

In the south, from 40°S to 55°S, two factors have been identified as barriers to the dispersal and establishment of species; first at a historical scale, the influence of the Last Glacial Maximum determined that during the Pleistocene all these areas were covered with glaciers, resulting in migration and refuge of taxa in Central Chile, while at an ecological scale, in this region the presence of westerly winds determines the occurrence of extremely high precipitation events (>6000 mm/year). This scenario produces low species richness in this region, limited to Holocene colonizer species adapted to these climatic conditions (Samaniego and Marquet 2009; Segovia et al. 2013; Scherson et al. 2014). In contrast to *H. axyridis*, native and endemic

coccinellids are also distributed in the extremes of the country, particularly in the north, with native species present also in neighboring countries (Peru and Bolivia in the north, and Argentina in the South) (González 2006), occupying other ecosystems.

The distribution of *H. axyridis*, native and endemic coccinellids is consistent with their climatic niche requirements. For *H. axyridis* the model shows a peak in the probability of presence where mean temperatures are less than 20 C° (BIO8 and BIO9), agreeing with laboratory studies which show a preference of *H. axyridis* for moderate temperatures (Barahona-Segovia et al. 2015), favoring colonization of temperate regions (Roy et al. 2016). Native coccinellids have higher probability of presence where there is high precipitation in winter (BIO19, peak between 800 mm and 1400 mm), low amounts of precipitation in summer (BIO18) and summer temperatures from 15°C to 30°C (BIO5), characteristics of Mediterranean and temperate climates (Di Castri and Hajek 1976). Endemic coccinellids respond similarly to natives in relation to temperature and precipitation, however for them precipitation seasonality (BIO15) is an important variable, with a bimodal curve with a peak in low seasonality (0) and another in high seasonality (200). This bimodal pattern of seasonality could reflect the existence of two groups of endemic species: species of the central zone, characterized by a Mediterranean climate with high seasonality, and species of the northern coastal zone, with an extremely low seasonality and low precipitation during all the year (Supplementary Material Fig. S4).

Given that these three coccinellid groups are mostly distributed in central Chile, it is not surprising that the highest probabilities (very high and high) of interaction of *H. axyridis* with native and endemic coccinellids predicted by our model occur in this region. Nevertheless, the area of very high interaction with endemics is much larger than the area with natives. This could imply that endemic coccinellids are at higher risk of being affected by the invasion of *H. axyridis* than natives, which have a larger distribution along Chile and thus have some refuge areas.

These spatial interactions additionally are modulated by the bioclimatic suitability in the land cover types and by the area occupied by these cover types. For example, we found that *H. axyridis* could colonize most cover types present between 30 and 40°S in Chile, nevertheless in the country it has a strong preference for croplands (Grez et al. 2013, 2016), which are very frequent in this region. Croplands and scrublands also have high suitability for native and endemic coccinellids, thus representing large areas where spatial interactions with *H. axyridis* could occur. Arborescent scrublands have the highest bioclimatic suitability for all coccinellids, but their frequency is very low in Central Chile, constituting only a small area of potential interaction. On the contrary, primary native forests include some areas with high bioclimatic suitability (> 0.6) and large areas with medium bioclimatic suitability (0.3 – 0.5) for native and endemic coccinellids but not for *H. axyridis*, resulting in a low probability of interaction in this cover type.

Most likely, spatial co-occurrence of *H. axyridis* with native and endemic coccinellids will result in an impoverished coccinellid biodiversity, because it has been well

documented that this invasive species in many parts of the world, including Chile, negatively impacts other coccinellids through competition and intra-guild predation (Grez et al. 2016; Roy and Brown 2015; Roy et al. 2016). Our model suggests that this negative effect could occur in 80% of the croplands in Chile, where the probability of interaction between these coccinellids is high or very high. This could alter the outcome of biological control service, since this guild of predatory insects are important natural enemies of crop pests (Obrycki and Kring 1998), where native species play an important role (Brown et al. 2011; Grez et al. 2014) However, our results also highlight the importance of closely following these interactions in some natural land cover types, such as scrublands of central Chile, particularly for conservation and invasion mitigation purposes.

Chile includes one of the 35 worldwide biodiversity hotspots, between 30° and 40°S (Mittermeier et al. 2004), where native and endemic coccinellids concentrate. However, this region is also where *H. axyridis* inhabits, representing a threat for the conservation of biological diversity in this Mediterranean hotspot. The identification of sites with higher interaction probabilities with local species is fundamental to understand the possible impacts on biodiversity at regional scales. The approach of analysis of ecological interactions between species used in the present study is an improvement over the approaches mostly used up to now, and could be a useful tool to study invasions in other regions of the world, or to predict other kinds of ecological interactions.

Conclusions

According to our results, central Chile is the area with highest probability of spatial interactions between the invasive *H. axyridis* in Chile and native and endemic coccinellids. The spatial configuration of bioclimatic suitability, as well as the land cover distribution, show that *H. axyridis* may interact with native and endemic coccinellids not only in croplands but also in some natural land cover types such as scrublands, becoming a concern for the conservation of coccinellids in these habitats. Our methodology represents a powerful tool to estimate areas where ecological interactions could be occurring.

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Conclusiones

El presente estudio, aplicado al caso particular de *H. axyridis* y coccinélidos nativos y endémicos, propone una herramienta novedosa para la identificación de potenciales interacciones espaciales entre organismos. Entre los alcances prácticos del presente trabajo destaca la aplicabilidad en un amplio ámbito de usos en ecología, especialmente para la conservación biológica y el control de especies invasoras. Se demostró que los MDE son una herramienta útil para la estimación de dichas interacciones espaciales. Sin embargo, entre las recomendaciones que emanan del presente estudio se desprende la necesidad por implementar investigaciones a nivel local, que permitan respaldar la interacción que se busca modelar con datos empíricos. Los estudios ecológicos locales permiten identificar los efectos de forma directa, por lo cual modelos pueden entregar una probabilidad de que tal interacción esté ocurriendo a gran escala. No obstante, la ocurrencia efectiva de la interacción dependerá de factores complejos y locales, tales como la disponibilidad de recursos, presas, competidores, manejo, etc.

El tema del sesgo en el muestreo y colecta de datos de ocurrencia de especies representa una de las mayores limitaciones de los estudios basados en modelación de especies, y en especial en un grupo tan ampliamente diverso y críptico como los insectos. Sin embargo, en el presente estudio se trató de reducir dicho problema mediante la búsqueda de información de forma acuciosa, logrando generar la base de datos espacial más amplia de coccinélidos nativos y endémicos para Chile, construida a partir de 17 colecciones entomológicas de todo Chile.

Entre las proyecciones de este estudio, destaca la capacidad de replicación de la metodología a diferentes escalas y contextos, por lo cual podría ser utilizada en áreas de alto valor ecológico para la conservación (e. g parques nacionales o sitios prioritarios) para estimar el posible impacto de esta u otras especies invasoras sobre las comunidades nativas y endémicas de dichos lugares.

Referencias Bibliográficas

Alaniz AJ, Bacigalupo A, Cattan PE (2017) Spatial quantification of the world population potentially exposed to Zika virus. *Int J Epidemiol*.

Bahlai CA, Colunga-Garcia M, Gage SH, Landis DA (2015) The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring. *Biol Invasions* 17:1005–1024

Barahona-Segovia RM, Grez AA, Bozinovic F (2015) Testing the hypothesis of greater eurythermality in invasive than in native ladybird species: From physiological performance to life-history strategies. *Ecol Entomol* 182–191.

Bidinger K, Lotters S, Rodder D, Veith M (2012) Species distribution models for the alien invasive Asian Harlequin ladybird (*Harmonia axyridis*). *J Appl Entomol* 136:109–123.

Bradley C (1985) The Absolute Correlation Coefficient. Maht. Gazette 69(447), 12-17.

Brown JL (2014) SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol Evol* 5:694–700.

Brown PMJ, Frost R, Doberski J, et al (2011) Decline in native ladybirds in response to the arrival of *Harmonia axyridis*: Early evidence from England. *Ecol Entomol* 36:231–240.

Carlton JT (2001) Introduced species in U.S. coastal waters: Environmental impacts and management priorities. Pew report. Pew Oceans Commission. Available at: http://www.iatp.org/files/Introduced_Species_in_US_Coastal_Waters_Enviro.htm Accessed 31 March 2016

Di Castri F, Hajek ER (1976) Bioclimatología de Chile. Editorial Universidad Católica de Chile. Santiago, Chile. 128 pp.

Elith J, Leathwick J (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Evol Syst* 40:677–697.

Elith J (2016) Predicting distributions of invasive species. 1–28. Available at: https://arxiv.org/ftp/arxiv/papers/1312/1312.0851.pdf Accessed 31 January 2017

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. *Methods Ecol Evol* 1:330–342.

Elith J, Phillips SJ, Hastie T, et al (2011) A statistical explanation of MaxEnt for ecologists. *Divers Distrib* 17:43–57.

Ferraz KMPM de B, Ferraz SF de B, de Paula RC, et al (2012) Species distribution modeling for conservation purposes. Nat a Conserv 10:214–220. doi: 10.4322/natcon.2012.032 Gallien L, Douzet R, Pratte S, et al (2012) Invasive species distribution models - how violating the equilibrium assumption can create new insights. *Glob Ecol Biogeogr* 21:1126–1136.

Gardiner MM, Landis DA (2007) Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on Aphis glycines (Hemiptera: Aphididae) biological control in cage studies. *Biol Control* 40:386–395.

Gardiner MM, Landis DA, Gratton C, et al (2009) Landscape composition influences patterns of native and exotic lady beetle abundance. *Divers Distrib* 15:554–564.

Gerick AA, Munshaw RG, Palen WJ, et al (2014) Thermal physiology and species distribution models reveal climate vulnerability of temperate amphibians. *J Biogeogr* 41:713–723.

Gonzalez G (2006) Los Coccinellidae de Chile [online]. Available at: http://www.coccinellidae.cl. Accessed 31 march 2016

González G (2014) Lista actualizada de especies de Coccinellidae (Insecta: Coleoptera) presentes en Chile. Available at: http://www.coccinellidae.cl/paginasWebChile/PDFs/Lista Coccinellidae de Chile 30 06 2014.pdf. Accessed 31 march 2016

Grez A, Zaviezo T, Gonzalez G, Rothman S (2010) *Harmonia axyridis* in Chile: a new threat. *Cienc E Investig Agrar* 37:145–149.

Grez AA, Zaviezo T, Gardiner MM (2014a) Local predator composition and landscape affects biological control of aphids in alfalfa fields. *Biol Control* 76:1–9.

Grez AA, Zaviezo T, Hernández J, et al (2014b) The heterogeneity and composition of agricultural landscapes influence native and exotic coccinellids in alfalfa fields. *Agric. For. Entom* 382–390.

Grez AA, Zaviezo T, Roy HE, et al (2016) Rapid spread of *Harmonia axyridis* in Chile and its effects on local coccinellid biodiversity. *Divers Distrib* 982–994.

Hirzel AH, Le Lay G (2008) Habitat suitability modelling and niche theory. *J Appl Ecol* 45:1372–1381.

Hirzel AH, Le Lay G, Helfer V, et al (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecol Modell* 199:142–152.

Illoldi-Rangel P, Rivaldi C, Sissel B, et al (2012) Species Distribution Models and Ecological Suitability Analysis for Potential Tick Vectors of Lyme Disease in Mexico. *J Trop Med* 2012:1–10.

Koch RL, Galvan TL (2008) Bad side of a good beetle: The North American experience with *Harmonia axyridis. Biol Control* 53:23–35.

Koch RL (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. J Insect Sci 3:32. doi: 10.1093/jis/3.1.32

Lim Y, Gopinath M, Chan S, Harte M (2011) Predicting Potential Invasive Species Distribution : An Application to New Zealand Mudsnails in the Pacific Northwest Youngah Lim Munisamy Gopinath Michael Harte. In: Agricultural & Applied Economics Association AAEA & NAREA Joint Annual Meeting. Pittsburgh, Pennsylvania, p 26

Linder C, Lorenzini F, Kehrli P (2009) Potential impact of processed *Harmonia axyridis* on the taste of “Chasselas” and “Pinot noir” wines. Vitis - *J Grapevine Res* 48:101–102.

Losey JE, Allee LL, Stephens E, et al (2014) Lady Beetles in New York: Insidious Invasions, Erstwhile Extirpations, and Recent Rediscoveries. *Northeast Nat* 21:271–284.

Mittermeier RA, Robles Gil P, Hoffman M, et al (2004) Hotspots Revisited: Earth’s Biologically Richest and Most Endangered Terrestrial Ecoregions. CEMEX, 0-392.

Obrycki JJ, Kring TJ (1998) Predaceous coccinellidae in biological control. *Anny Rev Entomol*, 43, 295–321.

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12:361–371.

Pellissier L, Anne Bråthen K, Pottier J, et al (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography* 33:1004–1014.

Phillips SJ, Dudik M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. In Proceedings of the Twenty-First International Conference on Machine Learning, 655-662.

Phillips SJ, Anderson RP, Schapire SP (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259.

Pliscoff P, Luebert F, Hilger HH, Guisan A (2014) Effects of alternative sets of climatic predictors on species distribution models and associated estimates of extinction risk: A test with plants in an arid environment. *Ecol Modell* 288:166–177.

Polce C, Termansen M, Aguirre-Gutierrez J, et al (2013) Species Distribution Models for Crop Pollination: A Modelling Framework Applied to Great Britain. *PLoS One.* 8(10): e76308

Porfirio LL, Harris RMB, Lefroy EC, et al (2014) Improving the use of species distribution models in conservation planning and management under climate change. *PLoS One* 9:1–21.

Poutsma J, Loomans AJM, Aukema B, Heijerman T (2008) Predicting the potential geographical distribution of the harlequin ladybird, *Harmonia axyridis*, using the CLIMEX model. BioControl 53:103–125.

Pyke CR, Andelman SJ, Midgley G (2005) Identifying priority areas for bioclimatic representation under climate change: A case study for Proteaceae in the Cape Floristic Region, South Africa. *Biol Conserv* 125:1–9.

Roy HE, Brown PMJ (2015) Ten years of invasion: *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Britain. *Ecol Entomol* 40:336–348.

Roy HE, Adriaens T, Isaac NJB, et al (2012) Invasive alien predator causes rapid declines of native European ladybirds. *Divers Distrib* 18:717–725.

Roy HE, Brown PMJ, Adriaens T, et al (2016) The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. *Biol Invasions* 18:997–1044.

Royston P (1982) An extension of Shapiro and Wilks's W test for normality to large samples. *J. Appl. Stat*, 31, 115–124.

Royston P (1983) A simple method for evaluating the Shapiro–Francia W' test of non-normality*. Statistician,* 32, 297–300.

Samaniego H, Marquet PA (2009) Mammal and butterfly species richness in Chile: Taxonomic covariation and history. *Rev Chil Hist Nat* 82:135–151.

Scherson RA, Albornoz AA, Moreira-Muñoz AS, Urbina-Casanova R (2014) Endemicity and evolutionary value: A study of Chilean endemic vascular plant genera. *Ecol Evol* 4:806–816.

Schurr FM, Pagel J, Cabral JS, et al (2012) How to understand species' niches and range dynamics: A demographic research agenda for biogeography*. J Biogeogr* 39:2146–2162.

Segovia RA, Hinojosa LF, Pérez MF, Hawkins BA (2013) Biogeographic anomalies in the species richness of Chilean forests: Incorporating evolution into a climatic - historic scenario. *Austral Ecol* 38:905–914.

Silva DP, Gonzalez VH, Melo GAR, et al (2014) Seeking the flowers for the bees: Integrating biotic interactions into niche models to assess the distribution of the exotic bee species Lithurgus huberi in South America. *Ecol Modell* 273:200–209.

Vásclavick T, Meentemeyer RK (2009) Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions ? *Ecol Modell 220*:3248–3258.

Veran S, Piry S, Ternois V, et al (2016) Modeling spatial expansion of invasive alien species: Relative contributions of environmental and anthropogenic factors to the spreading of the harlequin ladybird in France. *Ecography* 39:665–675.

Villagran C, Hinojosa LF (1997) Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. *Rev Chil Hist Nat* 70:241–267.

Warren DL, Glor RE, Turelli M (2010) ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography* 33:607–611.

Woodin SA, Hilbish TJ, Helmuth B, et al (2013) Climate change, species distribution models, and physiological performance metrics: Predicting when biogeographic models are likely to fail. *Ecol Evol* 3:3334–3346.

Zhang M-G, Zhou Z-K, Chen W-Y, et al (2012) Using species distribution modeling to improve conservation and land use planning of Yunnan, China. *Biol Conserv* 153:257–264.

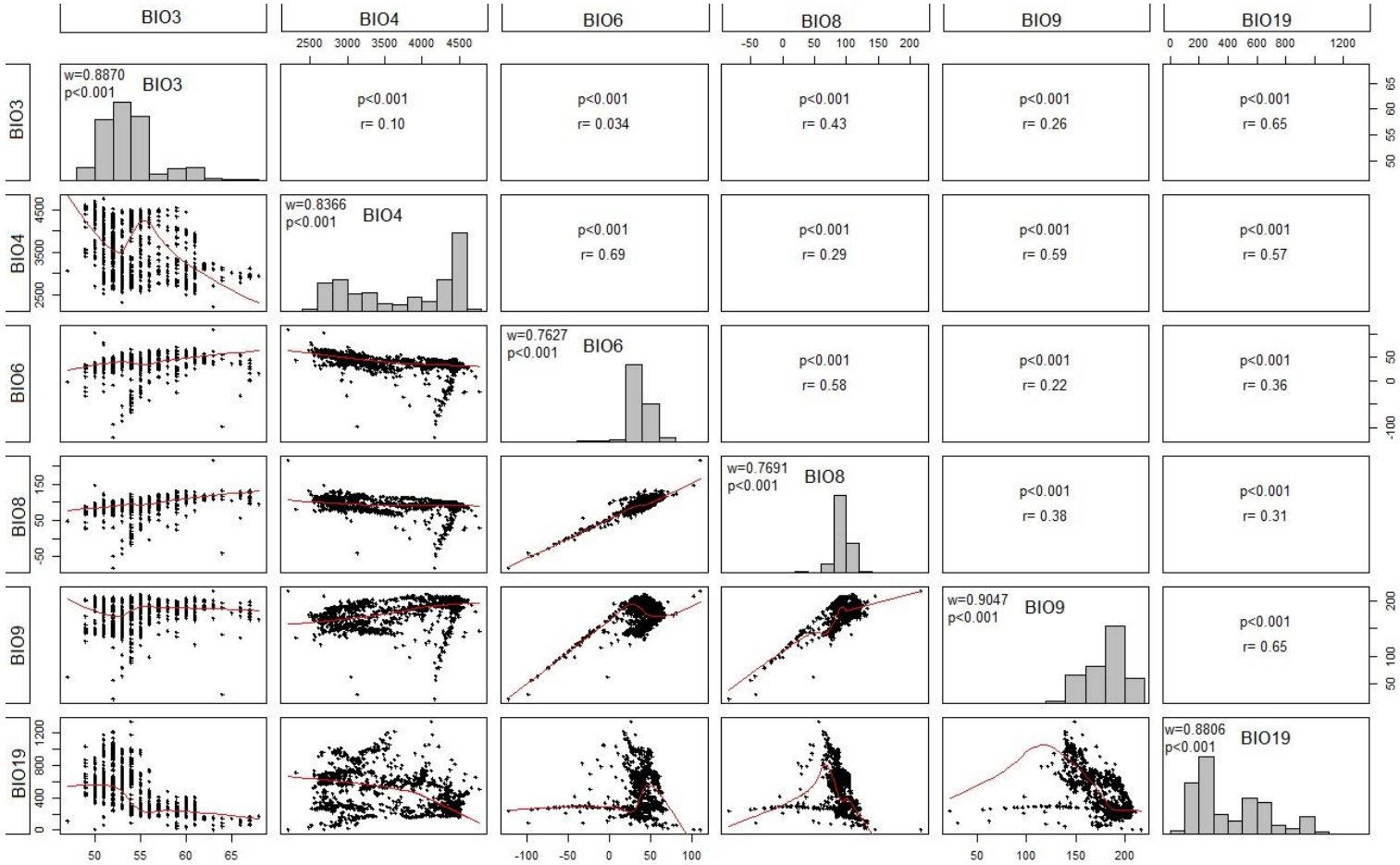
Zhao Y, Feng D, Yu L, et al (2016) Detailed dynamic land cover mapping of Chile: Accuracy improvement by integrating multi-temporal data. *Remote Sens Environ* 183:170–185.

Material suplementario

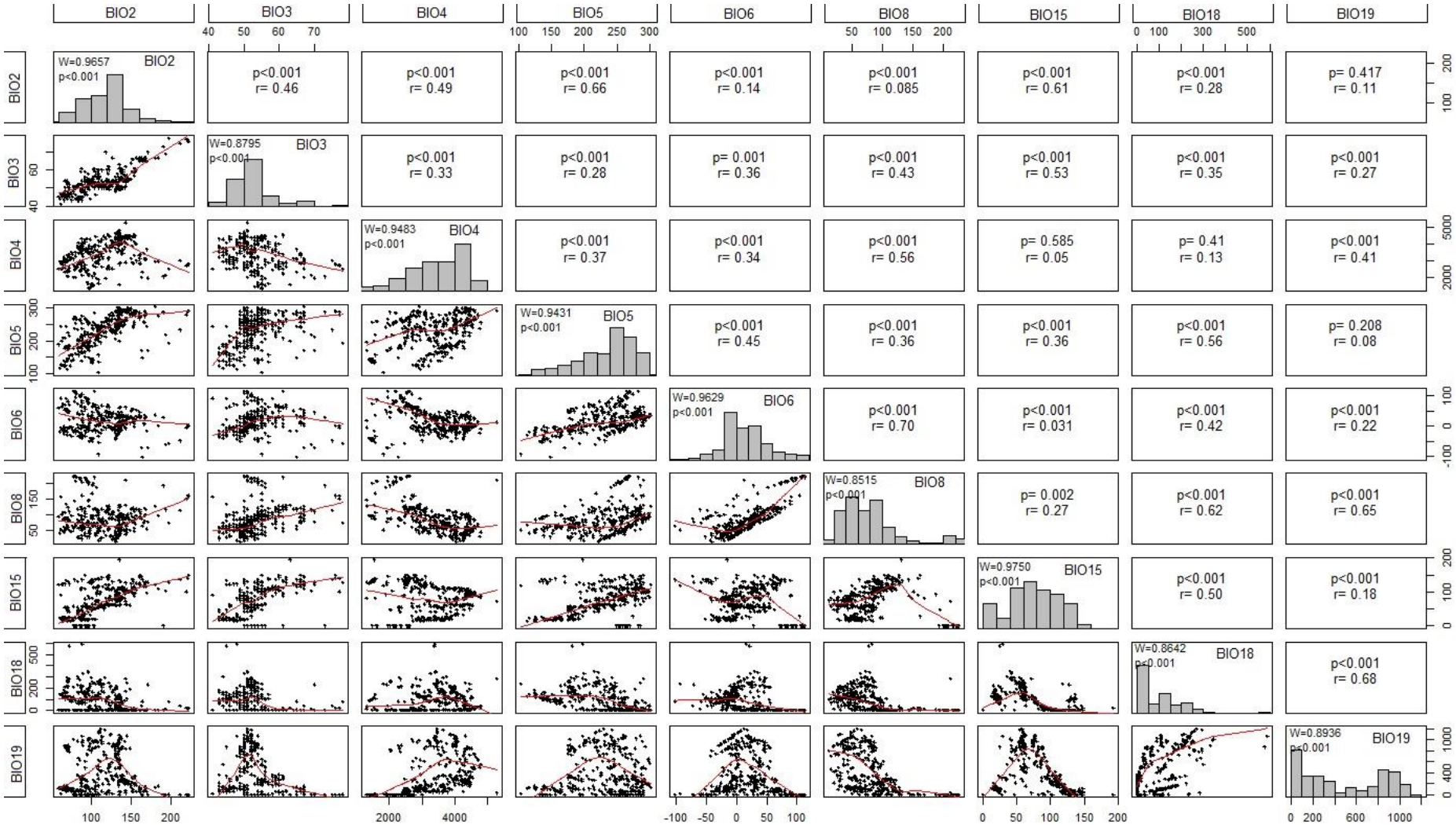
Figure S 1: *Correlation matrix of SDM variables.*

Panel of scatter plots (below the diagonal) of selected variables of final models with the 40-fold cross-validation technique, generated using R. 3.3.3 (Panel Cor function). Above the diagonal: absolute correlation coefficients and the statistical significance of each pair of variables. Boxes on the diagonal are the histograms of each variable and the respective Shapiro-Wilk values (W) and probabilities.

A) Scatter plots of variables of the *Harmonia axyridi* model.



B) Scatter plots of variables of the native coccinellid model.



C) Scatter plots of variables of the endemic coccinellid model.

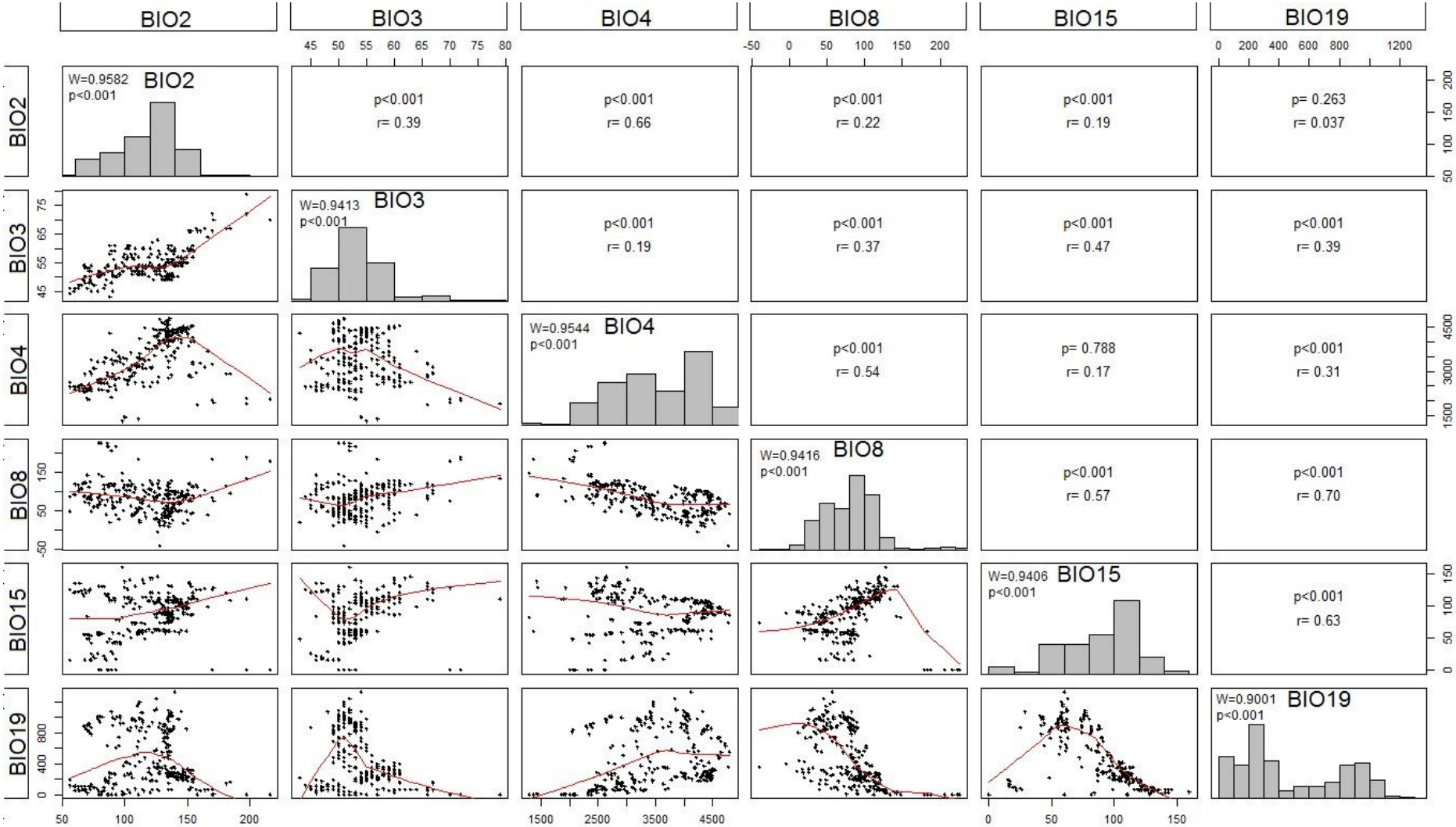


Figure S 2: *AUC curves and Omission/predicted rate.*

Plots of the accuracy of each model with 40-fold cross-validation technique. The upper plots correspond to ROC curves of each model, which represent the area under the curve (AUC). Lower plots show the omission rate and predicted area as function of cumulative threshold, averaged over the replicate runs (40).

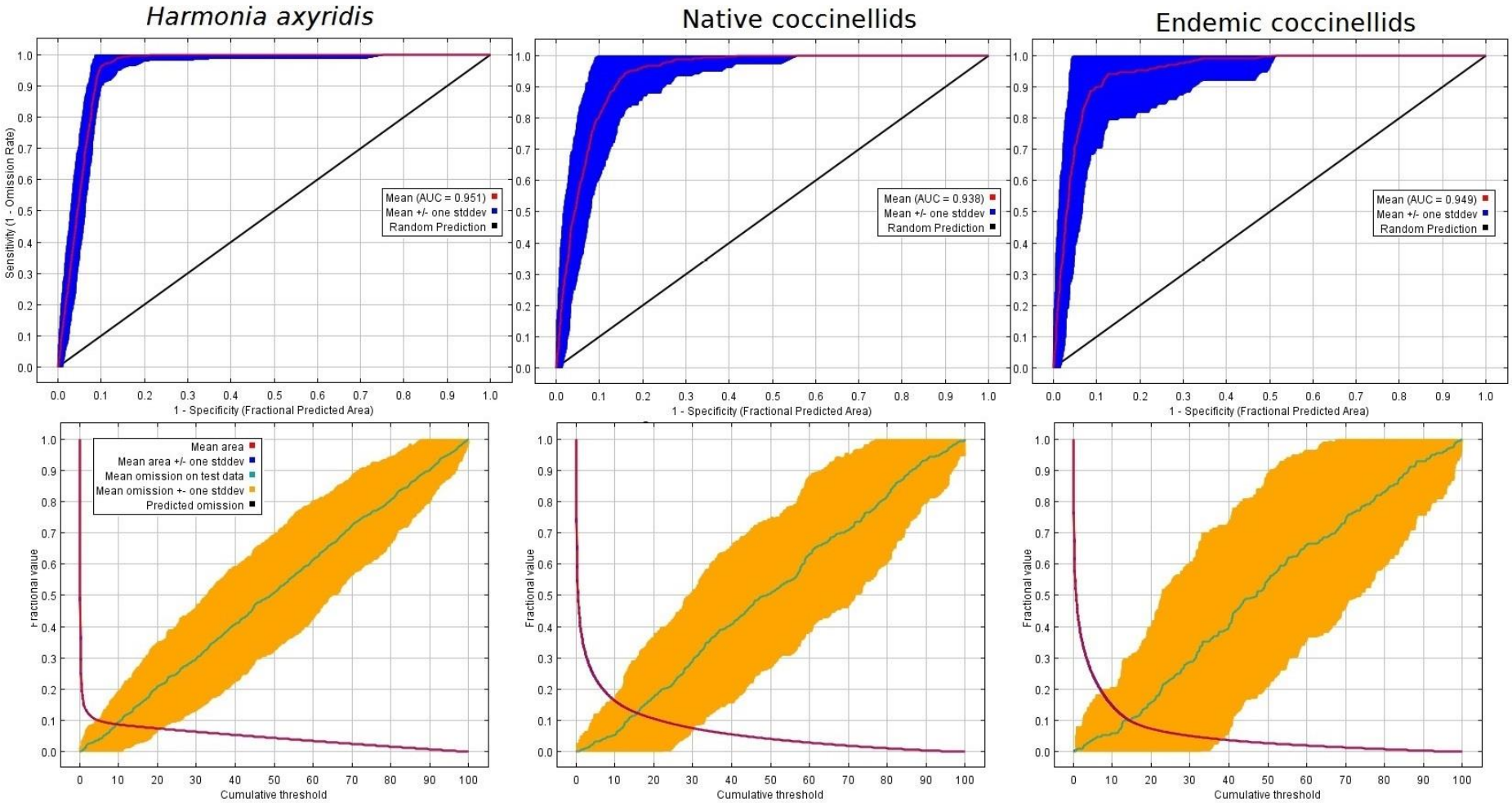


Table S 1: *Classification of land cover classes used in this study.*

It shows the grouping of land cover classes of Zhao *et al.* (2016) and the new classes used in this study. * The waterproof surface was only considered for spatial interaction, because this land cover in the northern represents rocks and other types of land cover; only in the central zone of the country does it represent urban cover. ** We avoid using land classes that Coccinellidae cannot use, including bare soil, wetlands or water bodies.

Land cover classes of Zhao *et al.* 2016	**Land cover classes used in this paper**
Rice paddies	Cropland
Greenhouses	
Other croplands	
Orchards	
Fallow	
Native Broad-Leaf- Primary	Primary native forest
Native of Conifers - Primary	
Mixed forest - Primary	
Native Broad-Leaf- Secondary	Secondary native forest
Native of Conifers - Secondary	
Mixed forest - Secondary	
Broad-leafed plantations - Adult	Exotic plantations
Broad-leafed plantations - Harvested	
Conifers plantations - Adult	
Conifers plantations - Harvested	
Annual meadow	Grassland
perennial meadow	
Other meadows	
Arid meadows	
Scrubland	Scrubland
Other scrubland	
Plantation of scrubland	
Succulents	
Other arid scrubland	
Arborescent scrubland	Arborescent scrubland
Waterproof surfaces*	Urban
Marshes	Not used**
Swamps	
Other wetlands	
Lakes	
Reservoirs	

Rivers	
Ocean	
Salares	
Sandy soil	
Rocks	
Gravel	
Snow	
Ice	
Clouds	

Figure S 3: *Map of land cover types used in this study.*

It shows the new classes used in this study, based on Zhao *et al.* (2016) (see Figure 5).

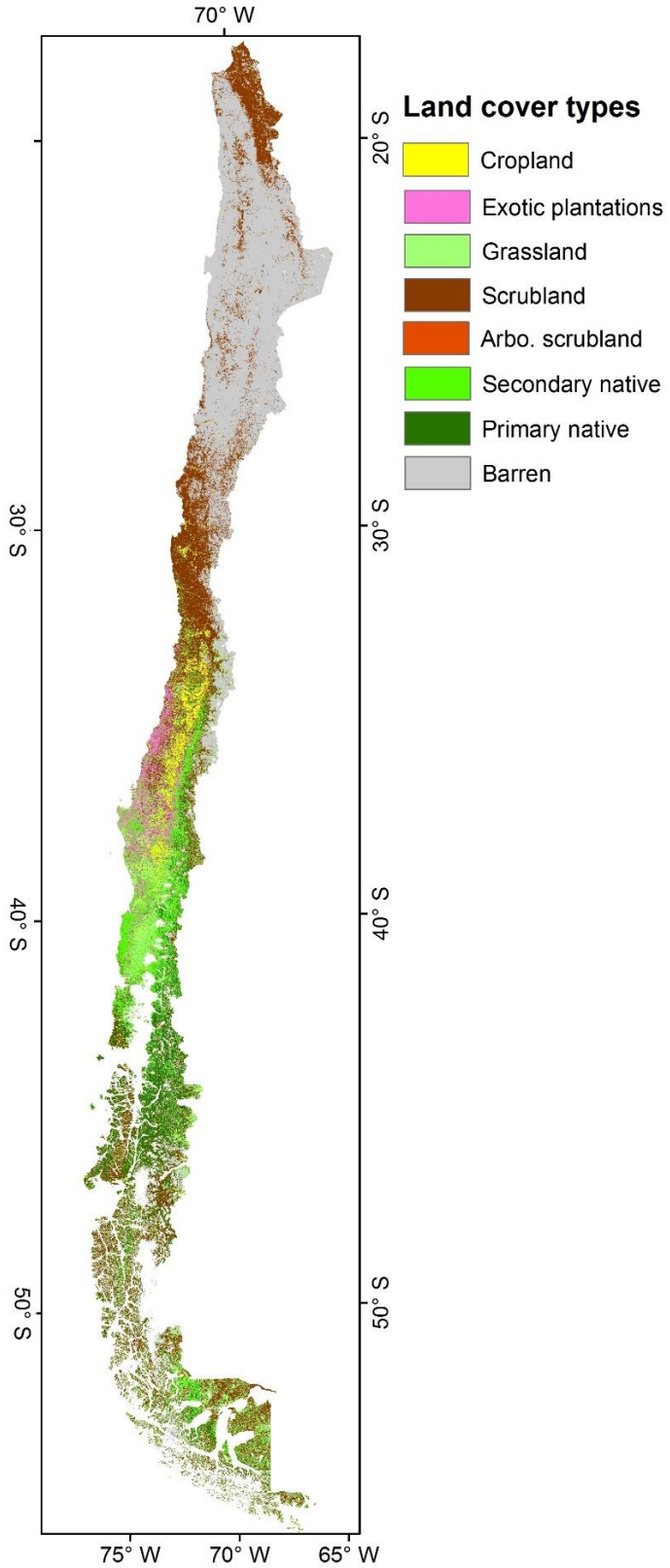
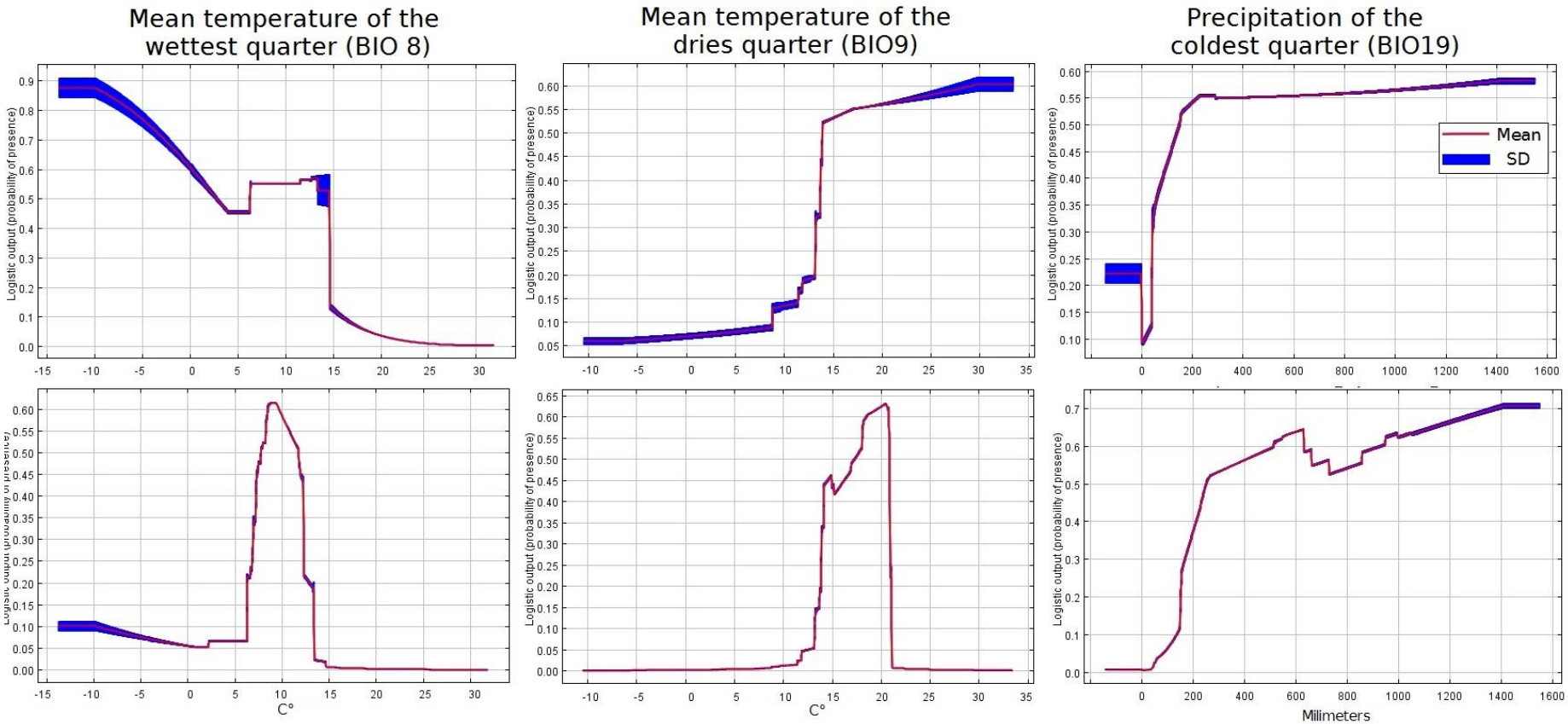


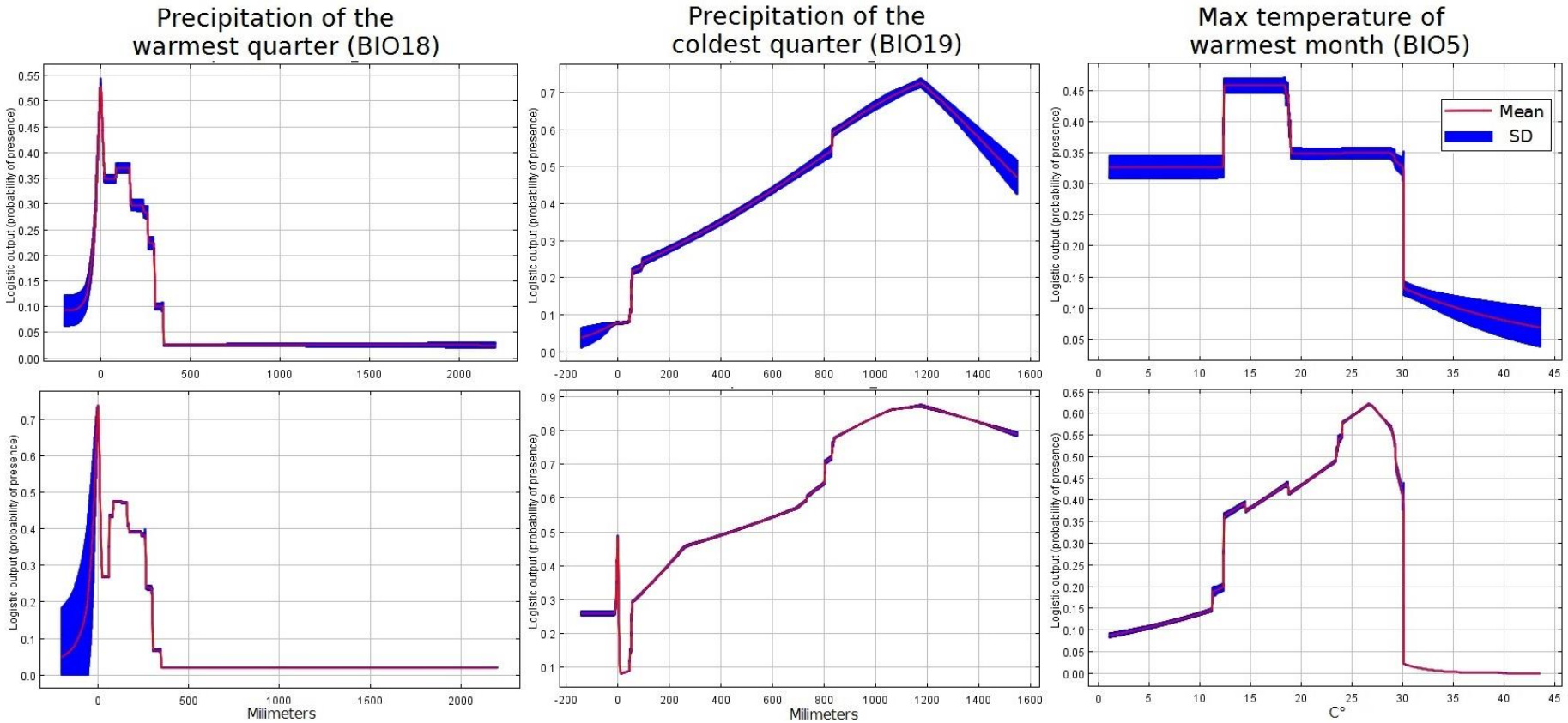
Figure S 4: *Curves of response of the each final model.*

The curves show how each environmental variable affects the prediction of probability of presence or bioclimatic suitability in the model generated by Maxent. The Y axis represents the probability of presence or suitability, the X axis is the magnitude of each variable (millimeters or degrees Celsius). The upper graphs represent the behavior of probability of presence keeping all the other environmental variables constant; the lower graphs show the behavior of probability of presence with a model using only the corresponding variable.

A) Response curves of *Hamonía axyridis*



B) Response curves of native coccinellids



B) Response curves of endemic coccinellids