Native bees in Mediterranean semi-arid agroecosystems: Unravelling the effects of biophysical habitat, floral resource, and honeybees

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ABSTRACT

The sustainable provision of pollination services in large regions of the Nearctic and Neotropics usually involves the coexistence of a rich assemblage of native bees and introduced bees in the same agroecosystem. This requires identifying biotic and abiotic conditions that improve the quality of semi-natural habitats surrounding agricultural crops aiming to enhance native bee survival. Here we unravel the contribution of habitat conditions, diversity of flowering plants, and honeybee abundance to the taxonomic diversity, flower visitation rates and functional trait distribution of native bees. We have selected three 1.2 km diameter experimental landscapes in a Mediterranean semi-arid agroecosystem of Central Chile, where wild bees, honeybees, and flowering plants were sampled in 83 10 × 10 m plots. The effects of eleven remote-sensing indices characterizing the habitat conditions, and their interactions with honeybee abundance have been analysed. Native bees were taxonomically richer in semi-natural habitats, with higher surface temperatures and near citrus crops. The flower visitation rates of native bees were positively affected by canopy closure and decreased in sites with a higher terrain slope. Highlands had lower honeybee abundance and native bees were more specialized. We found higher flower visitation rates of native bees on large patches with low abundance of honeybees and small patches with high abundance of honeybees. Visitation rate was also higher in sites with high flowering plant richness and with high abundance of honeybees. These findings suggest that native bees and honeybees differ in their habitat use and flowering resources. This partitioning may enhance, coexistence between these pollinator groups. We suggest that management of Mediterranean agroecosystems be focused on increasing forest canopy closure on the remnants of semi-natural habitats, while maintaining the flower diversity near crops and highlands.

1. Introduction

The abrupt decline of bee populations is of great concern for food security and sustainable management. In fact, three-quarters of fruit, vegetable, and seed production rely on pollinating insects like bees (Potts et al., 2010). Wild bees provide a pollination service either additive or synergistic to that offered by honeybees (*Apis mellifera*), which becomes increasingly important as honeybee populations decrease (Garibaldi et al., 2013; Winfree et al., 2018). The conservation of a diverse assemblage of wild bees, in terms of species and functional traits (e.g., body size and tongue length), may contribute to enhance crop pollination (Dicks et al., 2016; Winfree et al., 2018), and to support a high diversity of native plant species (Coutinho et al., 2018; Frund et al., 2013; Garibaldi et al., 2013).

Semi-natural habitats surrounding croplands serve as reservoirs of bee diversity and potential sources of pollinators for nearby cultivated crops. Hence maintaining or restoring those habitats is a strategy for sustainable agriculture (Kratschmer et al., 2018; Riojas-López et al., 2019). Human-induced land use change causes the loss and fragmentation of habitats that serve for nesting, resting, and reproduction habitat of pollinating insects. This process detrimentally, affect population persistence of pollinators impoverishing species assemblages

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(Kratschmer et al., 2018; Potts et al., 2010; Teuling et al., 2017). The degradation of seminatural habitats remaining in human - modified landscapes exerts additional negative effects on populations of pollinating insects and their interactions with plants, but these effects may be less evident and often result from different environmental drivers (Carman and Jenkins, 2016; Potts et al., 2010).

Anthropogenic habitat disturbances may cause a reduction in resource availability, intensification of negative interactions with other species (such as exotic ones), and detrimental changes in environmental conditions (e. g. microclimate stress or intensive agriculture), which ultimately causes a decrease of individual fitness and population size of wildlife (IPCC, 2015; Mortelliti et al., 2011). The effects of habitat degradation are often difficult to quantify (Kratschmer et al., 2018), which generates uncertainties when aiming to ensure the pollination service offered by wild bees based on the improvement of foraging and nesting habitat conditions (Dainese et al., 2018; Knapp et al., 2019). Bees are more abundant and diverse in flower-rich sites that provide pollen and nectar, but also in habitat fragments where they find suitable nesting or oviposition microhabitats (Kohler et al., 2008; Kratschmer et al., 2018). However, other biotic and abiotic factors may determine habitat suitability for wild bees. First, the availability of flowering resources may decrease for wild pollinators as competition with honeybees and other commercial pollinators increases, as evidenced by increased levels of niche overlap between native and exotic bee species (Trillo et al., 2019). Second, habitat structure, and biophysical conditions (e.g., local climate) indirectly affect bees through affecting abundance and phenology of their host plants. However, these factors also exert direct influences on their life history, behaviour, reproduction, and mortality, which become more marked as climate change progresses (Andersson et al., 2017; Nielsen et al., 2017). Since insects are particularly sensitive to variations in abiotic factors like temperature and humidity due to their ectothermic physiology, the structural properties of vegetation (e.g., canopy closure) play an important role in providing them with protection against extreme thermal conditions (da Silva et al., 2017). Degraded habitats usually support a reduced taxonomic diversity of bees, but also act as ecological filters for functional traits, ultimately undermining the pollination service (Hopfenmüller et al., 2014). Therefore, assessing the role of semi-natural habitats as reservoirs of wild bee diversity in agricultural landscapes requires assessing how introduced pollinators and habitat conditions limit the use of foraging and nesting resources.

In this study we have identified the major ecological drivers of habitat quality for native bees in a Mediterranean semi-arid agroecosystem of Central Chile, a region with high diversity of native pollinating insects but also characterized by intensive agricultural land use regimes (Montalva and Ruz, 2010). Conventional agriculture in Central Chile has relied on the use of commercial exotic pollinators, like honeybees and bumblebees, whose populations have spread and naturalized in native sclerophyllous forest and shrubland (Montalva et al., 2011). In this sense, the identification of habitat conditions that ensure the provision of pollinators for adjacent farm crops becomes challenging, especially when Central Chile is considered as a region increasingly prone to drought. Sustainable agriculture in this semi-arid region involves promoting the coexistence of exotic pollinators with a rich assemblage of native bees. The achievement of this sustainability goal rests on identifying suitable habitat conditions for native bees, but, in addition, it is critical to determine how different exotic and native bees are in terms of habitat and floral resource requirements. We have addressed habitat quality by combining remote-sensing estimates of habitat conditions (e.g. biophysical) with field measurements of floral resource availability and data of native and exotic honeybees visiting flowering plants. We particularly address the following questions:

1 What habitat variables better explain the taxonomic diversity, functional traits, and flower visitation rates of bees?

2 How important are flowering plants in explaining the taxonomic diversity, functional traits, and flower visitation rates of bees?

3 How important are honeybees and their interactions with habitat conditions in explaining the taxonomic diversity, functional traits, and flower visitation rates by bees?

4 How similar are native bees and honeybees in terms of their use of available floral resources?

2. Materials and methods

2.1. Study area

The study was performed in agricultural landscapes of Central Chile (33° 39`S, 71°14`W), a Mediterranean semi-arid zone with mean annual temperature of 14 °C and where rain (mean rainfall: 360 mm yr^{-1}) is concentrated during the austral winter while summers are extremely dry and hot (Sarricolea et al., 2017). Agricultural landscapes include a mosaic of fruit crops (mostly citrus, avocado, strawberry, melon, tomato, and apple) and semi-natural habitats, including sclerophyllous forest and shrubland (see below; Fig. 1). Honeybees are the most abundant non-native pollinators of fruit trees in the study area. Shrubland vegetation, the dominant cover type, is a heterogeneous habitat that includes *Acacia caven* savanna (with acacia trees scattered across prairies), in addition to dense and sparse sclerophyllous shrubs, dominated by evergreen species such as *Lithraea caustica*, *Baccharis paniculata*, and *Colliguaja odorifera* (Armesto and Pickett, 1985).

2.2. Selection of sampling units

Three non-overlapping 1.2 km diameter agricultural landscapes were selected for our study, based on the dispersion distances of European Apoidea species with size similar to that of native species in our study area (Fig. 1; Gathmann and Tscharntke, 2002). Land cover classes (habitat types) were characterized in each landscape using high-resolution Google Earth (WorldView 2, Geoeye and Spot 5) images, analyzed in two steps. First, an object-based classification (segmentation procedure) in the Orfeo package of Qgis 3.0 (Grizonnet et al., 2017) to determine the polygons, and then a photointerpretation in Qgis 3.0 calibrated with a field campaign to classify these polygons into ten categories (forest, shrubland, grassland, water bodies, citrus crops, avocado crop, annual crops, bare soil, roads and built area).

2.3. Sampling of bees and flowering plants

Bee sampling was conducted once a month during the austral spring (from September to November 2017), thus adjusting sampling dates to
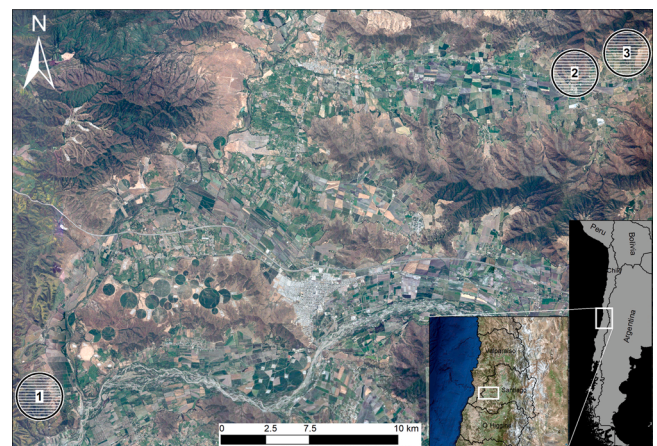

Fig. 1. Study area with the three landscape units (1.2 km diameter circles) located in a semi-arid Mediterranean agricultural landscape in central Chile.

the phenology of wild and fruit plants. Wild bees, honeybees, and flowering plants were sampled in 10 × 10 m squared plots randomly distributed across patches of semi-natural habitats (sclerophyllous forest and shrubland) identified from the land cover classification map (see above). Sampling was conducted on 83 plots (26, 31 and 26 plots in the landscapes), separated by more than 100 m from each other. The small size of the plots (100 m^2) provided intensive (unbiased) observations of flower visitation frequencies, while controlling for the total number of flowers locally available. In addition, the plot size was consistent with the spatial resolution of the remote sensing imagery employed (see below). All native and exotic flowering plants within the plots were identified at the species level, and their phenology was monitored along the study period. The taxonomic diversity of flowering plants was measured in each plot as: A) Chao's species richness index which determines the total species richness and deals with potential sample-size bias and, B) Shannon diversity index that takes the relative abundance of taxonomic units into consideration (Gotelli and Colwell, 2011).

Plots were sampled between 10:00 and 16:00 h local time, during days with sunny weather conditions and air temperatures above 18 °C, thus ensuring the samples to be comparable in terms of weather conditions. Observation sessions were conducted by two trained observers who counted all the bee's flower visits on ten focal flowering plants. The criterion used to select the focal flowering plants was based on ensuring the representation of most of native and exotic species present in the plot, thus avoiding replicating the same plant species in the sampled plot. All wild bees were collected with sweep nets after being observed visiting the flowers of focal plants. The collected bee individuals were identified at the species level in the laboratory.

Based on the collected data, we estimated the following variables that were later specified as response variables in statistical models (see Data analysis section):

1) Taxonomic diversity of native bee species, including Chao's species richness index and Shannon's diversity index.
2) Flower visitation rate of native bees, measured as the total number of native bees recorded visiting flowers in each plot during the sampling period, totalizing a sampling effort of 18 h per plot (6 h / month per 3 month). Similarly, the abundance of honeybees was quantified as the total number of honeybees visiting flowers in each plot.
3) Community-weighted means of four functional response traits of native bees were recorded in each plot, including size-corrected linear morphological measurements and the volumetric proportions of eight generalized prey items. Response traits are considered as the traits that modulate the occurrence and abundance of species in relation with environmental filters (Coutinho et al., 2018; Wood et al., 2015).We selected bee traits linked with dispersal, trophic and specialization behaviours (Cane, 1987; Greenleaf et al., 2007), including tongue length (mm), pollen specialization (oligolectic vs. polylectic), pollen transport (thorax vs. metasoma), and inter-regular distance (mm).

2.4. Habitat variables

A number of biophysical and structural habitat variables (hereafter referred to as "habitat" variables) was estimated to characterize the biotic and abiotic environmental conditions in each sampling plot. We particularly focused on variables considered to be important for bees, aiming to represent vegetation characteristics, disturbances, habitat structure and composition, climate and physiography (Andersson et al., 2017; Elias et al., 2017; Hopfenmüller et al., 2014). The biophysical characterization of ecosystems (Pettorelli et al., 2017) was performed using different remote sensing products accessed and processed in Google Earth Engine, a cloud based-platform for managing geospatial information without processing limits (Gorelick et al., 2017). To reduce the bias arising from using only one satellite image/product, we used the median during the sampling year, but for some indexes we also included

information for the last two years to capture the history of each pixel. In addition, cloudy images were discarded. All biophysical and structural habitat variables included in this study are detailed in Table 1, including: wildness index (WI), surface temperature, vegetation humidity (Normalized difference water index NDWI), fire disturbances (Burned area index; BAI), canopy closure (Vegetation continuous fields; VCF) and vigour of vegetation (Normalized difference vegetation index; NDVI) (Fig. 2). We also included additional topographic variables and spatial patch metrics (Table 1). Metrics of individual patches of sclerophyllous forest and shrubland (shape, area, perimeter and edge distance) and distances of these patches to different habitat types were estimated based on the land cover classification, in addition to the elevation, slope and exposition of the terrain in each plot, estimated using different remote sensing data (Table 1; Fig. 2).

2.5. Data analysis

We used Generalized Linear Mixed Models (GLMMs) to test for the effects of habitat variables (Table 1), flowering plants and honeybee abundance on the taxonomic diversity, mean functional traits and flower visitation rates of native bees quantified in each plot. Aiming to address the third research question we included additive and interaction terms of honeybee abundance with habitat variables. Significant honeybees × habitat interactions were interpreted using contour biplots. Using the *dispersion_glmer* function of the R package blmeco we found over dispersion in discrete response variables. Thus, GLMM with Gaussian and Negative Binominal distributed errors were implemented using *lmer* and *glmer.nb* functions of the R package lme4, with the landscape unit being included as a random effect (intercept) aiming to reduce spatial autocorrelation (Bates et al., 2015). The *Dredge* function of the MuMIn package in R was applied to determine the best models built with all possible combinations of explanatory variables (Barton, 2009). Models were selected based on the Akaike's information Criterion corrected for small sample sizes (AICc), ranking them using the AICc differences (ΔAICc) from the best model and Akaike weights (ω). Models with ΔAICc < 2 were considered to be equally supported by the data. Variance inflation factors (VIF), implemented with the *vif* function of the R package car, and Spearman correlations (rs) were used to test for multicollinearity in the predictors. Thus, models containing collinear variables ($r_s > 0.70$ and VIF > 3) were excluded from model selection (Fox and Weisberg, 2019). We checked for absence of spatial autocorrelation in the residuals of best-supported models using the Moran's I statistic (i.e, no Moran's I test was found to be significant; Table A1). All predictors were standardized to obtain comparable effect sizes. The *model.avg* function in the MuMIn R package was used to estimate the significance (p-value) and AIC-weighted importance of each model-averaged coefficient.

We combined Principal Component Analysis (PCA) and Hierarchical Cluster Analysis (HCA) to determine how similar native bees and honeybees are in the use of flowering plant species. First, we ordered bee species according to the plant species visited by them using a PCA on standardized flower visitation data. PCA allows us to reduce the data dimensionality (i.e., multiple species of plants) into a set of few uncorrelated factors, thus facilitating the interpretation of results. Loading variables that exceed a value of 0.5 were considered as "significant" in any of the factors of the PCA. The explained variance (R^2) and the cos2 of each variable on the PCA were used as goodness-of-fit criteria. Factors with an eigenvalue greater than the unity were considered significant and used in the HCA (see above). Second, we performed an HCA using mean's method, which calculates the distance between two clusters as the mean of the dissimilarity between the points in one cluster and those in the other cluster, separating the groups by the gain in inertia. PCA and HCA were performed using the FactoMiner and factoextra packages in R (Kassambara, 2020; Lê et al., 2008).

Table 1
Description of remote sensing derived variables of habitat estimated at the plot level. Variables include topographic attributes, spatial patch metrics, land cover (habitat types) and abiotic habitat (habitat structure, disturbance and climate).

Variable (code)	Description
Altitude (srtm)	Meters above sea level, based on SRTM version 3.0 of NASA (pixel resolution of 30 m), which capture the topography of the land surface with a radar-type active sensor (ALOS Palsar sensor).
Exposition (asp)	Solar exposition, estimated as the orientation of the topography with respect to north (expressed in degrees).
Slope (slp)	Slope of the land calculated using the difference in elevation between two pixels (expressed in degrees) and generated with the "Relief" tool of QGis.
Wildness index (WI)	Each land cover class is assigned to a level of wildness, as based on Grez et al. (2019) from the most (0) to the least disturbed (15) habitat: Buildings, roads, bare soil, annual crops, avocados, citrus crops, grape orchards, linear vegetation, grassland, open scrubland, mid-open scrubland, close scrubland, open forest, mid-open forest and close forest.
Distances to Forest (fd), Shrubland (sd), citrus crops (cd), Avocado (ad) and Building (bd).	Distance of the plot to the edge of different land cover classes using Qgis 3.0
Patch shape (shp), area (area), perimeter (edg) and edge distance (ed)	Metrics of semi-natural habitat patches estimated with Fragstat 4.2.1 (McGarigal et al., 2012)
Normalized Difference Vegetation Index (ndvi)	Index for the vigour of the vegetation based on the chlorophyll balance reflected in the infrared portion of the electromagnetic spectrum (36 images processed)
Normalized Difference Water Index (ndwi)	Vegetation humidity index sensitive to the amount of liquid water in the canopy calculated as the normalized difference between the near and middle infrared, with values from -1 to 1; higher values indicate greater humidity of the canopy. We used images generated since 2015, to generate a more robust index (147 images processed)
Burned Area Index (bai)	Index that shows perturbations associated with the occurrence of fires from the spectral distance between the red and near infrared in relation to a spectral reference point associated with charcoal (burned vegetation). We considered fires from the year 2013, which allowed including the history of fire perturbations of each pixel (180 images processed)
Vegetation continuous fields (vcf)	Index of canopy closure, equivalent to aerial biomass, including vegetation canopy cover of more than 5 m height expressed as the percentage of canopy closure (0–100). This product was generated based on a time series of Landsat 7 satellite images and phenological analyses of the world, which is available in the Global Forest Change platform (Hansen et al., 2013)
Surface temperature (temp)	Surface temperature detected using infrared (degrees Kelvin). We generated the mean of the thermal 13 infrared band of the satellite product "L1T Radiance" of Aster, which estimates the surface temperature expressed in degrees Kelvin. We used the median of the 13 band for the study months (54 images processed)

3. Results

A total of 334 bee individuals were collected (59 % were native and 41 % were honeybees) while visiting 379 individual flowering plants belonging to 39 species, and then classified into 21 bee species. The plant species most visited by native bee species were *Alonsoa meridionalis*, *Solanum crispum*, *Podanthus mitique*, *Cryptocarya alba*, *Escallonia pulverulenta*, *Flourensia thurifera* and *Alstroemeria pulchra*. Honeybees were observed visiting 26 plant species, while *Ruizanthedella mutabilis* was the native bee species visiting more plant species (8 plant species).

3.1. Effects of habitat variables and flowering plants

Habitat variables affected both native bees and honeybees, as shown by the best supported GLMM (Table 2, Fig. A1 and A2; see the best supported models and their averaged coefficients in Tables A1 and A2, respectively). The taxonomic richness and Shannon diversity of native bees decreased in sloping habitats (slp) and increased as the habitat became more pristine, i.e., with large wildness Index (WI) values (Fig. 3). The richness of native bees also increased with higher surface temperatures (temp; Table 2; Fig. 3). The flower visitation rate of native bees markedly decreased with the slope of the terrain and increased with canopy closure (vcf; Table 2; Fig. 3). The abundance of honeybees increased with habitat altitudes (srtm; Table 2; Fig. 3). The functional attributes of native bees were also affected by altitude, with bees increasing their pollen specialization, but decreasing the pollen load carried in their metasoma at higher altitudes (Table 2; Fig. A.2). Honeybees and native bees were also affected by the distance to certain habitat types. First, the abundance of honeybees increased with distance to sclerophyllous forests (ed; Table 2; Fig. 4) Second, the taxonomic richness and inter-tegular distance of native bees decreased with distance to citrus crops (cd; Table 2; Fig. 4).

3.2. Effects of honeybees

We did not find support for an additive effect of honeybees on native bees. Instead, foraging activity and functional traits of native bees were affected by the interactions of honeybee abundance with habitat variables (Table 2; Fig. 5 and A1). The flower visitation rate of native bees was found to be high in large habitat patches (> 50 ha) that present a low abundance of honeybees (< 1 in./plot), but also in small patches (<10 ha) with high abundances of honeybees (> 6 in./plot). Flower visitation rates reached the lowest levels (< 2 visits/plot) at large patches (> 30 ha) with high abundances (> 4 in./plot) of honeybees (Fig. 5). We found the opposite pattern for the interaction between honeybee abundance and richness of flowering plants, according which native bees are expected to have higher flower visitation rates (>4 visits/plot) at habitats rich in flowering plants (>5 species/plot) and with high abundance of honeybees (Fig. 5 and A1). Recorded native bees had, on average, higher inter-tegular distances in large patches (> 50 ha) and in presence of high abundances of honeybees (> 6 in./plot).

3.3. Flower resource use similarity between native bees and honeybees

Principal Component Analysis (PCA) showed that the two first explained approximately 58.7 % of the total variance of the relation of bee and flower assemblages (Fig. A3; Tables A4 and A5). The first component, which explained 46.4 % of the variance, showed a negative association of 19 species of native bees with honeybees in terms of the plant species visited. The second component, which explained 12.3 % of the variance showed the native bee, *Ruizanthedella mutabilis* (Halictidae) to be negatively associated with honeybees and 15 native bee species. Honeybees contributed 87.71 % of the variance of the first component, while the rest of the species contributed with less than 1 % (Table A4). The native bees, *R. mutabilis* (77.83 %) and *Ruizanthedella cerdai* (5.67 %) made the greatest contribution to the second component, while the
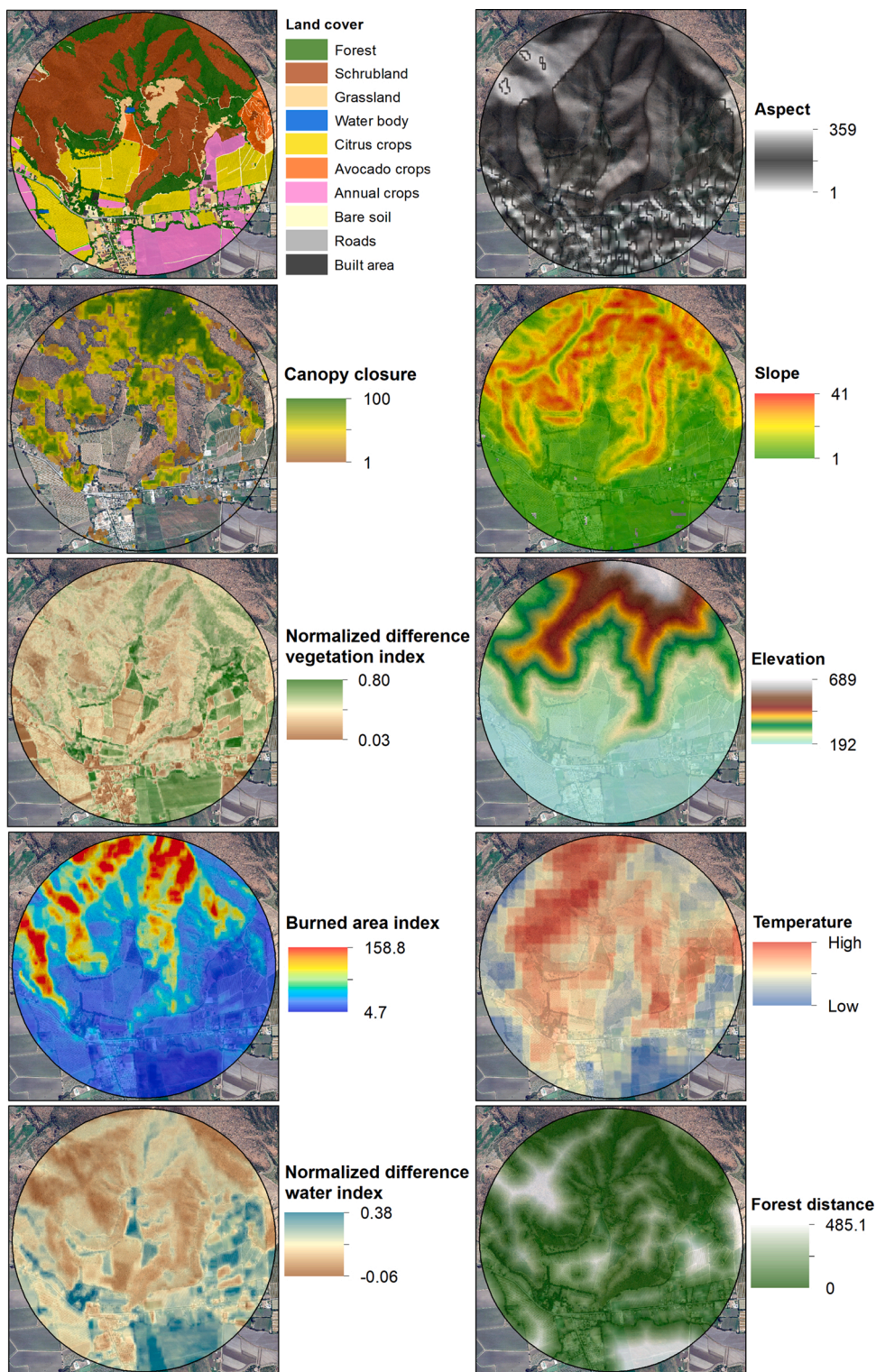
Fig. 2. Remote-sensing derived variables of land cover, abiotic habitat, topography and spatial patch metrics characterizing one of the three landscapes included in this study.

other bee species contributed with less than 2 %. A 46.2 % of the plants visited by honeybees were exotic ones, while 60 % of the plants visited by *R. mutabilis* were also exotic (Fig. A3). Hierarchical Cluster Analysis (HCA) identified six groups of bee species with different flower preferences (Fig. A4). HCA showed that honeybees exhibit marked foraging differences with the native bee species (Fig. A4). However, *R. mutabilis* was classified by HCA to be different from the other native bee species,

followed by a third cluster composed of *A. gayi* and *C. cyanopygus*. Besides, we identified three more clusters, two of them composed of only one species and a third composed of the other 15 native bee species (Fig. A2).

Table 2
Significant (p < 0.05) model-averaged coefficients of the best-supported (ΔAIC < 2) GLMM explaining taxonomic and functional variables of bee assemblages in the studied plots. Predictor codes correspond to those of habitat variables explained in Table 1, included their interactions (×) with the abundance of honeybees (Patch area with honeybee as area×Honey; Richness of plants with honeybees as Plant richness ×Honey). The detailed full list of coefficients and candidate GLMM are provided in Table A2.

Response variables		Predictors								
		Edge distance (ed)	Wildness Index (WI)	Distance to citrus crop (cd)	Slope (slp)	Elevation (srtm)	Temperature (temp)	Canopy closure (vcf)	area×Honey	Plant richness ×Honey
Taxonomic	Honeybee abundance	(0.62)*				(-0.27)*				
	Flower visitation rate of native bees				(-0.99)**			(0.72)**	(-0.66)***	(0.004)*
	Richness of native bees		(0.93)*	(-0.29)*	(-0.39)**		(0.35)*			
	Shannon diversity of native bees		(0.87)*		(-0.33)**					
Functional	Inter-tegular distance			(-0.24)*					(0.18)*	
	Tongue length									
	Pollen specialization					(0.62)*				
	Pollen transport					(-0.58)*				

0.01≤ p < 0.05*, 0.001 ≤ p < 0.01**, p < 0.001*.

4. Discussion

Habitat quality for native bees was a composite variable that included the availability of flowering resources and other habitat conditions (e.g., biophysical variables), but that also covaries with the abundance of honeybees. Our findings are consistent in suggesting that both native bees and honeybees differ in their patterns of habitat use in the landscape, while at fine-grained levels they exhibit segregation in the use of flowering resources.

The availability of flowering plants and habitat conditions were important predictors of the taxonomic diversity, community functional traits and flower visitation rates of native bee species. The positive influence of canopy closure on flower visitation rates suggests that the conservation of seminatural habitat remnants (forests) should be considered among the actions to be implemented for the sustainable management of Mediterranean agroecosystems. The canopy closure would contribute in enhancing suitability of local climate conditions for bees in warm climatic regimes like Mediterranean ones, offering them with an opportunity to adjust their body temperature to physiological requirements during foraging and reproductive activities (Coutinho et al., 2018; Papanikolaou et al., 2017). Stressful microclimate conditions from the openness of forest or shrubland may result in reduced survival, reproduction and movement rates. However, warm conditions benefited richness of native bee species, as shown by previous studies reporting the same pattern (Frund et al., 2013). Sclerophyllous forest and shrubland vegetation in Central Chile have been used for growing cows and goats, causing increased erosion and herbivory. Besides, these habitats have historically been affected by fires and fuelwood extraction (Schulz et al., 2010). Moreover, our results support that the wildness of vegetation prevailing in semi-natural habitats in Central Chile acts as an important driver of habitat quality, being responsible for a rich assemblage of native bee species. Our results also reveal spatial components of habitat quality, with an impoverishment of the native bee assemblage in sites located far (>1 km) from citrus crops. Native bees benefit from citrus crops from which they obtain alternative floral resources (Grajales-Conesa et al., 2013). Crops surrounded by native forest may be particularly favoured by a taxonomically diverse pool of bee species that eventually pollinate the flowers of cultivated plants (Riojas-López et al., 2019). Functional characteristics of native bees were also associated with habitat conditions. We showed that bee species located near citrus crops tend to be larger, which suggests that under certain environmental conditions the body size could have an effect for bees. Olygolectic bees

were more concentrated at higher altitudes, while polylectic preferred lowlands. This suggests that specialist species find suitable flowering plant species in highlands, while generalist bees are favoured by a broader offer of flowering plants in lowland sites and closer to the agricultural crops. Our findings suggest that the management on Mediterranean agroecosystems consider the differences of functional response traits between native bee species. First, conservation of oligolectic bees should be focused on the ecological maintenance and restoration of semi-natural habitats in highlands. Second, small-size native bees do probably not benefit from available flowering resource near citrus crops, contrasting with the large-sized ones, which highlights the importance of semi-natural lowland habitats surrounding citrus crops.

We found that native bees and honeybees co-occurred in lowlands of the valleys, where croplands and the native habitats surrounding croplands should offer a broad spectrum of food resources for both type of species, as found in previous studies for native bees (Grajales-Conesa et al., 2013). In this sense, the generalist behaviour of honeybees in relation to their use of habitat and floral resources could represent a potential threat to specialist native bees, arising mainly from resource competition and the potential transmission of pathogens (Stout and Morales, 2009). However, the foraging activity of native bees was more intense in sites with high floral resources and high abundance of honeybees, indicating that a high amount of flower resources reduces competition levels, offsetting a numeric increase in honeybees. Additionally, the large native bees occupying the large patches with a high abundance of honeybees indicate that the spatial overlap between honeybees and large-sized bees in large patches not necessarily results in high competition levels, probably due to a high availability of floral resources in those large habitat remnants.

Honeybees were the most frequent bee species observed feeding on flowering plants, including 65 % of plant species. The generalist behaviour of honeybees (Benelli et al., 2017) and their higher competitive ability respect to the native bees make them successful pollinators of a broad spectrum of floral resources (González-Varo and Vilà, 2017). The introduction of honeybees in cultivated areas promotes the spread of their populations across the adjacent semi-natural habitats (González-Varo and Vilà, 2017). About half of the flowering plants visited by honeybees were introduced plants, unlike the native bee species that preferred native plant flowers. The proportionally larger use of the introduced flowering plants as feeding resources by honeybees, as compared to native bees could generate a reduction on the niche overlap between honeybees and native bees (e.g., Fig. 7), which is a necessary
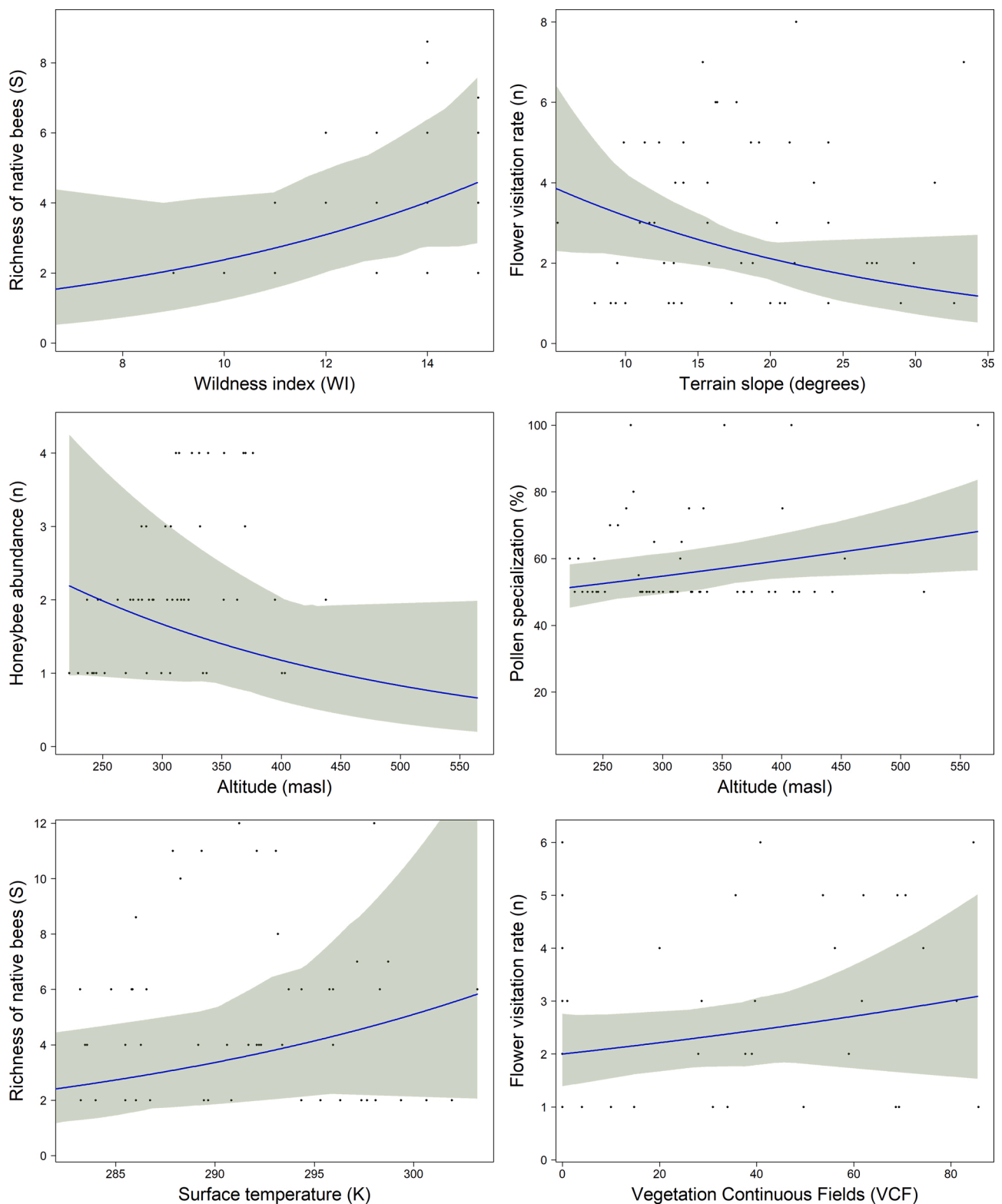
Fig. 3. Predictions from Generalized Linear Mixed-effects Model (GLMM) for the effects of habitat conditions (Table 1) on taxonomic (species richness, Shannon diversity and flower visitation rate) and functional (pollen specialization is quantified as the percentage of oligolectic species) variables of native bees as well as the abundance of honeybees.

condition for species coexistence (Frund et al., 2013). The generalist behaviour of honeybees and the adoption of pollination practices based on the use of hives within crops may explain their high abundance at low altitudes. However, we observed a reduced honeybee abundance in sites near sclerophyllous forests, which raises evidence against the invasion

of semi-natural forest ecosystems by honeybees.

Native bee species were heterogeneous in terms of their flower visitation rates and preferences for flowering plants. *R. mutabilis* was the most frequent native bee species visiting a great variety of flowering plants (Fig. 6), which is consistent with the category of polylectic
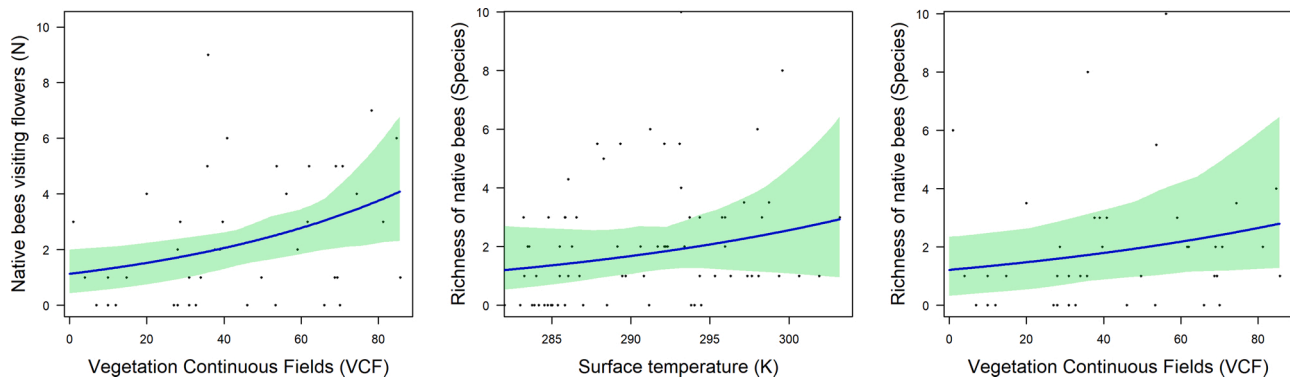
Fig. 4. Predictions from GLMM for the variation in honeybee abundance, taxonomic richness of native bees and Inter-tegular distance with distance to native forest and distance to citrus crops.
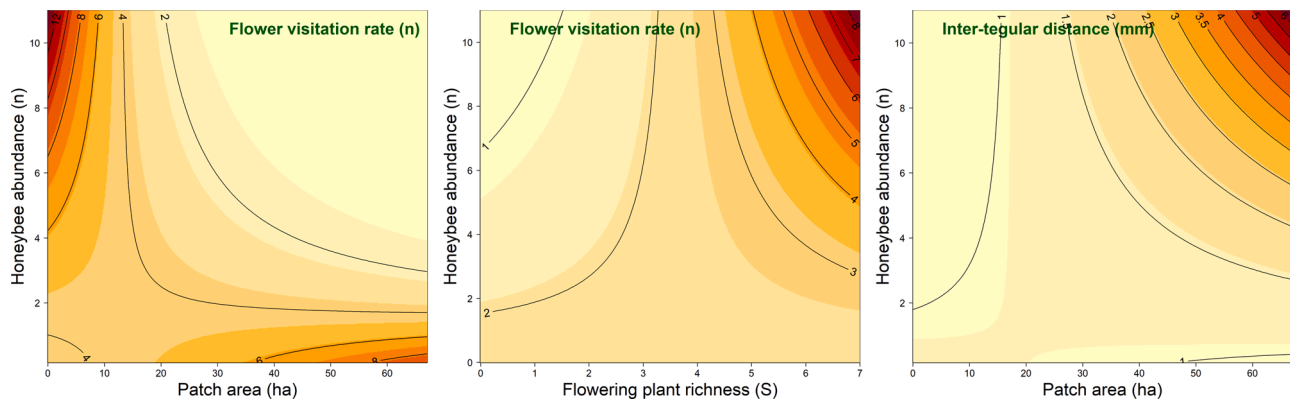
Fig. 5. Bivariate contour plots of GLMM predicting the flower visitation rate (left and centre plots) and Inter-tegular distance (right plot) of native bee species as functions of the interaction of honeybee abundance with habitat variables (patch size and flowering plant richness). Response variable is described in the upper part of the graph (green letters). Black contour lines are labelled with the response variable value, while yellow-dark brown colour gradient indicates a low to high gradient of the response variable (darker brown = high values; lighter yellow = low values). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

species. However, the ability of *R. mutabilis* to switch its preference to the flowering plants with larger availability under different habitat conditions (Polidori et al., 2010) suggests *R. mutabilis* behaves as a habitat generalist. Previous studies show higher abundance of Halictidae bees, like *R. mutabilis,* in structurally less complex landscapes (Morrison et al., 2017), as typically observed in agricultural landscapes where honeybees are the main pollinators (Hendrix et al., 2018).

4.1. Implications for landscape management

The quality of an ecosystem service is frequently associated with the biological diversity of the ecosystem (Daily et al., 2009; Dawson and Martin, 2015), a relation supported by the hypotheses of assurance of resources and biotic resistance (Tilman et al., 2014). Numerous studies support the importance of native bees as providers of pollination services in agroecosystems (Kremen, 2018; Schöb et al., 2018), highlighting the value of bee diversity (Wang et al., 2009). In this sense, our study provides new insights for the sustainable landscape-scale planning focused on agricultural areas surrounded by semi-natural Mediterranean habitats. Remnants of native sclerophyllous forest were found to be key ecosystems for the conservation of both native bee-plant interactions and bee populations of individual bee species. Semi-natural less disturbed habitats support a great diversity of native bees due to the presence of high-quality nesting areas and areas rich in floral resources, among other factors (Evans et al., 2018). The accelerated replacement of native sclerophyllous forest by avocado crops in areas where traditional agriculture had not been adopted (i.e., highland areas) is a major

concern for the conservation of natural habitats in this Mediterranean region (Alaniz, 2019). This pattern of land use change may cause adverse impacts on the specialized species of native bees that inhabit highlands, which in turn may not benefit from the flowering resources provided by avocado crops, thus compelling farmers to use honeybees.

Wildness index and forest canopy cover had a profound impact on the activity and richness of native bees in the vicinity of cultivated areas. Preserving the functional diversity of bees promotes the pollination of the native flora (Fig. 4) while causing pollination spillover-effects from bees dispersing to nearby crops (Goulson et al., 2015). Here, we suggest the high abundance and diversity of native bees found along the borders of agricultural lowlands in the valley may result in bee species providing pollination services while relaxing the need of overpopulate crops with honeybees. Functionally and taxonomically diverse assemblages of native bees should be highly effective in providing pollination service to croplands due to that different bee species are expected to partition the timing of their visits, as predicted by the resource assurance hypothesis (Garibaldi et al., 2013).

The use of beehives of honeybees for the pollination of crops is a common practice despite of having negative impacts on native bees living in natural habitats by competitive displacing (González-Varo and Vilà, 2017). However, sustainable agricultural practices should minimize negative interactions between native bees and honeybees by maintaining or restoring semi-natural habitats that act as reservoirs of native bee species. Since the XVI century, natural sclerophyllous habitats in Mediterranean semi-arid agroecosystems of central Chile have been lost due to the expansion of intensive agriculture, and, more

recently, by the increase of urban areas. In this region, agricultural lowlands and highland semi-natural habitats have historically co-occurred, with the latter being degraded, among other reasons by cattle overgrazing and firewood collection (Alaniz, 2019). Native bees in central Chile are vulnerable to the regional decrease in rainfall, which will possibly lead to an impoverishment of floral resources. Therefore, landscape planning intended to the functional integration of semi-natural habitats with agricultural practices are needed to achieve the conservation of native bee communities.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:10.1016/j.agee.2020.107188.

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