Article

Functional Traits Mediate the Natural Enemy Response to Land Use at the Local Scale

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Abstract: Arthropods are key nodes for the provision of ecosystem services such as pest control, but their response to land-use change is highly variable depending on the scale of analysis and the natural enemies' life histories. We evaluate the effects of landscape- and local-scale variables of natural enemies' communities on small-scale agriculture. We consider functional response traits to attain a mechanistic understanding of the effect of land-use changes on the biodiversity and resilience of natural enemies' communities. Predator and parasitoid arthropods were collected from thirteen raspberry farms to estimate functional diversity, complementarity, and redundancy indices. We found no effects of landscape heterogeneity, local habitat, or management practices on natural enemies' functional diversity. Regarding resilience, complementarity was high at most of the sites and was not affected by the landscape or local variables. However, redundancy was affected by two management practices. Weed control decreased natural enemies' abundance as well as the abundance of walker generalist predators and flying specialist parasitoids, while habitat richness decreased flying generalist predators. These results highlight the importance of management when the landscape matrix is heterogeneous. We conclude that small-scale agriculture in a heterogeneous landscape supports a functionally diverse enemy community, potentially promoting the resilience of pest control to land-use change.

Keywords: landscape heterogeneity; biological pest control; agricultural management

1. Introduction

Globally, there is consistent evidence of biodiversity declines due to landscape simplifications and agricultural intensification and the negative consequences on ecosystem functioning and the services they provide. In order to address these issues, the recognition of the fundamental role that biodiversity plays in supporting human well-being is a cornerstone [1]. In agroecosystems, beneficial arthropods, such as natural enemies and pollinators, are considered key nodes for ecosystem functioning and the provision of services, such as pest control and crop productivity [2]. Several studies have examined the relationship between natural enemy diversity and landscape heterogeneity, finding, in general, a positive relationship [3–5], mainly because of the presence of species capable of differential resource usage [6–8]. However, several other studies have shown the complexity of such a relationship, limiting our capacity for generalization [9,10]. Some possible causes of such a complex response to landscape heterogeneity (composition and configuration [11]) are the scale of analysis, the effect of within-farm management practices, and natural enemies' life histories [6,12–14]. In this sense, a mechanistic understanding of the biophysical controls on the natural enemy community is essential for decision making at the local and landscape levels.

The consideration of functional diversity is a promising tool, as it implies the understanding of the role that species play in agroecosystems and their responses to changes in environmental drivers [15,16]. In particular, response functional traits are eco-morpho-physiological characteristics of individuals related to the response of organisms to disturbances or habitat change [17,18]. In this sense, the differential responses of natural enemies to a particular landscape configuration, such as the proportions of crop and non-crop habitats, could be determined by species' dietary, dispersal, and overwintering traits [19]. Arthropod traits, such as life history and diet type, correspond to ecological strategies that are closely related to habitat use. For example, Lami et al. [20] evaluated how landscape changes can influence the habitat specialization of natural enemy communities and found that traits such as diet specialization (i.e., organisms with limited foraging flexibility) determine the ability to respond to landscape changes. Additionally, Martin et al. [19] found that a distinguishing trait of natural enemies in response to the landscape is the overwintering place: while non-crop overwintering organisms are enhanced by connectivity independently of the semi-natural cover amount, crop overwintering organisms are more abundant in less connected landscapes and in those with higher proportions of arable cover. Moreover, Dominik et al. [21] and Galle et al. [22] demonstrated that the effects of landscape on arthropod abundance depend on body size. Additionally, Hillaeret et al. [23] concluded that larger invertebrates occupy more isolated natural areas. Thus, relating response trait diversity with land-use change will allow the understanding of the ecological mechanism behind arthropods' responses. Moreover, focusing on the functional diversity of natural enemies can lead to a better understanding of the effect of land-use change on pest control ecosystem services.

The ecological resilience and stability of pest control in response to land-use change is also expected to depend upon landscape heterogeneity. In this sense, more heterogeneous landscapes are expected to harbor greater functional complementarity, given by the presence of species performing different roles for an ecosystem function. Moreover, the probability of finding species that perform similar functions but respond differently to the same disturbance could also be higher. Accordingly, the system has a "guarantee" or "insurance" to continue providing ecosystem functions despite land-use changes. This mechanism is known as the Insurance Hypothesis [24]. For example, patches of natural area composed of trees and shrubs correspond to landscape elements of greater structural complexity (different canopy strata) where greater species diversity is expected, as opposed to grassland patches, which are mostly composed of low herbaceous species. Thus, landscapes with higher proportions of natural areas (a measure of composition) can result in greater habitat availability for more diverse natural enemies. In turn, the connectivity of these patches, calculated as the edge density (a measure of configuration), allows for greater mobility of organisms between patches, functioning as biological corridors [25]. Therefore, it is expected that in more heterogeneous landscapes (higher proportions of natural areas and more dense patches), greater diversity of natural enemies will be found, fulfilling different ways of responding to land use (functional response diversity) and thus providing complementarity and redundancy in biological pest control.

There is significant evidence of the role of landscape heterogeneity in providing natural contributions to human beings, but this information is often contradictory. On the one hand, several authors have found a strong positive relation between non-arable areas and natural enemies' abundance and diversity [3,12,14,26], emphasizing the importance of heterogeneous landscapes in determining biological pest control [5,14]. On the other hand, numerous studies have shown that natural enemies' responses to landscape heterogeneity may also be neutral or negative [4,9,27], featuring a context-dependent result (sometimes including management practices or other farm-level drivers). The main objective of this study is to assess the key functional response traits of natural enemies' communities to landscape and local drivers as well as the resilience and stability of pest control to land-use changes. First, we hypothesize that heterogeneous landscapes, characterized by diverse configurations and compositions, promote more diverse natural enemies, but the

effect may be determined by response traits related to resource availability. We predict that the presence of species with a higher mobility capacity (i.e., flyers with larger body sizes) will be mainly affected by landscape variables, while the presence of species with a lower mobility capacity (walkers, small body size) will be mainly determined by local management practices. Second, we hypothesize that heterogeneous landscapes ensure greater resilience to land-use change in natural enemies' communities due to the importance of non-crop habitat heterogeneity. We predict that the functional response complementarity and functional redundancy in pest control will be mainly affected by the landscape, rather than by local management strategies.

2. Materials and Methods

2.1. Study Site

This study was carried out in the Andean valley region of Comarca Andina del Paralelo 42°, comprising territories located between 41°30′ and 44°55′ south and 71°20′ and 71°42′ west (Río Negro and Chubut provinces), Argentina. This region belongs to the Patagonian Andean Forests eco-region and is bordered to the west by the Andes Mountain Range, which conditions the precipitation regime on the leeward side [28]. The landscape is characterized by a matrix of native and feral forests interrupted by urban areas, agricultural patches, and grasslands with multiple uses. The latter are usually old clearings for extensive cattle grazing, mostly composed of spontaneous herbaceous vegetation. The agricultural patches are mainly fruit crops (mostly berries), horticulture productions, and hop farms to a lesser extent.

2.2. Sample and Identification of Natural Enemies

Thirteen farms producing raspberry (*Rubus ideaus* L.) of the Autumn Bliss variety were selected in order to represent landscape heterogeneity (i.e., from 14% to 84% natural area in a 500 m radius). During January 2021, four pitfall traps (8 cm in diameter) were placed at each farm in the center of the biggest raspberry stand (henceforth, the focal point) at distances of 3 m from each other. Traps consisted of plastic containers with lids and three "windows", buried so that the windows were flush with the ground. The containers were half-filled with water with a drop of soap in order to break the surface tension so that the arthropods falling into them could not escape. Traps were left in the field for seven days, and then the contents were placed in a solution of 70% alcohol for later classification.

All individuals were identified in the laboratory to the order level under a stereoscopic magnifying glass, simultaneously selecting those that could be potential natural enemies (predators and parasitoids). Using dichotomous keys [29–31], each individual was classified into a family or superfamily, and morphospecies were differentiated based on morphological characteristics (wing shapes, color, body size, etc.). For each morphospecies, particular functional response traits identified in the literature [32,33] were recorded: life habit (predatory or parasitoid); dispersal strategy (walker, flyer, or both); diet breadth (generalist or specialist); diet in life history (the same when it has the same diet at all stages and different when it changes diet, e.g., Syrphidae has predatory larvae and nectivorous adults); and body size (measured by the captured morphospecies, in mm).

2.3. Landscape-Level Variables

A land cover map was created around the focal points (by sampling the midpoint of each farm) using the advanced digitization tool in QGis software (Figure 1). We worked with an existing forest type and land cover classification for the region [34] (CIEFAP (Andean Patagonian Forestry Research and Extension Center; Spanish acronym) classification) with a 10 m resolution. Firstly, the layer of the first level of classification (native forest, non-native forest, or other land cover) was selected and used to create polygons of native forest, semi-natural vegetation (shrubs and exotic trees), grasslands (open fields of spontaneous or sown herbaceous vegetation), forest plantations (mostly exotic pinaceous), and urban areas. Secondly, we used satellite images from Google Satellite and Google Earth in two periods

of the year 2021 (summer and winter) to generate the necessary contrast to identify the different land uses and land covers. Additional and new digitalization was also carried out to update the polygons of the preview classification that have undergone changes in recent years since the original inventory was formed (i.e., housing development of rural areas, clearing of native forest or forestation). For the delimitation of national and provincial roads, the primary road network layer (line) provided by the National Geographic Institute (IGN) of Argentina was used with buffers of 10 and 7 m respectively, so that the resulting polygons incorporated roadsides and bicycle paths where appropriate.
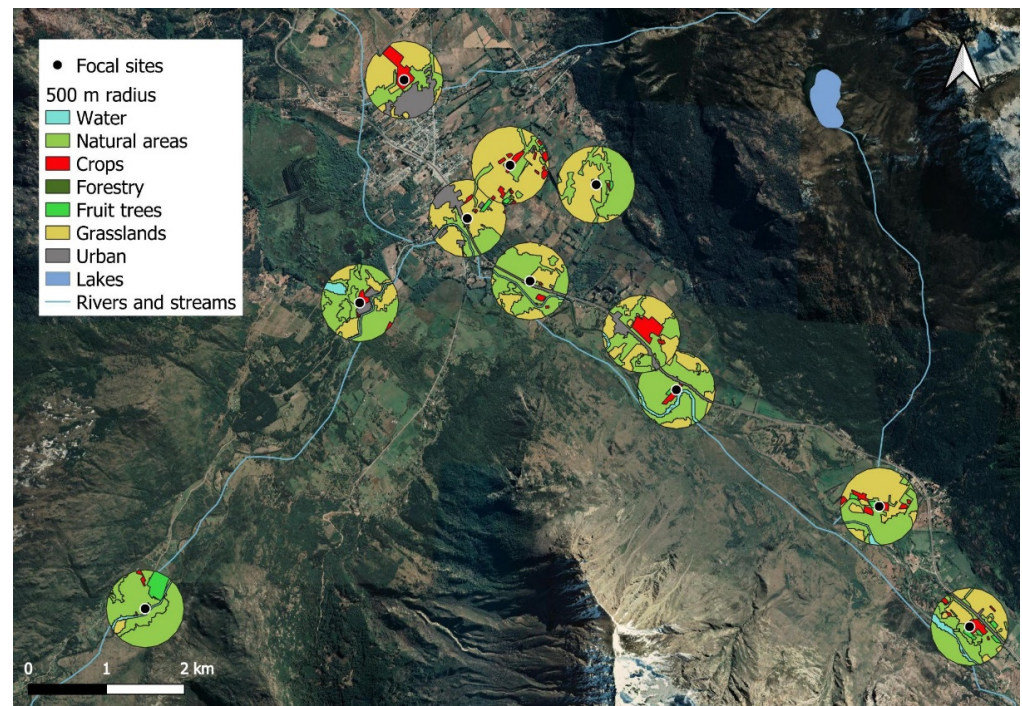

Figure 1. Extract of the created land cover map for the study sites. Circles around focal points represent the 500 m radius.

The resulting land cover map was then used to calculate the proportion of each landscape cover category (Table 1) at a 500 m radius from the focal point. Each cover proportion was a landscape compositional variable (explanatory variable). We also calculated the edge density for natural area patches as the sum of every patch perimeter divided by the total area. The edge density is a configurational landscape variable (explanatory variable).

Table 1. Landscape cover categories. Brief descriptions of patches and the methodologies used. CIEFAP = Andean Patagonian Forestry Research and Extension Center—Spanish acronym.

Category	Description	Methodology
Crops	Berry crops (*Rubus* sp., *Fragaria* sp., *Ribes*., etc): deciduous perennials; hops (*Humulus lupulus*): large squares in interannual cultivation with soil movement in winter; interannual horticultural crops with frequent rotation	Advanced digitizing
Fruit farm	Pome or stone fruit trees. Evenly or randomly distributed	Advanced digitizing
Grassland	Open fields with or without grazing. Natural grassland or sown pasture.	Advanced digitizing
Urban	At least 50% of the area covered or occupied by construction, streets, or roads	Advanced digitizing, CIEFAP classification, IGN road network route layer

Table 1. *Cont.*

Category	Description	Methodology
Natural areas	Exotic and native spontaneous shrub and tree vegetation	CIEFAP classification, Level 1, category "TF" and "OTF; Level 3, category "ArlesEx" and "ArbEx"
Forestry	Pinaceae forestation	CIEFAP classification, Level 3, category "Forest"
Ecotone	Mountain rockery, High altitude herbaceous vegetation	Advanced digitizing

2.4. Farm-Level Variables

From each focal point, four transects were drawn in the four cardinal point directions (N, S, E, W). In each transect, the type of habitat (crop, fruit bush, spontaneous herbaceous, spontaneous shrub, etc.) was recorded at five points from the focal point (10 m, 20 m, 40 m, 80 m, and 160 m), and the GPS coordinates of each point were recorded. With these data, we obtained the farm-level explanatory variables: habitat richness (number of different cover types) and habitat dominance ($D_i = \ln N + \Sigma P_i \ln P_i$.; D = habitat dominance. N = total number of land covers. P_i = Proportion of I land cover.) (habitat dominance = 1 means that a single habitat type occupies all recorded points, while habitat dominance = 0 means that all habitat types are equally represented in the points) [35,36]. Moreover, a brief interview of the owner or manager of each farm was conducted to record current and historical management practices: the presence or absence of weed control (regardless of the methods) and the type of irrigation system used (irrigation: drip or sprinkler). These were also used as explanatory variables in the models.

2.5. Data Analysis

2.5.1. Functional Diversity Indices

To evaluate the effect of surrounding vegetation and management on the natural enemy (NE) biodiversity, we obtained four biodiversity indices (response variables). As we had four subsamples per farm, the first step was to calculate the mean abundance per NE morphospecies in each farm. Then, we calculated two functional diversity indices: functional dispersion (Fdis) and functional divergence (Fdiv). Fdis is a multidimensional index calculated as the mean distance of individual morphospecies to the centroid of all morphospecies in the community [37]. Fdiv represents the morphospecies abundance distribution on the functional traits range [38].

2.5.2. Resilience Indicators

Several species performing similar roles in a community contribute to functional redundancy in ecological function (i.e., acting as natural enemies) [24,39,40]. Redundancy in biological control ecosystem function was determined by analyzing the abundance of natural enemies (Ab_NE). Additionally, the abundance of functional groups was used to estimate the redundancy of each functional trait within the biological control function (i.e., walker predators or flyer parasitoids). Functional groups were identified by performing a cluster analysis using the Ward linkage method. For this, we calculated a dissimilarity matrix based on the Gower dissimilarity index.

Complementarity, understood as species fulfilling different roles in the same ecosystem function [24,39,40], was measured as the proportions of functionally unique morphospecies (NE_sing) and functional group (FG) richness (NE_sing/NE_richness). FG richness was calculated as the sum of FG at each site. The proportion of functionally unique morphospecies with respect to the NE richness was calculated in order to assess the level of complementarity. This index is highly dependent upon the number and type of functional traits, highlighting the importance of selecting traits according to the ecosystem functioning of disturbance that needs to be addressed [38]. If all natural enemy morphospecies are functionally different, then NE_sing/NE_richness will be 1, indicating the greater value of functional complementarity of that community [41].

Functional diversity indices, cluster analysis, and NE_sing were calculated using the "FD" package [41]. All analyses were performed using R software, version 4.2.2 [42].

2.5.3. Statistical Analysis

Multimodel inferences were performed for each level of analysis: landscape (five land-use cover and edge density variables) and farm level (habitat richness and habitat dominance) across all combinations of explanatory variables using the MuMIn 1.47.1 package in R [43]. The model with the best fit was selected using a parsimonious criterion based on the lowest AIC [44]. Given that patches of different cover are repeated across the landscape and that the studied invertebrates have different dispersal distances, a conceptual focus of the work was to assess whether the same type of variable is important at different scales; thus, we analysed each study scale separately (see [45]). We performed linear regressions for most of the response variables to analyse the effects of five landscape variables on functional indices as well as abundance variables. Fruit trees, forestry, and ecotone covers were not used for the analysis because of their sporadic presence at each site. Normality and homoscedasticity assumptions were fulfilled due to input data that represented the mean values of the subsamples. FG richness was the only variable with a non-normal distribution, and thus, it was analysed using a generalized linear model with a Poisson distribution. We performed a Durbin–Watson test to evaluate the spatial correlations between residuals, resulting in non-significant differences. An ANOVA analysis (type I) was performed for the management variables (weed control and irrigation system). For significant ANOVA results (alpha = 0.05), we conducted a Bonferroni adjustment. All analyses were performed using R software [42].

3. Results

A total of 8287 individuals belonging to 20 different orders were collected from 13 communities. Of these, 919 were classified as natural enemies due to their predatory or parasitic nature, representing 65 morphospecies (Table S1). In one farm, two pitfall traps were lost (removed by animals), resulting in a very small representative community. Therefore, we decided to dismiss this community from the analysis.

The cluster analysis resulted in 4 functional groups (Figure 2). FG 1 and 3 were composed by generalist predators with the same diet throughout their lives. The main difference between the two groups was the dispersal type. While FG 1 (10 morphospecies) was composed exclusively of walkers (mostly spiders), FG 3 (17 morphospecies) was walkers/flyers (mostly beetles). FG 2 was the most abundant (34 morphospecies), and it was mainly composed of flying parasitoids (mostly wasps) that were all specialists with different diets through their life history. It was also the FG with the smallest average body size (2.5 mm), although some specimens reached 10 mm. FG 4 (4 morphospecies) was represented by flies and wasps, all flying, three generalist predators, and one generalist parasitoid with the same diet throughout their life history and a wide size range (2 to 15 mm).

3.1. Functional Diversity

We found no effect of landscape heterogeneity on natural enemies' functional diversity for either the compositional variables analyzed (the proportion of each landscape cover) or the configurational variables (edge density of natural areas). Both Fdis and Fdiv indices' null models showed the highest AIC in the multimodal inference analysis. Additionally, we found no significant effect of the vegetation cover on the functional diversity (Table S2). Moreover, the different management practices evaluated in this study had no significant effect on the functional diversity indices. Functional diversity did not change due to weedy or sprinkler irrigated stands with respect to stands without weeds and those that were drip irrigated (Table S2).

3.2. Resilience

Regarding complementarity indicators, at least 3 functional groups were identified at each of the twelve communities analyzed, indicating a great representation of every group of key functional traits. The FG absent in each case was FG4 which, in turn, exhibited the lowest richness (Figure 2). The NE_sing/NE_richness proportion indicated high complementarity on almost every farm (Table 2): at least 70% of the natural enemy (NE) morphospecies were functionally unique in eleven of the twelve farms. The results of multimodel inference indicated that the null model was the best fitted for both the FG richness and the number of functionally unique morphospecies (NE_sing). Furthermore, the ANOVA analysis showed no significant effects of the management variables on the FG richness and NE_ sing.
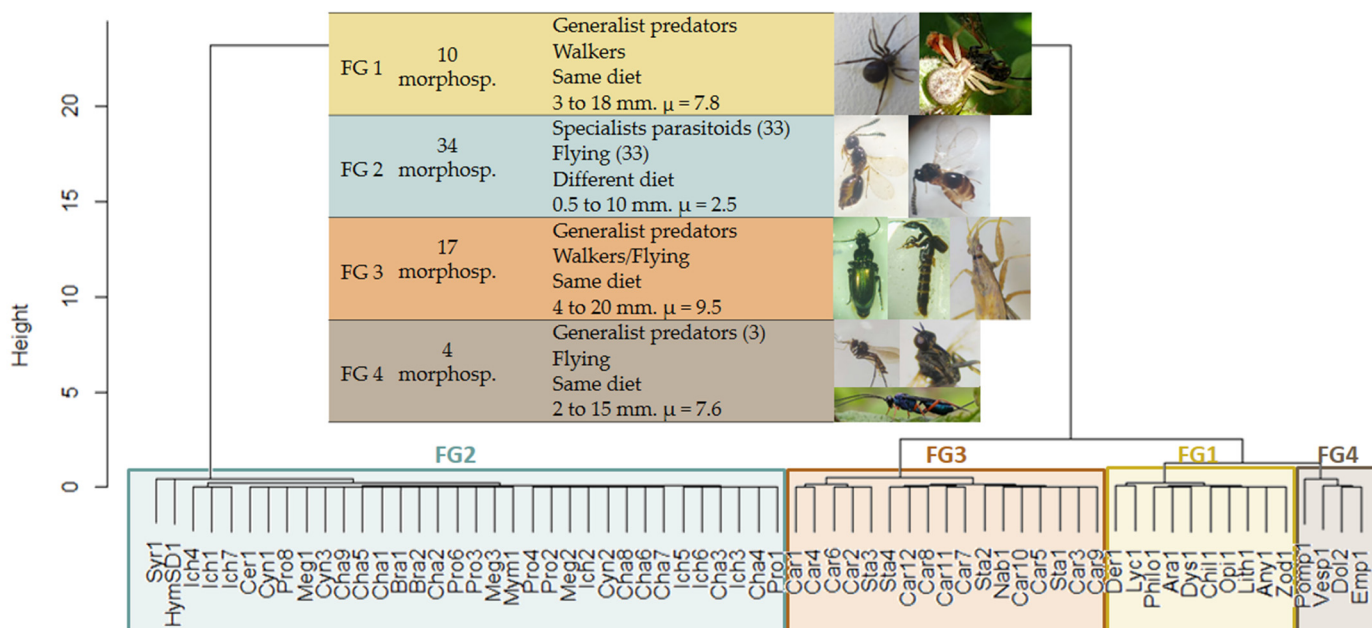

Figure 2. Cluster analysis results and functional response traits characterizing each functional group (FG). Each colored rectangle represents a different functional group, and names (in vertical) represent each morphospecies. The table inside the figure summarizes the functional trait information. Numbers in parenthesis refer to the number of morphospecies that correspond to the trait next to it. Images are representative morphospecies at each FG.

Table 2. Functionally unique morphospecies (NE_sing) proportions with respect to natural enemy (NE) richness. Every morphospecies in a farm has a unique combination of functional traits when NE_sing/NE_richness = 1.

FARM ID	NE RICHNESS	NE SING	NE_SING/NE_RICHNESS
1	29	23	0.79
5	18	16	0.89
6	23	19	0.83
7	10	9	0.90
8	12	11	0.92
9	20	19	0.95
11	22	17	0.77
12	14	11	0.79
13	27	17	0.63
14	23	16	0.70
15	23	19	0.83
16	21	17	0.81

Biological control redundancy indicators, such as the abundance of natural enemies, were not affected by the landscape or habitat variables, but they were significantly affected by weed control. Stands with no weed control showed a higher abundance of natural enemies than those in which weeds were controlled.

With regard to the different functional response traits related to biological control, multimodel inference indicated that neither landscape- nor farm-level variables significantly affected the abundance of FG 1, 2, and 3, but FG 4 was negatively correlated with the habitat richness (Figure 3c). However, when farm-level variables were considered, there was a significant effect of weed control on FG1 and FG2 abundance: farms without weed control had a higher abundance of FG1 and FG2 than those where weeding was carried out (Figure 3).
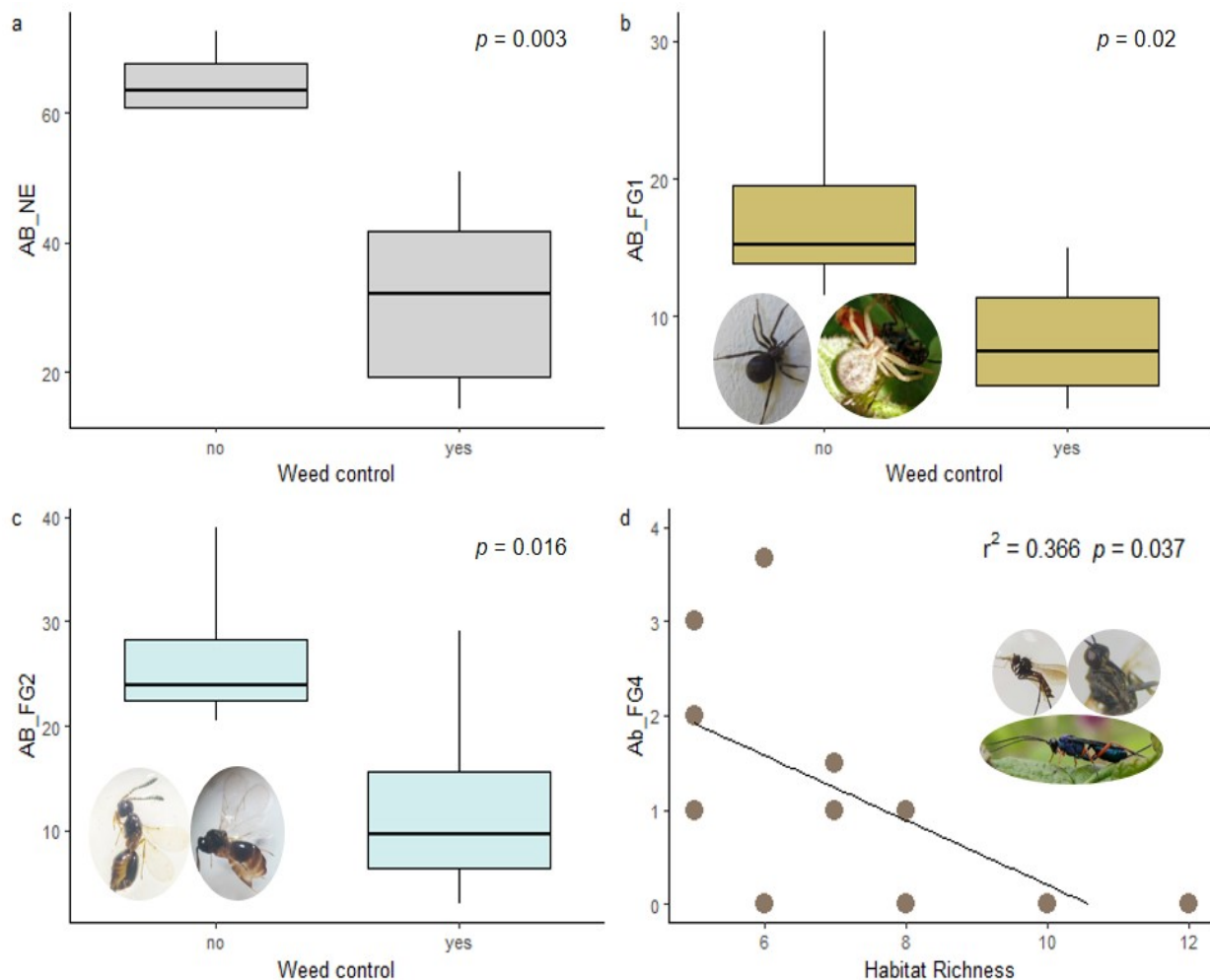

Figure 3. Farm-level variables with significant effects on functional group abundance. (**a**) Effect of weed control on the abundance of natural enemy morphospecies (Ab_NE). (**b**) Effect of weed control on the abundance of functional group 1 (Ab_FG1). (**c**) Effect of weed control on the abundance of functional group 2 (Ab_FG2). (**d**) Effect of the habitat richness on the abundance of functional group 4 (Ab_FG4).

4. Discussion

Worldwide, the design of landscapes that provide suitable habitats for beneficial arthropods, such as natural enemies, is essential for sustainable agriculture. In this study, we assessed key functional response traits of natural enemies' communities to landscape and local drivers as well as the resilience of natural enemies' communities to land-use changes in heterogeneous landscapes.

We found that, in the productive valleys of the northern Andean Patagonian region of Argentina, the natural enemies' functional diversity is not affected by changes in the landscape heterogeneity or by local (farm)-level variables. Neither the land cover type composition nor the landscape configuration (edge density) had effects on the functional diversity indices. Such results are not in accordance with our first hypothesis, which postulated that heterogeneous landscapes promote higher natural enemy diversity. On the contrary, farms surrounded by a matrix composed of 84% or 14% of forests and shrublands did not show significant differences in the diversity of natural enemies. Furthermore, the enemy diversity was not sensitive to changes in the farm-level variables, such as the habitat availability or management strategies. Consequently, there was no significant difference in enemy diversity between farms with a large crop size (high habitat dominance) or few alternative vegetation types (low habitat richness) and farms with a small crop size and many alternative vegetation types, corresponding to more resources and shelters. The same results were found with respect to management practices: neither weed control nor irrigation type had effects on natural enemies' functional diversity indices.

The differential responses of each functional group might be a reason for the absence of landscape and farm practice effects on diversity indices. Specialist parasitoids were the most abundant group in the natural enemies' communities, followed by generalist predators, represented by carabid and staphylinid beetles. It is known that these groups are less affected at the landscape scale because of their poor dispersal ability [4,46]. However, in highly modified landscapes, small changes in the natural area proportion may affect parasitoids [47]. Furthermore, there is evidence of different responses between diet generalist and specialist arthropods, indicating that specialists are mostly sensitive to landscape complexity at smaller scales [27]. Another important issue is evidence of a greater positive effect of forest cover on natural enemy diversity when fragments are well-connected and spatially distributed [48] or when crop sizes are as small as possible [49]. Our results may be in line with these findings, as forest cover and edge density presented high values in our study system, whereby agricultural production systems inserted in low-human-modified and heterogeneous landscapes may sustain a great natural enemy community.

Our second hypothesis was partly confirmed, as while the landscape ensures complementarity, farm-level effects were also significant. Firstly, we found that landscapes in the study region provided high complementarity in natural enemies' response traits to land-use change, and this was independent of changes in the composition and configuration of land cover. In other words, changes in our study region were not large enough to affect natural enemies' complementarity. Four functional groups (FGs) were present, characterized by a combination of different functional traits that influence the responses of individuals to land-use changes: diet breadth, diet over the life history, body size, life habits, and dispersal strategy. On the one hand, at least three FGs were represented on every farm, while 8 of the 12 farms harbored four FGs, and the absent group was always the flying generalist predator group. In other agricultural systems, such as rice or coffee fields, land heterogeneity resulted in a higher number of functional groups compared to that found in this study for raspberry systems, resulting in a wider gradient of functional group richness according to landscape and local variables [21,46,50]. On the other hand, the existing proportion of the number of functional unique morphospecies (NE_sing) with respect to natural enemies' richness (NE_richness) indicated high functional complementarity in most communities. Thus, in these heterogeneous landscapes, farm-level practices ensure a wide variety of functional traits in the studied region. This is particularly important for biological pest control, since enemies' trait complementarity could enhance ecosystem function: the more different the natural enemy community is, the better the resulting pest control contribution is [51,52].

Secondly, redundancy in functional response traits in the natural enemies' communities was shown to be sensitive to farm-level practices (i.e., weed control and habitat richness) but not to landscape-level variability. On the one hand, variation in natural enemies' abundance with respect to weed management resulted from an increase in walker generalist predators (FG 1) and flying specialist parasitoids (FG 2) under non-weed-controlled condi-

tions. These results indicate that walker generalist predators (spiders) and flying specialist parasitoids (microhymenotpera) are more sensitive to farm management than landscape changes. Moreover, flying generalist predators (FG 4) were more abundant when the habitat richness was lower. On the other hand, the number of arthropods fulfilling the same function, that is the natural enemies' abundance, was not significantly different in high heterogeneous landscapes with respect to those with lower heterogeneity. This is consistent with previous studies which indicated that natural enemies' abundance does not have a significant response to compositional and configurational landscape variables [19]. On the contrary, empirical evidence highlights the positive effects that landscape heterogeneity has on biological control resilience due to the enhanced redundancy of the process [53–55]. In summary, effects on redundancy of enemies' functions are highly dependent on each functional trait and its response to farm-level variables.

In summary, our results provide strong evidence for the agroecological paradigm [56], strengthening the proposal that small-scale farming can enhance natural processes that control beneficial arthropods such as natural enemies. In this sense, our findings indicate that a highly heterogeneous landscape in terms of having many different land covers, low human intervention, and a small-sized crop, is capable of providing the necessary resources for sustainable food production. Thus, the extrapolation of results to other systems (homogeneous modified landscapes with high external input production) is not only wrong but also dangerous for the trade-off between food production and conservation objectives. Management decisions are, therefore, the key tool to take into account when biological control is to be assessed on this type of system. It is important then that the scientific community looks forward into applied investigations on alternative agricultural systems representing wider (or minorities) areas and/or in-between situations with highly intensive agriculture to better understand the mechanisms behind the ecology of communities.

5. Conclusions

We studied the effects of landscape heterogeneity and farm-level management practices on the functional diversity and resilience of natural enemies' communities. Functional response traits were found to be affected by management variables, such as weed control and habitat richness. The landscape configuration in the studied region, dominated by natural areas and a small crop size with low agricultural intensification, presents a spatial heterogeneity that is capable of supporting highly diverse natural enemies, providing functionally diverse communities of natural enemies and high functional trait complementarity. Our findings represent an important contribution to the effective management of agroecosystems that address societal challenges and promote human well-being and biodiversity benefits in a global change context. Multiscale studies are needed to continue the exploration of small-scale agriculture systems in complex landscapes.

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