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Ant Diversity Is Enhanced by Ecological Infrastructures in Agroecosystems: A Case Study in Irrigated Mediterranean Farmland

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Abstract: We aimed at assessing the role of ecological infrastructures (EI) in promoting ant biodiversity in floodplain Mediterranean agricultural crops. We examined and compared ant communities at the interface between EI (remnant vegetation patches) and adjoining agricultural matrix (maize, rice, others) in irrigated farmland. The study was conducted in 2019, in two agricultural landscapes in the valleys of the rivers Tagus and Sorraia, Central Portugal. We used the Akaike information criterion for model selection and to distinguish among a set of possible models describing the relationship between: the ant richness in the agricultural matrix and drivers associated with the surrounding landscape and crop type; the ant richness in EI and the habitat quality of EI patches, the characteristics of the surrounding landscape, and the presence of invasive ant species. We found that: EI patches supported a higher ant diversity and an overall specialized ant community, distinctive from the agricultural matrix; location but not vegetation physiognomy influenced ant diversity; ant richness within the agricultural matrix decreased with the distance to the EI, and that this relationship was influenced by the crop type; and that ant richness in the EI was associated with the absence of the invasive Argentine ant and the area of terrestrial EI in the surrounding landscape.

Keywords: ants; biodiversity; Formicidae; green infrastructure; landscapes; Portugal; riverscapes

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1. Introduction

Agricultural land use is pointed out as one of the major drivers of land use change, representing around 40% of the land surface [1]. In this context, agricultural intensification, characterized by crop monocultures, high soil disturbance, and use of pesticides, is generally associated with landscape simplification and biodiversity losses, reducing ecosystem services on which agriculture depends [2–4]. To overcome these negative effects, a sound management plan should be adopted to enhance habitat heterogeneity and support biodiversity and ecosystem services by conserving and promoting ecological infrastructures (EI), including a network of natural, semi-natural, and restored patches at different spatial scales [5,6].

In agroecosystems, EI are considered of such ecological value that different eco-schemes (i.e., payment aids) were introduced in the European Union, through the Common Agriculture Policy (CAP), to encourage farmers to progressively dedicate a proportion of their arable land to non-productive biodiversity-friendly features [7,8]. One of the present Green Deal targets under the CAP strategic plan is to bring back at least 10% of agricultural areas under high-diversity landscape features by 2030 [8]. These may include hedges, rows of trees, field copses, ponds, or fallow land [7]. However, these ecological approaches have been focused mainly on quantitative aspects, with higher compensation for those who have larger areas devoted to EI. Above all, the landscape features that compose the EI must fulfill the purpose of providing suitable habitats (of good quality) for promoting biodiversity and ecosystem services (ES) [9]. Two of the most important factors influencing this are the landscape configuration of EI (i.e., the spatial arrangement of land use patches) and their composition (i.e., the relative proportion of habitat types) [10–12]. In the last decades, quality-based assessment tools have been developed to evaluate the potential value of a certain area to harbor biodiversity, such as the 'Indice de Biodiversité Potentielle' (IBP) [13] and the Habitat Ecological Infrastructure Diversity Index (HEIDI) [14]. Nevertheless, further knowledge is needed to guarantee successful green measures implementation, such as guidelines for selecting the best elements of the landscape (e.g., in terms of composition and configuration) and redesigning sustainable and resilient crop production systems [2].

In the Mediterranean region, drought conditions and water scarcity pushed land use activities to the vicinity of watercourses, and EI are usually distributed among cultivated plots, along roads, paths, or water features [15,16]. As a result, patches are few in number and present simple configurations [14]. Nevertheless, these patches are still high-value habitats playing a crucial role in supporting food, refuge, and breeding areas for several biological communities [17–20]. In this regard, there is a growing awareness that agroecosystems should be a priority in the biological conservation agenda because some agroecosystems are repositories of high levels of biodiversity, including ants [21]. Some studies have been carried out on ant communities in Mediterranean drylands (e.g., [22,23]). There is a lack of information concerning irrigated lands.

Ants (Hymenoptera, Formicidae) are a group of eusocial and colonial insects with more than 16,500 described species worldwide [24]. Eusociality confers marked advantages in terms of ecological dominance, resources foraging, defense against enemies, and may allow ants to adapt or tolerate future environmental change [25–27]. Ants have evolved into distinctive life strategies, resulting in the interaction with many different animal and plant communities [28–30]. They also carry out important ecological functions and services, such as nutrient cycling, decomposition, soil movement, seed dispersal, and pest regulation [31–33]. However, these services are dependent on ant biodiversity, which has been threatened worldwide by agricultural intensification [34–36]. For instance, the intensification of coffee plantations in the tropics (involving the conversion of rustic systems, with shaded trees, to unshaded monocultures) significantly reduced ant species richness [21]. In temperate regions, ant richness and abundance have been also affected by agriculture, and its impacts may vary depending on agricultural practices [34] and landscape components [37–39]. Although the Mediterranean basin is considered a hotspot for ant richness [40], intensive agricultural landscapes in this region exhibited low potential for ant biodiversity, when compared to more extensive agricultural systems [4,14]. Despite considerable efforts to protect ant biodiversity in human-disturbed landscapes, many of the existing refuges are small, fragmented, isolated, or of poor quality [14]. In addition, invasion by exotic species is often reported, and changes in competitive interactions or colonization processes may also affect ant assemblages in disturbed areas [41].

To broaden our understanding of the role of EI in ant biodiversity, particularly in annual cropping systems, we examined ant communities at the interface between EI and the adjoining agricultural matrix in two intensively irrigated agricultural areas located in the Sorraia and Tagus river valleys in Portugal. We aimed at assessing the role of EI in promoting ant biodiversity in floodplain Mediterranean agricultural crops. We made four hypotheses, as follows: (1) the reduced habitat structure and lower food resources availability in the agricultural matrix would likely affect ant richness and composition, in comparison with EI; (2) the effect of EI on ant diversity would differ with their typologies, namely, location and vegetation physiognomy; (3) the ant richness in the agricultural matrix is dependent on the type of crops produced, as well as on other drivers associated with the surrounding landscape; and (4) the ant richness in EI is influenced by the habitat quality of EI patches, but also by the characteristics of the surrounding landscape, and can be affected by the presence of invasive ant species.

The results from this study will enable a better understanding of the role of EI in ant biodiversity. They will provide valuable clues for the improvement of management plans when aiming at the conservation and restoration of Mediterranean agricultural floodplains.

2. Materials and Methods

2.1. Study Area

The study was conducted in 2019, in two agricultural landscapes in the valleys of the rivers Tagus and Sorraia, Central Portugal (Figure 1). Both landscapes comprise irrigated cropland, composed of annual crops, with a predominance of rice paddies (*Oryza sativa* L.) in the alluvial plains of the Sorraia river and maize fields (*Zea mays* L.) in the Tagus river valley.

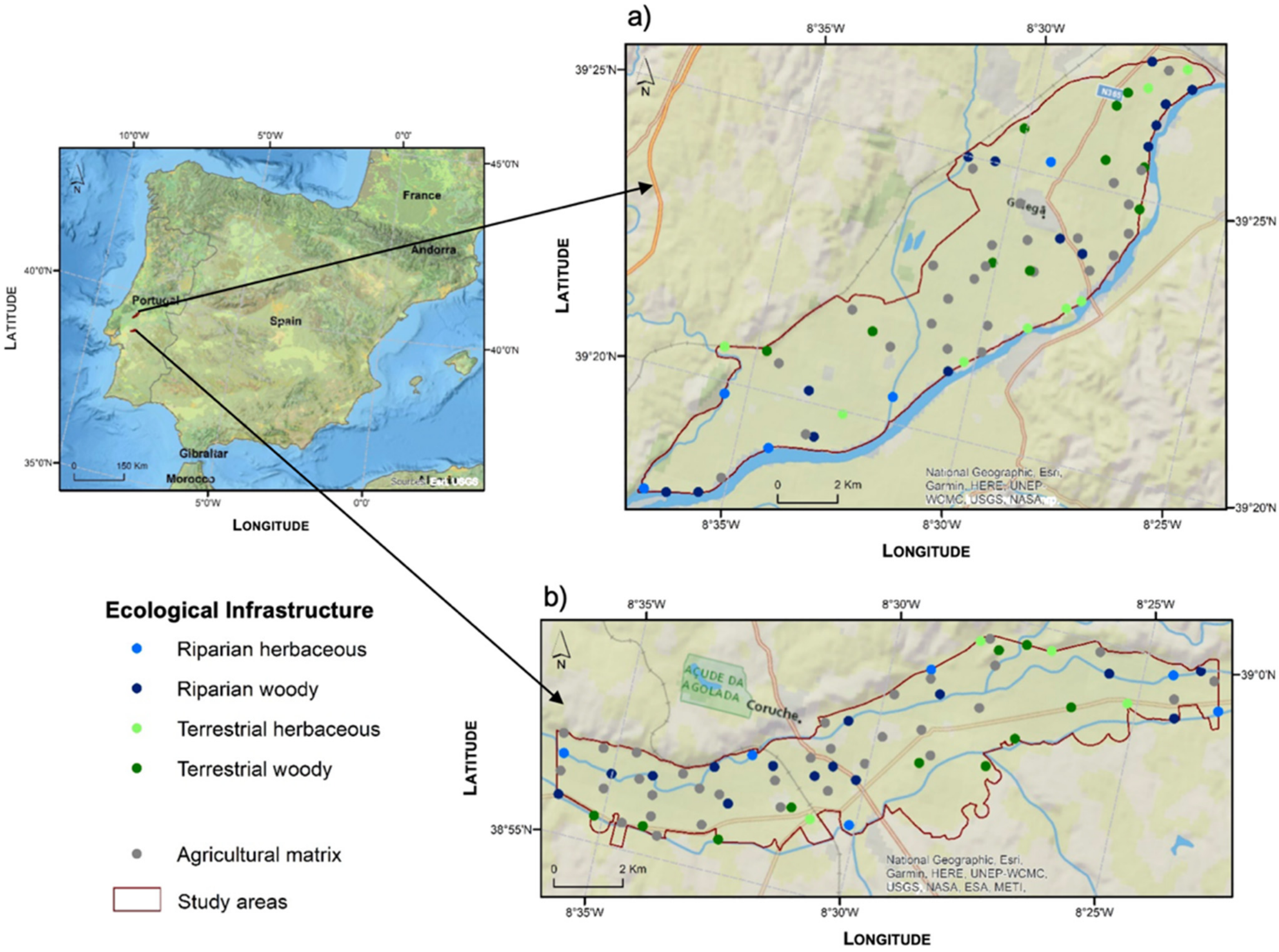

Figure 1. Geographic location of study areas and sampling sites. (**a**) Tagus and (**b**) Sorraia valleys.

The region is characterized by a mild climate with rainy winters (average rainfall of circa 900 mm) and hot, dry summers (average annual air temperature of around 15 °C), with values varying regularly throughout the year, with a maximum in August and a minimum in January [42]. The rainfall pattern exhibits strong seasonal and inter-annual variability, with high floods usually occurring in autumn or early winter, a gradual decline in discharge, and subsequent drying out during late spring and summer [43].

2.2. Sampling Design

Sampling was carried out in 130 sites, based on a balanced subset of randomly distributed points, including 59 sites within the agricultural matrix (27 and 32 in the Tagus and Sorraia basin, respectively) and 71 sites in the EI patches (37 and 34 in the Tagus and Sorraia basin, respectively). We used field data and a geographic information system (GIS) image-based approach to characterize the sampling sites. The agricultural matrix and EI patches were manually and individually digitized through a visual analysis of the Esri World Imagery layer (1:1000 scale) [44]. We selected a minimum mapping unit of 200 m^2, with a minimum width of 5 m and a minimum gap distance among patches of 10 m [45,46]. These mapping thresholds were established to represent the minimum patch size and minimum distance between patches that are considered ecologically meaningful for Mediterranean ant communities [47,48]. The EI vegetation patches were then classified according to the vegetation physiognomy, i.e., those dominated by trees and shrubs (hereafter referred to as "woody EI"), and those where trees were absent or rare, including open areas with scarce vegetation or dominated by herbaceous plants and low bushes (hereafter referred to as "herbaceous EI"). We also classified EI vegetation patches according to their location, i.e., those located contiguous to a watercourse (hereafter referred to as "riparian EI") and those that were non-contiguous to a watercourse (hereafter referred to as "terrestrial EI").

A description of the variables used in the study is summarized in Table 1. Variables related to proximity and area/density were calculated using the Patch Analyst Vector format (ArcGis10.6) extension [49]. A 200 m buffer radius was considered around each sampling site to measure the total area occupied by the EI patch types and the agricultural land [37,38]. Habitat quality variables included shrub richness, the occurrence of the invasive Argentine ant, *Linepithema humile* (Mayr), and a measure of the potential habitat quality of the EI–HEIDI index, *sensu* Fonseca et al. [14]. Through the information collected in the field, we used different metrics to calculate the HEIDI index, including: vegetation structure (e.g., native-invasive plant species, vertical strata); the presence of specific habitats (e.g., microhabitat at trees, dead wood trunks on the ground, leaf litter cover); vegetation management (e.g., understory clearing); and floristic suitability (i.e., the ecological value of plant taxa for the provision of ES such as their potential for myrmecochory) (see Fonseca et al. [14] for a detailed description of the HEIDI index development).

2.3. Ant Sampling and Identification

Ant sampling was carried out in early summer, between June and July, i.e., the period with the highest activity for Mediterranean ant communities [50]. The sampling was performed using pitfall traps, a method that has been used in many studies of ant communities worldwide (e.g., [51–53]). It is a simple, cost-effective method for collecting epigaeic ants that provides good results in assessing species richness and composition patterns while allowing for continuous day and night sampling [54–57].

The sampling design consisted of five pitfall traps per site, distributed in a linear transect, with the middle trap considered as the geo-referenced point. A similar number of pitfall traps per site has been used by different authors (e.g., [58–61]). Each trap was five meters apart from the neighboring ones. Pitfall traps consisted of 100 mL plastic containers placed flush with the ground, and partially filled with a solution of 30% propylene glycol and a few drops of detergent, to retain and preserve the intercepted ants. They were left in the field for about 48 h. This sampling time was shown to be more cost effective and robust enough to estimate ant diversity, in comparison with 14-day sampling [62]. The ants collected per site were put together for sorting and identification.

All the entomological material was sorted and identified by the first author, who has more than 10 years of experience in the study and taxonomic identification of ants. Identification was carried out at the species level (except for *Solenopsis* spp.), under a stereomicroscope, using taxonomic keys for Portugal and Iberian Peninsula and knowledge expertise [63–65]. All identified specimens were preserved in 96% alcohol and kept at the laboratory of entomology of Instituto Superior de Agronomia.

Table 1. Description of the variables used in the study.

Applied To:	Variable Name	Abbreviation	Category	Type, Units, and Range	Description
Agricultural matrix data	Distance to the closest EI patch	Dist_EI	Proximity	Continuous: meters; [0, ∞]	Distance to the closest remnant habitat patch–EI edge
	Distance to urban area	Dist_urban	Proximity	Continuous: meters; [0, ∞]	Distance to the closest urban area using Level 4 of COS 2018 layer (i.e., the Portuguese Land use and Occupancy Charter of 2018, www.dgterritorio.pt (accessed on 26 March 2021))
	Distance to river	Dist_river	Proximity	Continuous: meters; [0, ∞]	Distance to the closest watercourse defined by the adapted HIDCOD layer (i.e., the Portuguese waterline layer based on the Digital Elevation Model of 25 m)
	Crop type	Crop_type	Habitat quality	Nominal: maize field, rice paddy, others (mixed types)	Crop type characterization within the agricultural matrix
Ecological infrastructure (EI) data	Agricultural land	Agricultural_matrix	Area/density	Continuous: ha; [0, ∞]	Area of the agricultural matrix in a 200 m buffer contained within the study area
	Area of riparian EI	Riparian_EI_area	Area/density	Continuous: ha; [0, ∞]	Sum of the areas of riparian EI; basic statistics of the spatial configuration
	Area of terrestrial EI	Terrestrial_EI_area	Area/density	Continuous: ha; [0, ∞]	Sum of the areas of terrestrial EI; basic statistics of the spatial configuration.
	Shrub richness	Shrub_richness	Habitat quality	Continuous: none; [0, ∞]	Number of shrub plant species in the EI patches
	HEIDI quality index	HEIDI_index	Habitat quality	Continuous: none; [0, ∞]	HEIDI value for short distance dispersers in the EI patches *sensu* Fonseca et al. [14]
	Argentine ant occurrence	Argentine_ant	Habitat quality	Nominal Bolean: presence, absence	Argentine ant occurrence in the EI patches

2.4. Statistical Analysis

For testing Hypotheses 1 and 2, we used the ant richness (i.e., number of observed species in each sampling site) and ant species composition occurring in the EI and within the agricultural matrix. A one-way ANOVA (aov function in R package stats [66]) was used to determine statistically significant differences between and among independent groups (EI vs. agricultural matrix, herbaceous EI vs. woody EI vs. agricultural matrix, and riparian EI vs. terrestrial EI vs. agricultural matrix). If the p-value was statistically significant ($p < 0.05$) a post-hoc for multiple comparisons was performed using Tukey's HSD Test (TukeyHSD function in R package stats [66]). Boxplots were created using graphics and ggplot2 R packages [66,67].

The differences among the communities were investigated using a permutational multivariate analysis of variance (PERMANOVA) (adonis function in R package vegan [68]) based on a Bray–Curtis distance matrix with 999 permutations. We used a site-per-species matrix containing incidence data for ant species at each sampling site. Ordination plots were created using metaMDS and ordiellipse functions in R package vegan [68].

To test Hypothesis 3, we performed generalized linear mixed models (GLMMs) (glmmTMB function in R package glmmTMB [69]). We used ant species richness sampled within the agricultural matrix as a dependent variable, and the models were fitted with a negative binomial distribution to handle overdispersion. The predictors were included as fixed factors, and all continuous ones were standardized (i.e., rescaled to the same unit), enabling comparisons of effect magnitude. We used the Akaike information criterion corrected for small sample size (AICc) to test the statistical relevance of including crop types (maize fields, rice paddies, and other mixed crops) [70]. The Argentine ant occurrence (present, absence) and sampling month (June, July) alone or together were added as random effects to account for the sampling design. Of these, we only include crop types as a predictor. Validation of the full multivariate models was carried out using DHArMa and performance R packages [71,72] with the help of diagnostic plots (Figure A1). We generated all possible models based on the full one and performed model selection with the MuMIn package [73]. Models were selected based on Akaike weights and AIC differences (ΔAIC) from the best-fitted model and were considered to be equally supported if AIC was less than two units [70]. Based on model-averaging, we estimate the predicted responses of ant species richness with associated 95% confidence intervals [74]. We performed also GLMMs in a similar way to test Hypothesis 4, using ant species richness sampled in the EI, and further assessed whether the influence of different predictors (the % area of agricultural matrix, riparian EI, and terrestrial EI, in a 200 m buffer; shrub richness; the HEIDI quality index *sensu* Fonseca et al. [14]; and the Argentine ant presence) could shape ant communities in the EI.

Data were stored in spreadsheets Microsoft® Excel for Mac version 16.16.27 (201012), and all analyses were conducted in the R environment [66].

3. Results

3.1. Agricultural Matrix Versus Ecological Infrastructures (Hypothesis 1)

3.1.1. Species Richness

We recorded 17 072 ants belonging to 47 species from 20 genera. We observed higher species richness in EI than in the agricultural matrix (Figure 2). Mean species richness was significantly different between EI and the agricultural matrix ($p < 0.01$, 95% C.I. = [1.72, 3.51]; Figure 2a), riparian EI and the agricultural matrix ($p = 0.02$, 95% C.I. = [−2.72, −0.22]), and between terrestrial EI and the agricultural matrix ($p < 0.01$, 95% C.I. = [0.46, 3.13]; Figure 2c).

3.1.2. Community Composition

Ant communities in EIs were significantly different from those in the agricultural matrix ($F_{1,117} = 5.22$, $p = 0.007$; Figures 3a and 4). All 20 species observed in the agricultural matrix were also present in the EI, except for *Cardiocondyla mauritanica* Forel, which was only identified in the agricultural matrix; 27 ant species were only observed in association with the EI. *Linepithema humile* and *Tapinoma nigerrimum* Nylander were the most frequent species in EI and the agricultural matrix, respectively. In most of the cases, ant species were more frequent in EI, in comparison with the agricultural matrix. However, the opposite was observed in the case of *T. nigerrimum*, *Tetramorium forte* Forel, *Hypoponera eduardi* Forel, *Messor bouvieri* Bondroit, and *Formica cunicularia* Latreille.

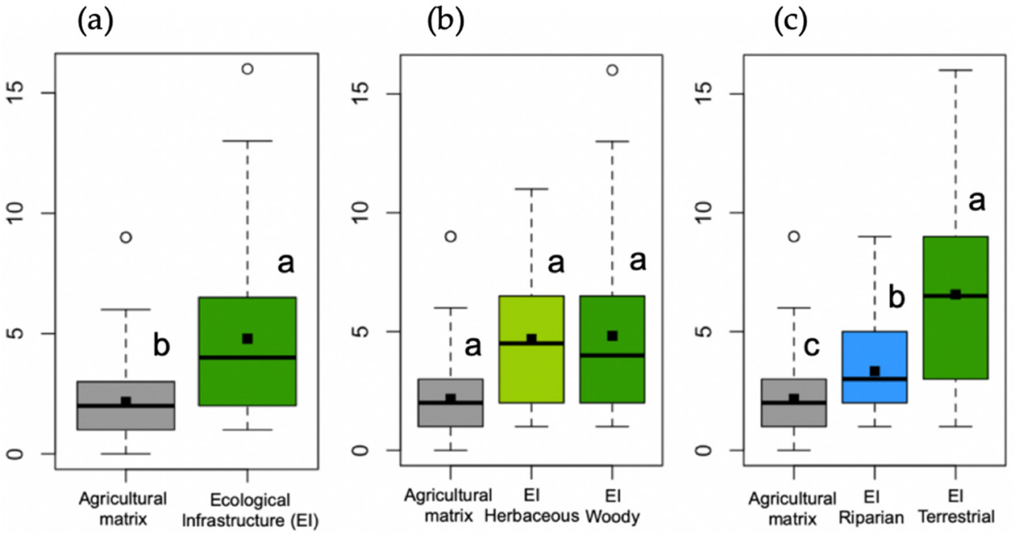

Figure 2. Boxplots represent the ant species richness among groups. (**a**) Ecological infrastructures (EI) vs. agricultural matrices; (**b**) woody EI vs. herbaceous EI vs. agricultural matrices; (**c**) terrestrial EI vs. riparian EI vs. agricultural matrices. Different letters show significant differences between and among groups (Tukey's HSD test).

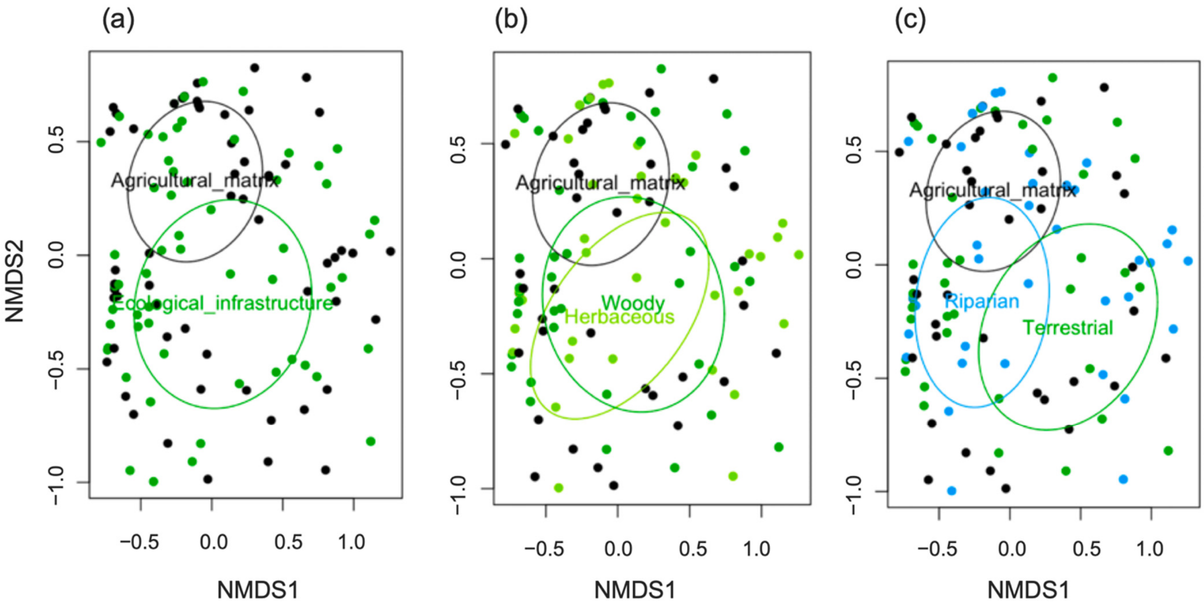

Figure 3. Ordination plots of species composition of ant communities in Ecological infrastructures (EI) and the agricultural matrix assemblages based on Bray–Curtis dissimilarities: (**a**) EI vs. agricultural matrices; (**b**) woody EI vs. herbaceous EI vs. agricultural matrices; (**c**) terrestrial EI vs. riparian EI vs. agricultural matrices Legend: EI—ecological infrastructures (green); MATRIX—agricultural matrix (black); W—woody EI (dark green); H—herbaceous EI (light green); T—terrestrial EI (green); R—riparian EI (blue).

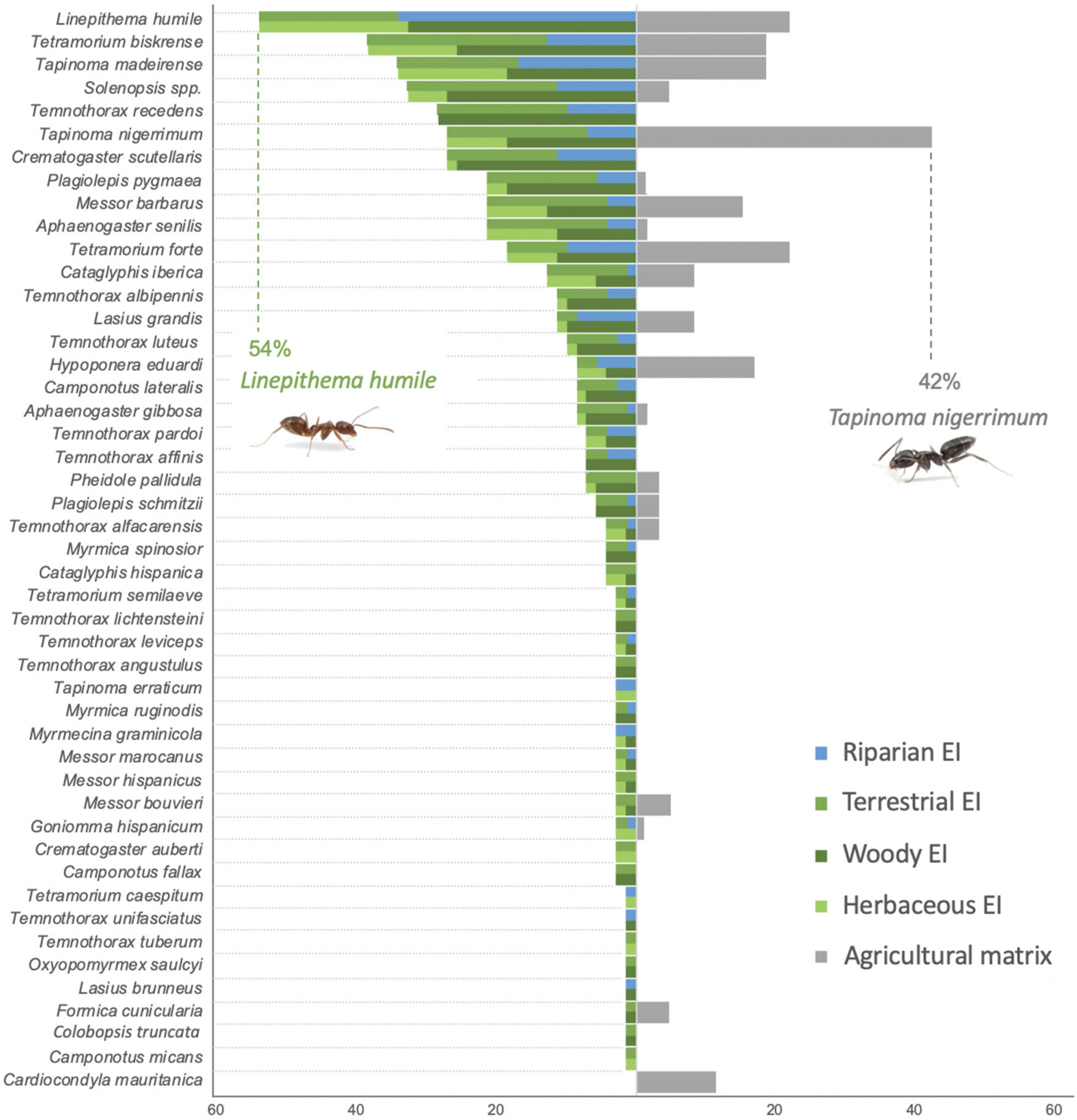

Figure 4. Frequency distribution of ant species occurrence (in percentage) as a function of the sites sampled in the ecological infrastructures (EI) (left blue-green bars) and the agricultural matrix (right gray bars).

3.2. *Effect of the Ecological Infrastructure Typology (Hypothesis 2)*

3.2.1. Species Richness

Ant species richness in terrestrial EI was significantly higher than in riparian EI ($p < 0.01$, 95% C.I. = [1.81, 4.72]; Figure 2c). No significant differences in ant species richness were observed regarding vegetation physiognomy, i.e., woody EI vs. herbaceous EI ($F_{1,\,126} = 0.03$, $p = 0.86$; Figure 2b). Nevertheless, the total number of ant species identified in woody EI (40 species) was higher than in herbaceous EI (33 species) (Figure 4).

3.2.2. Community Composition

Ant communities in riparian EI were significantly different from those in terrestrial EI ($F_{1,117} = 4.18$, $p = 0.009$; Figure 3c). Of the 27 ant species observed only in EI, 10 and 5 species were specific to terrestrial and riparian EI, respectively. Most of the ant species were more frequent in the terrestrial EI than in the riparian EI, except *L. humile* and *Lasius grandis* Forel, which were favored by riparian habitats (Figure 4).

No significant differences were found between ant communities of herbaceous EI and woody EI ($F_{1,117} = 1.61$, $p = 0.150$; Figure 3b). Nevertheless, most ant species were more frequent in woody EI, occupying a total area of 564.95 ha, in comparison with herbaceous EI, which occupied 117.54 ha. Some ant species were identified only in one type of EI. For example, *Tapinoma erraticum* (Latreille), *Goniomma hispanicum* (André), *Crematogaster auberti* Emery, *Tetramorium caespitum* (Linnaeus), *Temnothorax tuberum* (Fabricius), and *Camponotus micans* (Nylander) were observed only in herbaceous EI, whereas *T. lichtensteini* (Bondroit), *T. angustulus* (Nylander), *Myrmica ruginodis* Nylander, *C. fallax* (Nylander), *T. unifasciatus* (Latreille), *Oxyopomyrmex saulcyi* Emery, *Lasius brunneus* (Latreille), *F. cunicularia*, and *Colobopsis truncata* (Spinola) were found only in woody EI.

3.3. Drivers of Ant Richness in the Agricultural Matrix (Hypothesis 3)

Ant species richness within the agricultural matrix was significantly associated with the distance to the EI and crop type, but not with the distance to the river or to urban areas (Table 2, Figure 5).

Table 2. Summary of the GLMM best-fitted model compared with the Null and Full models, to test Hypothesis 3. Significant *p*-values ($p < 0.05$) are displayed in bold.

	Null Model			**Best-Fitted Model**			**Full Model**		
Predictors	**Incidence Rate Ratio (95% Confidence Interval)**	**Statistic**	***p*-Value**	**Incidence Rate Ratio (95% Confidence Interval)**	**Statistic**	***p*-Value**	**Incidence Rate Ratio (95% Confidence Interval)**	**Statistic**	***p*-Value**
(Intercept)	2.17 (1.70–2.78)	6.16	**<0.001**	3.23 (2.35–4.44)	7.23	**<0.001**	3.16 (2.24–4.47)	6.52	**<0.001**
Crop [Maize_field]				0.39 (0.24–0.65)	–3.68	**<0.001**	0.41 (0.23–0.71)	–3.17	**0.002**
Crop [Other_mixed_types]				0.69 (0.40–1.18)	–1.37	0.172	0.69 (0.40–1.20)	–1.31	0.191
Dist_EI				0.68 (0.50–0.92)	–2.47	**0.013**	0.68 (0.49–0.94)	–2.33	**0.020**
Dist_urban							0.98 (0.76–1.26)	–0.19	0.847
Dist_river							0.97 (0.73–1.29)	–0.22	0.828

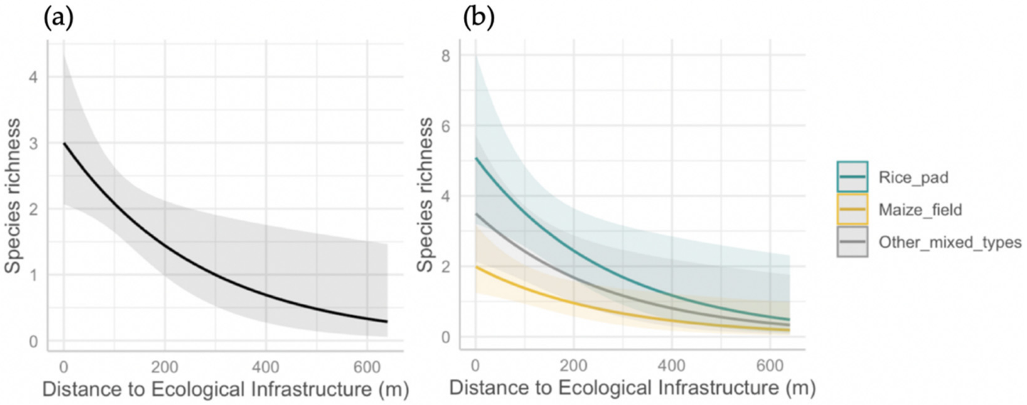

Figure 5. Predicted responses of the ant species richness within the agricultural matrix in relation to the distance to the nearest ecological infrastructure, (**a**) overall and (**b**) considering the crop type. Model predictions from GLMMs and associated 95% confidence intervals are represented by the solid lines and shaded areas, respectively.

The best-fitted model included two out of four variables, i.e., the distance to EI and crop type. This model performed better than the others as it carried 52% of the cumulative model weight and has the lowest AIC score (Table A1). In addition, the next-two-best models and the null model were more than two AIC units higher (2.4, 2.4, and 11.1, respectively) and carried only 15.7%, 15.6%, and 0.2%, respectively, of the cumulative model weight (Table A1).

Predicted responses of the ant species richness within the agricultural matrix showed a significant negative effect of the distance to the nearest EI, indicating that ant species richness decreases with increasing distance to EI (Table 1, Figure 5). The number of ant species is predicted to drop to half if the EI patch is at a 200 m distance and almost zero if at a 600 m distance. This trend effect is irrespective of the crop type, yet is more pronounced in crops with higher ant species richness, such as rice paddies (Figure 5). Our model suggested that this type of crop is predicted to harbor a significantly higher number of species when compared with maize fields (Table 2, Figure 5). Nevertheless, these are both low levels of ant richness and are predicted to aggravate without the presence of EI patches at a short distance (Figure 5).

3.4. Effect of Ecological Infrastructure Habitat Quality and Characteristics of the Surrounding Landscape (Hypothesis 4)

Ant species richness in the EI was significantly associated with the absence of Argentine ant and the area of terrestrial EI in the surrounding landscape but not with the area of riparian EI or agricultural land, shrub richness, or HEIDI quality index (Table A2, Figure 6). Three models showed a ΔAIC < 2, yet the most parsimonious model of the three appear to be the one including fewer parameters (two out of six), i.e., the Argentine ant occurrence and the area of terrestrial EI in the surrounding landscape (Table 3, Table A2). The model with the lowest AIC includes another parameter, i.e., the area of riparian EI in the surrounding landscape. These two models explained 37.4% of the cumulative weight (Table A2).

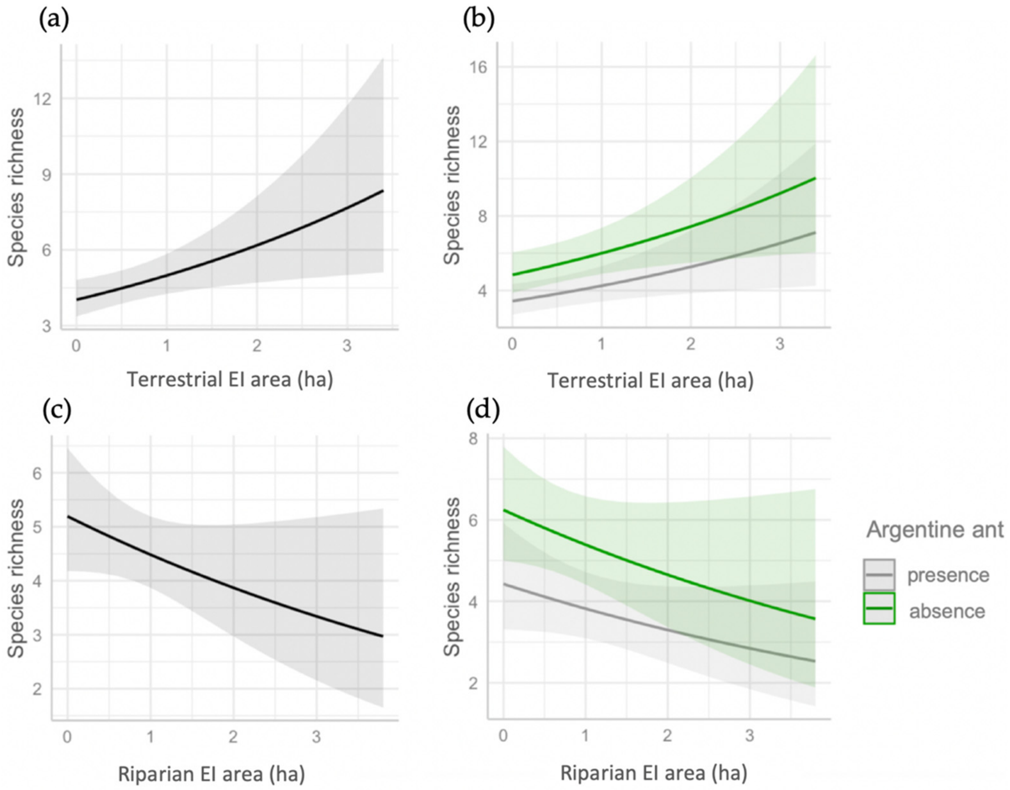

Figure 6. Predicted responses of the ant species richness in relation to the riparian and terrestrial ecological infrastructure (EI) proportional area in the 200 m buffer, overall (**a**,**c**) and considering the Argentine ant presence (**b**,**d**). Model predictions from GLMMs and associated 95% confidence intervals are represented by the solid lines and shaded areas, respectively.

Table 3. Summary of the GLMMs model with the lowest AIC, compared with the Null and Full models, to test Hypothesis 4. Significant *p*-values ($p < 0.05$) are displayed in bold.

	Null model			**Best-fitted model**			**Full model**		
Predictors	**Incidence Rate Ratio (95% Confidence Interval)**	**Statistic**	***p*-Value**	**Incidence Rate Ratio (95% Confidence Interval)**	**Statistic**	***p*-Value**	**Incidence Rate Ratio (95% Confidence Interval)**	**Statistic**	***p*-Value**
(Intercept)	4.79 (4.09–5.61)	19.41	**<0.001**	3.85 (3.13–4.74)	12.72	**<0.001**	3.88 (3.15–4.78)	12.71	**<0.001**
Argentine ant [absence]				1.41 (1.06–1.87)	2.37	**0.018**	1.38 (1.03–1.85)	2.18	**0.030**
Riparian area				0.87 (0.73–1.04)	−1.53	0.127	0.88 (0.73–1.07)	−1.29	0.196
Terrestrial area				1.17 (1.04–1.33)	2.54	**0.011**	1.20 (1.04–1.38)	2.52	**0.012**
Matrix area							1.04 (0.90–1.21)	0.51	0.613
Shrub richness							0.98 (0.84–1.13)	−0.30	0.763
HEIDI quality index							0.98 (0.85–1.13)	−0.28	0.780

Predicted responses of the ant species richness in the EI, showed a significant positive effect on the area occupied by EI in the surrounding landscape (Figure 6). The opposite effect is predicted to occur with the area occupied by the riparian EI in the surrounding landscape although it was not statistically significant (Table 3, Figure 6).

4. Discussion

We are facing the challenge of managing trade-offs between food production and conserving biodiversity under intensive cropland systems [1]. Our results provide evidence that EI may have an important role in conserving ant biodiversity in agricultural landscapes and that its effect is influenced by its typology and habitat quality.

Focusing on ants, a key group in providing valuable insights into disturbed habitats and in promoting ecosystem functions and services across agroecosystems, we aimed at assessing the importance of landscape components in promoting ant biodiversity in a floodplain Mediterranean agricultural mosaic. We first hypothesized that the reduced habitat structure and lower food resource availability in the agricultural matrix would likely affect ant richness and community composition, in comparison with EI (Hypothesis 1). As expected we found higher ant species richness in EI (46 species) than in the agricultural matrix (20 species). Few other studies also provided support for this hypothesis. For example, Dauber and Wolters [35] registered higher ant species richness in more complex habitats including fallow lands (13 species) and meadows (11 species), than in arable land (8 species), in Central Europe. This is possibly related to the level of disturbance inherent to the agricultural production system and its clear differences in habitat complexity [35,75], in accordance with the "habitat heterogeneity hypothesis" [76,77], which predicts that more structurally complex habitats, with further vegetation layers, can provide additional ecological niches and resources, thus supporting more species. The unique requirements of specialized ant fauna [35], associated with life-history species traits, such as feeding habits, colony size, dispersal capabilities [78], and their ability to cope with disturbance [79], may also contribute to the observed differences in ant species communities between EI and agricultural land. In fact, ant species communities observed foraging in EI were significantly different from those in the agricultural matrix. We found 27 species only occurring in the EI patches, whereas all species observed in the agricultural matrix were also present in the EI, except *C. mauritanica*, which is an invasive species favored by semi-arid areas and anthropogenic disturbance [80]. It seems that the agricultural matrix is dominated by opportunist species, such as *T. nigerrimum*, *T. forte*, and other broadly adapted omnivorous (e.g., *F. cunicularia*) and generalist (e.g., *Pheidole pallidula* Nylander) species, with wide habitat tolerance and higher dispersal capabilities, able of exploiting disturbed areas [81,82]. Landscape conversion to monocultures has been reported to favor generalist ants with large colonies [78]. These ant species, which might be less affected by local or landscape heterogeneity, can play an important role in pest management, such as *T. nigerrimum* [83–85] and *F. cunicularia* [29], or in decomposition, such as *T. nigerrimum*, *L. humile*, *Tetramorium* spp., *P. pallidula*, and *Cataglyphis* spp. They are scavengers and active foragers, collecting and consuming living prey and dead (carrion) animal matter [32,86,87]. Nevertheless, other ecosystem services might be also influenced. For instance, weed control is a potential service mediated by harvester ants, e.g., *Messor* spp. [88], that might be valuable in crops that resort to the use of herbicide applications, such as maize [89]. On the other hand, some ant species may be associated with disservices [29,32]. For example, *L. humile* became a major pest in many areas around the world [90], and can affect pollination [91], natural ant seed dispersal [92], and biological control of pests in agroecosystems [93].

Regarding the effect of EI typology (Hypothesis 2), we found significant differences between terrestrial and riparian EI but not between herbaceous and woody EI. Ant species richness in terrestrial EI (41 species) was higher than in riparian EI (33 species). Most of the ant species occurring in both EI locations were more frequent in terrestrial than in riparian EI, except *L. grandis* and *L. humile*, which were favored by riparian habitats. These are numerically dominant species known to resist anthropogenic disturbances, and with efficient foraging recruitment mechanisms [94,95]. The lower species richness observed in riparian EI may be explained, at least in part, by the higher frequency of *L. humile* in these habitats, in comparison with terrestrial EI. In fact, the negative impact of this invasive species on the diversity of native ants has been documented in different ecosystems [96–99].

The presence of alien invasive plant species in the riparian EI may also influence ant species richness. In Mediterranean irrigated cropland, riparian habitats suffer from the introduction and establishment of invasive plant species, such as the giant reed *Arundo donax* L. [100], that might affect the availability of crucial habitat resources for ant species, provided by native vegetation [36].

On the other hand, ant species richness and species composition were not influenced by vegetation physiognomy, i.e., woody EI vs. herbaceous EI. We would expect a different result, since woody EI are more complex than herbaceous EI and thus are likely to provide more diverse and suitable habitats for ants, reported recently for intensive agricultural landscapes [14]. Nevertheless, most ant species were more frequent in woody than in herbaceous EI.

We further hypothesized that ant richness in the agricultural matrix would be dependent on the crop type, as well as on drivers associated with the surrounding landscape, including the distance to EI, urban areas, and water lines (Hypothesis 3). We found that ant species richness within the agricultural matrix decreased with the distance to the EI and that this relationship was influenced by the crop type. Similar results were reported by Armbrecht and Perfecto [101] in Mexican intensive farmland, which observed a dramatic reduction of ant species richness in function of the distance to the forest fragment. These results and, as mentioned before, the fact that almost all ant species observed in the agricultural matrix were also present in the EI suggest that ant assemblages in agricultural lands depend on the recruitment of ant species from EI. The EI may act as refuges, buffering the negative consequences of insecticide application in adjacent fields [102], and reservoirs with less disturbed habitats increasing the ant species richness of adjacent higher disturbed habitats [35]. The survival of specialist ant species relies on the existence of EI where they can find food, nesting, and foraging resources [41,103].

However, no association was found between ant richness in the agricultural matrix with distance to the river or urban areas, as hypothesized. We would expect a positive effect with the river proximity, since several studies suggested that species richness and diversity of invertebrate communities are positively correlated with the structure and composition of riparian vegetation patches [104–106]. The observed lack of relationship between ant richness and river proximity might be related to the relatively low quality of riparian patches in the studied agricultural systems [14], since well-preserved riparian corridors are essential for the long-term maintenance of myrmecofauna [107]. The higher frequency of the Argentine ant presence in riparian habitats, and the expected negative impact on ant richness might also have contributed to this lack of relationship. Regarding urban areas, studies examining the impacts of urbanization on ant richness report diversity loss [108] and changes in ecological interactions [109]. We also would expect similar results with a negative effect on ant richness in the proximity of urban areas. However, urban environments may still provide habitat heterogeneity for small organisms such as ants [110], and in particular, for dry-adapted, heat-tolerant ant species [111].

In terms of crop type, our model suggested that rice paddies are predicted to harbor a significantly higher number of ant species when compared with maize fields. This might be due to differences in higher land crop type occupation and intensification [112]. Maize is the major cereal crop in Portugal, corresponding to 66% of cereal-producing farms, in 2016, while rice represented only 1% of the farms, usually associated with areas of lower cultivation value [113]. Due to sampling conflicts inherent to the crop being flooded (rice paddies), the sampling was carried out exclusively at the edges of the plots in the dry bunds (i.e., levees). Nevertheless, edges between different land use types did not increase ant species richness at the landscape scale, nor were they unique habitats for specialized ant fauna [35]. Furthermore, rice paddies are likely to have more resources, since they harbor both aquatic and terrestrial organisms, including a high-rich arthropod fauna inhabiting the vegetation, water, and surrounding bunds [114,115].

Finally, we hypothesized that the ant richness in EI would be influenced by the habitat quality of EI patches, but also by the characteristics of the surrounding landscape, and could be affected by the presence of invasive ant species (Hypothesis 4). We found that ant species richness in the EI was associated with the absence of the invasive Argentine ant and the area of terrestrial EI in the surrounding landscape. This is consistent with other studies that found an increase in ant species richness with an increasing percentage cover of forest or fallow land [37,116]. Our predicted responses of the ant species richness in the EI showed a positive effect on the area occupied by EI in the surrounding landscape. However, the selected habitat quality variables were not significant contributors to explaining ant species richness. This contradicts our initial expectation that both habitat quality and landscape features should contribute to the prediction of ant species richness, as Mediterranean ants are strongly linked to both patch and landscape variables [37]. Nevertheless, the regression model in our study showed low values of explained variance, so the habitat quality variables used, i.e., shrub richness and HEIDI index, might not be suitable for ants. Furthermore, these are highly disturbed areas with low variability. In addition, the relative importance of local and landscape factors may depend on the landscape context. Local allocation of habitats such as field boundaries and management practices seem to have a higher impact in structurally simple landscapes than in complex ones, demanding an even greater effort [117]. In our study region, agricultural land dominates most of the landscape.

The other relevant factor affecting ant species richness was the presence of the Argentine ant in EI patches. In fact, this invasive species is known to thrive in riparian, urban, and agricultural habitats with Mediterranean climates [118], and to disturb native ant communities [96–99]. The dispersion of the Argentine ant in the Iberian Peninsula was predicted to be possible mostly along the coast, but also into inland areas along river valleys [119], as in the case of the study area.

5. Conclusions

Agricultural intensification has been responsible for reducing biodiversity and ecosystem services. The conservation and increment of EI within the agricultural landscape have thus been proposed as an approach to mitigate the negative ecological impacts of intensification, by promoting functional biodiversity. Nevertheless, there is a need to assess the quantity and quality of semi-natural habitats in agricultural farmlands, and to better understand the role of different types of EI in enhancing biodiversity and ES in agricultural systems [9]. Here we investigated the effect of EI and its typologies (i.e., location and vegetation physiognomy) on ant species richness and community composition in floodplain

Mediterranean agricultural systems. Our results showed that ant diversity in agroecosystems is enhanced by EI and that ant assemblages present in agricultural lands are likely recruited from ant communities of EI. Therefore, EI may have a critical role in determining ant diversity and species composition of ant assemblages in agricultural farmlands, and consequently in the corresponding services and disservices. However, the effect of the EI on ant diversity was influenced by the EI location, the type of agricultural crops, as well as other drivers and characteristics of the surrounding landscape. In fact, whereas EI location was a significant factor influencing ant species richness and composition, with higher diversity registered in terrestrial than in riparian EI, vegetation physiognomy of EI seems to have no influence. On the other hand, ant diversity may be negatively affected by the presence of invasive species, such as the Argentine ant.

Our findings provide new insights into the role of EI in ant diversity conservation in agroecosystems and may help define habitat conservation and restoration guidelines. Nevertheless, management guidelines should also integrate knowledge about the different animal guilds and related services. For example, two other studies carried out in the same agricultural system showed that the EI location and vegetation physiognomy may influence differently different animal guilds and services [20,120]. These differences should be considered in the global management system.

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Appendix A

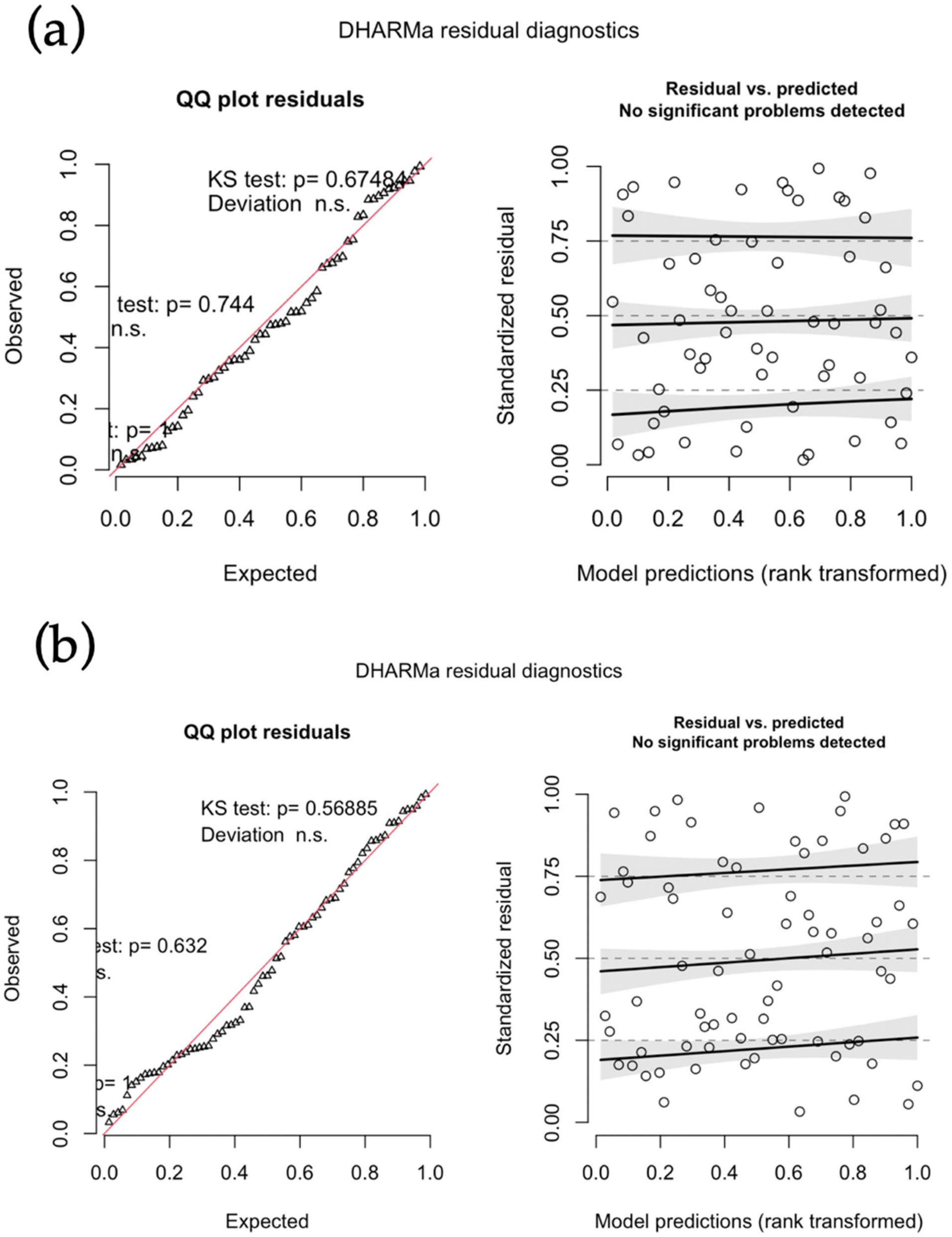

Figure A1. Diagnostic plots showing no significant problems detected in (**a**) GLMMs relating the effects of different predictors on the ant species richness in the agricultural matrix, and in (**b**) GLMMs relating the effects of different predictors on the ant species richness in the ecological infrastructures.

Table A1. Description of the GLMMs relating the effects of different predictors on the ant species richness in the agricultural matrix. Models are ranked in ascending order of AIC values and the number of parameters in the model (K), log-likelihood (logLik), AICc, ΔAICc, and AICc weight (ωi) are given for each model. The "+" signal means the inclusion of the nominal variables in the models.

Models	snd(Int)	dsp(Int)	Crop	Dist_EI	Dist_river	Dist_urban	K	logLik	AICc	ΔAICc	ωi
Richness~Crop + scale(Dist_EI)	1.17	+	+	−0.39			5	−105	222	0.0	0.518
Richness~Crop + scale(Dist_EI) + scale(Dist_river)	1.15	+	+	−0.37	−0.041		6	−105	224	2.4	0.157
Richness~Crop + scale(Dist_EI) + scale(Dist_urban)	1.17	+	+	−0.39		−0.035	6	−105	224	2.4	0.156
Richness~Crop	1.18	+	+				4	−109	227	4.7	0.049
Richness~Crop + scale(Dist_EI) + scale(Dist_river) + scale(Dist_urban)	1.15	+	+	−0.38	−0.032	−0.025	7	−105	227	4.9	0.044
Richness~Crop + scale(Dist_river)	1.11	+	+		−0.124		5	−109	228	6.4	0.021
Richness~Crop + scale(Dist_urban)	1.18	+	+			0.036	5	−109	229	7.0	0.015
Richness~scale(Dist_EI) + scale(Dist_river)	0.72	+		−0.28	−0.205		4	−110	230	7.9	0.010
Richness~scale(Dist_EI)	0.74	+		−0.31			3	−112	230	8.2	0.008
Richness~Crop + scale(Dist_river) + scale(Dist_urban)	1.12	+	+		−0.138	0.063	6	−108	230	8.7	0.007
Richness~scale(Dist_EI) + scale(Dist_urban)	0.73	+		−0.33		−0.116	4	−111	231	9.6	0.004
Richness~scale(Dist_river)	0.75	+			−0.257		3	−113	232	9.7	0.004
Richness~scale(Dist_EI) + scale(Dist_river) + scale(Dist_urban)	0.71	+		−0.29	−0.186	−0.048	5	−110	232	10.2	0.003
Richness~1 (Null model)	0.77	+					2	−114	233	11.1	0.002
Richness~scale(Dist_river) + scale(Dist_urban)	0.75	+			−0.255	−0.0036	4	−114	234	12.0	0.001
Richness~scale(Dist_urban)	0.77	+				−0.0814	3	−114	235	12.9	0.001

EI—ecological infrastructure; Dist_EI—Distance to the closest EI patch; Dist_river—Distance to river; Dist_urban—Distance to urban area; Crop—Crop type (maize field, rice paddy, others—mixed types). Please see Table 1 for a detailed description.

Table A2. Description of the GLMMs relating the effects of different predictors on the ant species richness in the ecological infrastructure (EI) patches. Models are ranked in ascending order of AIC values and the number of parameters in the model (K), log-likelihood (logLik), AICc, ΔAICc, and AICc weight (ωi) are given for each model. The "+" signal means the inclusion of the nominal variables in the models.

Models	snd(Int)	dsp(Int)	Arg_ant	Matrix_area	Riparian_area	Shrub_ richness	Terrestrial_area	HEIDI_index	K	logLik	AICc	ΔAICc	ωi
Richness~Arg_ant + scale(Riparian_area) + scale(Terrestrial_area)	1.3	+	+		−0.14		0.16		5	−165	340	0.00	0.192
Richness~Arg_ant + scale(Terrestrial_area)	1.3	+	+				0.20		4	−166	341	0.11	0.182
Richness~Arg_ant + scale(Matrix_area) + scale(Terrestrial_area)	1.3	+	+	0.06			0.21		5	−166	342	1.79	0.079
Richness~Arg_ant + scale(Terrestrial_area) + scale(HEIDI_index)	1.3	+	+				0.21	−0.038	5	−166	343	2.13	0.066
Richness~Arg_ant + scale(Matrix_area) + scale(Riparian_area) + scale(Terrestrial_area)	1.4	+	+	0.03	−0.13		0.17		6	−165	343	2.19	0.064
Richness~Arg_ant + scale(Shrub_richness) + scale(Terrestrial_area)	1.3	+	+			−0.03	0.21		5	−166	343	2.21	0.064
Richness~Arg_ant + scale(Riparian_area) + scale(Shrub_richness) + scale(Terrestrial_area)	1.4	+	+		−0.14	−0.025	0.17		6	−165	343	2.26	0.062
Richness~Arg_ant + scale(Riparian_area) + scale(Terrestrial_area) + scale(HEIDI_index)	1.3	+	+		−0.14		0.16	−0.23	6	−165	343	2.27	0.062
Richness~scale(Riparian_area) + scale(Terrestrial_area)	1.5	+			−0.20		0.16		4	−168	344	3.21	0.039
Richness~Arg_ant + scale(Riparian_area)	1.4	+	+		−0.23				4	−168	344	3.33	0.036
Richness~Arg_ant + scale(Matrix_area) + scale(Terrestrial_area) + scale(HEIDI_index)	1.3	+	+	0.06			0.22	−0.04	6	−165	344	3.80	0.029
Richness~Arg_ant + scale(Matrix_area) + scale(Shrub_richness)) + scale(Terrestrial_area)	1.3	+	+	0.06		−0.04	0.23		6	−166	344	3.90	0.027
Richness~Arg_ant + scale(Shrub_richness)) + scale(Terrestrial_area) + scale(HEIDI_index)	1.3	+	+			−0.02	0.21	−0.03	6	−166	345	4.43	0.021
Richness~Arg_ant + scale(Matrix_area) + scale(Riparian_area) + scale(Shrub_richness) + scale(Terrestrial_area)	1.4	+	+	0.04	−0.13	−0.03	0.18		7	−165	345	4.49	0.020
Richness~Arg_ant + scale(Matrix_area) + scale(Riparian_area)) + scale(Terrestrial_area) + scale(HEIDI_index)	1.4	+	+	0.04	−0.12		0.17	−0.03	7	−165	345	4.50	0.020
Richness~Arg_ant + scale(Riparian_area) + scale(Shrub_richness)) + scale(Terrestrial_area) + scale(HEIDI_index)	1.4	+	+		−0.14	−0.02	0.17	−0.02	7	−165	345	4.67	0.019
Richness~Arg_ant + scale(Matrix_area) + scale(Riparian_area)) + scale(Terrestrial_area)	1.5	+	+	0.07	−0.17		0.17		5	−167	345	4.79	0.018

EI—ecological infrastructure; Arg_ant—ecological infrastructure; Matrix area—Distance to the closest EI patch; Riparian area—Area of riparian EI; Terrestrial area—Area of terrestrial EI; Shrub_richness—Shrub richness; HEIDI_index—HEIDI quality index. Please see Table 1 for a detailed description.

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