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Contrasting effects of beekeeping and land use on plantpollinator networks and pathogen prevalence in Mediterranean semiarid ecosystems

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Pollinators are fundamental for plant reproduction in natural and agricultural ecosystems. However, their populations are declining worldwide, threatening the functioning of the ecosystem service they provide. The factors driving this change are manifold, but land use changes and interspecific transmission of pathogens between managed and wild bees are prominent. In this context, most research efforts have focused on specific taxa and rarely at the community level, limiting our ability to fully understand the effects of global change on the functioning of plant–pollinator interactions in ecosystems.

Here, we investigate the impact of human activities (beekeeping and land use intensity) on the spread of an emergent pathogen *Vairimorpha ceranae* in Mediterranean wild bee communities inhabiting landscapes with varying levels of anthropogenic disturbance. Plant–pollinator interactions were sampled in nine one-hectare plots along a gradient of land use (urban structures, croplands and natural vegetation) and beekeeping intensity. We analysed the impact of human disturbances on pollination networks and pathogen prevalence, and applied a network approach to examine whether total effects of species in networks (i.e. direct plus indirect interactions) explain pathogen spread through bee communities.

We found that *V. ceranae* prevalence in honey bees is not a good predictor of the pathogen spread through bee communities. There seems to be a temporal mismatch between pathogen dynamics in managed and wild bees. Networks with more diversity of interactions and more plants showed less pathogen prevalence, but total effect analyses (i.e. combining direct and indirect interactions) failed to explain pathogen transmission across pollination networks. Croplands increased wild bee density, and interactions and species diversity in networks, while shrublands had the opposite effect. Our results highlight the importance of studying pathogen dynamics at the community level and analysing species interaction patterns to improve our understanding of pathogen spread through communities.

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Introduction

Animal pollination is a fundamental ecosystem function because approximately 90% of angiosperm plants are pollinated by animals (Ollerton et al. 2011). This mutualistic interaction is also pivotal for humans because more than three-quarters of global food crops rely to some extent on animal pollination (Klein et al. 2007). Bees stand out among animals as the dominant pollinator group and the only one that totally relies on floral resources across its entire life cycle (Ollerton 2017). Therefore, there is increasing concern about the decline of pollinators detected in several areas worldwide (Potts et al. 2010, Goulson et al. 2015) which may trigger a disruption in ecosystem functioning, harming plant reproduction and crop productivity (Biesmeijer et al. 2006). The collapse of pollinator populations is caused by multiple factors (Goulson et al. 2015). However, land use changes and the interspecific transmission of pathogens between managed and wild pollinators can be highlighted among the main drivers of this decline (Proesmans et al. 2021). Most research efforts on understanding the factors of bee declines have focused on specific taxa and rarely at the community level, limiting our ability to fully understand the impact of global change drivers on the functioning of plant-pollinator interactions in ecosystems.

Growers generally rely on managed pollinators, such as the western honey bee Apis mellifera, for crop pollination (Morse 1991, Rucker et al. 2012). However, recent studies report a complementary role of managed and wild bees in crop pollination (Garibaldi et al. 2013, Hünicken et al. 2022). Currently, there is an open debate on the impact of managed bees on wild pollinators (Geslin et al. 2017, Geldmann and González-Varo 2018). There are controversial results on the competition between honey bees and wild bees for floral resources (Mallinger et al. 2017, Wojcik et al. 2018), but it seems that honey bees are replacing wild bees in many managed and unmanaged ecosystems (Herrera 2020, Garibaldi et al. 2021). Moreover, there is evidence on the spillover of pathogens and parasites from honey bees to wild bees (Graystock et al. 2016, Mallinger et al. 2017, Martínez-López et al. 2021, 2022) when they share flower resources (Graystock et al. 2015, Tehel et al. 2016, Figueroa et al. 2019).

Bee pathogens are related to emerging infectious diseases (EID, Manley et al. 2015). Among them, microsporidia have played a critical role in the collapse of honey bee colonies, especially in Mediterranean countries (Martín-Hernández et al. 2018). Microsporidia from the genus *Vairimorpha* (*Nosema*) have been detected in wild bees (Grupe and Quandt 2020, Martínez-López et al. 2021), and their effects on wild bee health have also been studied in different parts of the world such as central Europe (Fürst et al. 2014, Ravoet et al. 2014) and South America (Plischuk et al. 2009, Porrini et al. 2017). For instance, *Vairimorpha ceranae* has spread worldwide due

to the trade in honey bees and is now considered a growing pandemic in managed and wild bees (Grupe and Quandt 2020). *Vairimorpha ceranae* can spread when its primary hosts, honey bee colonies, are moved across the landscape, a process known as migratory beekeeping (Martínez-López et al. 2022). This pathogen has been found in several wild bee taxa, but information on the dissemination of this pathogen at the community level is scarce (Graystock et al. 2020, Figueroa et al. 2020, Martínez-López et al. 2021), especially in semiarid Mediterranean areas, which are recognised as hotspots of bee biodiversity (Orr et al. 2021).

Semi-natural areas are beneficial for wild bee populations because of the food and nesting resources they provide (Goulson et al. 2007, Winfree et al. 2009). When floral resources are scarce, managed and wild bees are more likely to interact via shared resources, increasing pathogen transmission due to the above-mentioned role of flowers as a contact point for pathogen exchange (Gravstock et al. 2015, Tehel et al. 2016). In contrast, mass flowering events have been found to cause a dilutive effect, reducing pathogen transmission (Piot et al. 2021). Semi-natural areas are disappearing due to changes in land use such as agricultural intensification and land abandonment (Robinson and Sutherland 2002, Robledano-Aymerich et al. 2014) which could have negative consequences for pollinators. For instance, intensive farming usually involves an intense use of pesticides, which can have negative impacts on pollinators (Henry et al. 2012, Whitehorn et al. 2012, Nicholson et al. 2023).

The interaction between bees and flowering plants in ecosystems forms complex networks whose structure can be studied to estimate the resilience of pollinator communities to anthropogenic disturbances, such as land use and global environmental changes (Bennett et al. 2020, Bascompte and Scheffer 2023), and to understand the functioning of communities (Heleno et al. 2014, Vizentin-Bugoni et al. 2018, Bennett et al. 2020). Moreover, network structure may shape pathogen transmission across pollinators within communities (Proesmans et al. 2021). Networks with a large diversity of species and many interactions may increase the likelihood of interspecific pathogen transmission (Strona et al. 2018). Conversely, a dilution effect on the spread of pathogens in plant-pollinator networks has been described when the proportion of potential links between species is high (i.e high connectance) (Figueroa et al. 2020). Research has focused on the impact of direct interactions within networks on pathogen spread (Proesmans et al. 2021). However, previous studies have demonstrated that the analysis of the total effects of species in networks (i.e. direct plus indirect interactions) may be more informative to predict the consequences of perturbations in network functioning (Pires et al. 2020). Landscape simplification derived from agricultural intensification and/ or land abandonment can erode plant-pollinator network structure, with important consequences for the functioning

of pollinator communities (Fortuna and Bascompte 2006, Spiesman and Inouye 2013, Shinohara et al. 2019, Colom et al. 2021). However, the effects of these changes in plant–pollinator interactions on the transmission and spread of pathogens are not fully understood.

Here, we investigate the impact of human activities (beekeeping and land use intensity) on the spread of a pathogen V. ceranae in Mediterranean wild bee communities inhabiting landscapes with varying levels of anthropogenic disturbance. We sampled plant-pollinator interactions in nine one-hectare plots distributed along a gradient of land use (urban structures, croplands and natural vegetation) and beekeeping intensity (low presence versus high presence of honey bees) in the southeast of the Iberian Peninsula under a Mediterranean semiarid climate. This region and overall Mediterranean climatic conditions are underrepresented in plant-pollinator and pollinator-pathogen studies, which have generally been conducted at northern latitudes in Europe and America. Specifically, our goals were: 1) to investigate the impact of different stressors (land use intensity and beekeeping) on plant-pollinator networks; and 2) to study whether direct paths and/or total effects (direct + indirect interactions) in plant-pollinator interaction networks explain pathogen spread through bee communities. We expect an effect of land use intensity and beekeeping on plant-pollinator networks reducing interaction diversity. Furthermore, we hypothesized that accounting for both direct and indirect paths connecting species is more effective in determining the spread of pathogens in pollination networks such that wild bees more strongly connected to honey bees through indirect paths would have higher pathogen prevalence.

Material and methods

Study site

Nine one-hectare sites $(100 \times 100 \text{ m})$ distributed along a transect of 20 km in the southeast of the Iberian peninsula (Fig. 1) were included in the study. Study sites were located in the surroundings of a protected area (Sierra Espuña Regional Park and Site of Community Importance of Sierra Espuña, ES ES0000173). Four samplings were performed from February to May 2017 to capture the variability in plant–pollinator interactions and pathogen prevalence.

The area has a semiarid Mediterranean climate with high temperature and low precipitation $(243.51 \pm 16.27 \text{ mm} \text{ and} 17.22 \pm 0.12 \,^{\circ}\text{C}$, La Calavera station, Alhama de Murcia, SIAM 1994–2018). The landscape is characterized by a matrix of crops (irrigated and rainfed crops), anthropogenic structures (urbanizations, roads, etc.) and natural vegetation patches (shrublands and pinewoods). Citrus trees and grapes are the most widespread irrigated crops, while almond and olive trees are the most common rainfed crops. Natural vegetation consists of reforested pinewoods of *Pinus halepensis* dating back to the end of the 19th century, and Mediterranean shrublands with several species such as *Anthyllis cytisoides*, *Helianthemum violaceum, Stipa tenacissima, Teucrium capitatum, Rosmarinus officinalis* and *Sideritis murgetana*.

Interaction sampling

Honey bees and wild bees were collected in four sampling periods from February to May (late winter, early spring, mid spring and late spring) (27.26 \pm 7.36 days between samplings). Samplings consisted of transects of 100 m length and



Figure 1. Study sites (red dots) distributed within the limits of Sierra Espuña protected area. Map elaborated with QGIS ver. 2.14.3 (QGIS Development Team 2022).

2 m width randomly distributed within the study plots. Field work was performed on sunny, windless days from 10:00 to 18:00 with uniform sampling effort for each site (1 h/sampling). Bee individuals were captured with hand nets and the flowering plants on which they foraged were recorded. The density of wild bees per site and sampling (bees/m²) were calculated at the community level. We also collected some bees within the plots outside the sampling scheme to increase sampling size for pathogen prevalence and pollination networks, but these individuals were not considered for density estimates. When honey bees appeared in large numbers, we collected only one in ten. However, we assessed the total number of honey bees to calculate densities.

The abundance and richness of bees is highly related to the availability of floral resources (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003). Therefore, we also assessed the flower density and the species richness of flowering plants of the study sites in the four samplings, by counting floral units in ten randomly distributed 1 m² plots within the study areas. Flowers belonging to the *Asteraceae* family were considered as a single floral unit. Plants were identified at either species or genus level.

Pollinators identification

Bees were identified in a previous study (Martínez-López et al. 2021) through an integrative taxonomy approach combining classical taxonomy and DNA barcoding. Briefly, we took individual pictures from each bee, which were sent to an expert taxonomist. Additionally, we amplified the barcoding *cox1* region (cytochrome c oxidase subunit I) of the mitochondrial DNA for each bee. Finally, we combined both sources of information to identify all individuals at least up to the genus level.

Network analyses

We calculated the structural features of the sampled pollination networks with the R package 'bipartite' (www.r-project. org, Dormann et al. 2008). The following parameters were computed: the number of bee species, the number of plant species visited by the sampled bees, the number of interactions, the ratio between the richness of animal and plants (web asymmetry), the Shannon diversity of the interactions, the proportion of possible links between species that are realized (connectance), nestedness (Almeida-Neto and Ulrich 2011) which is a measure of the level of interaction among generalist and specialist species (Bascompte et al. 2003), and specialization (Blüthgen et al. 2006) which measures the niche complementarity among species (i.e. whether bees in networks are generalist and interact with multiple plants or if bees are specialist and interact only with some plants).

Assuming bee pathogens spread from honey bees to wild bees indirectly, through the interactions they share with plants, we should be better able to understand pathogen transmission by investigating the indirect paths connecting species in plant–pollinator networks. Thus, we also examined

the matrix of total effects, which accounts for both direct and indirect paths between species (Pires et al. 2020). We calculated the total effects matrix by computing a dependence matrix **Q**, with dimensions $S \times S$, where q_{ii} represents the proportion of interactions of species *i* with species *j* over the total of interactions of species *i*. The total effects matrix is then computed as $T = (I - RQ)^{-1}$, where I is the determinant, **R** is a diagonal matrix that represents how relevant interactions are for each species, and Q is the dependence matrix. Because we are interested solely in the topology of the network and not on population dynamics, we chose a fixed value of $R_{ii} = 0.8$ for all species. Each element T_{ij} represents the total effects through direct and indirect paths of species j on species i. The sum of values over the columns, T_{out} , is a proxy for the overall influence of each species over the others (Pires et al 2020). We computed T_{out} for each species as an estimate of its potential to function as an infectious host, in the case of bees, or as a site of infection, in the case of plants. We also computed the T matrix for the networks representing each location and registered the potential influence of honey bees over other species of bees and plants locally.

Pathogen detection

Vairimorpha ceranae prevalence in the collected samples was determined in a previous study by molecular techniques (Martínez-López et al. 2021). Briefly, we used specific primers for the amplification of *V. ceranae* (Martín-Hernández et al. 2007). Negative and positive controls were included in all reactions. DNA of the pathogen was detected by PCR, so, we can confirm the presence of the pathogen in the positive samples. This does not guarantee that these bees were infected, and individuals could carry the pathogen without developing infections.

Land use intensity calculation

We assessed land use in all the study areas at four different distances from the center of the plot (250–500–750–1000 m). Information about land uses in the different areas was extracted from the Information System of Land Occupancy in Spain (Instituto Geográfico Nacional 2015) (SIOSE). Five categories were considered: 1) irrigated crops; 2) rainfed crops; 3) shrublands; 4) pinewoods; and 5) anthropogenic structures (i.e. roads, houses, etc.). Rainfed crops in the area are associated with traditional management and/or low use of pesticides and fertilizers, while irrigated crops are generally linked to intensive agricultural management. We used QGIS ver. 2.14.3 (QGIS 2022) to calculate the area of each land use for the study sites at all distances. We also assessed land use inside the study plots to consider its impact on the wild bee community.

Data analyses

To better understand the factors affecting wild bee density, we used generalized linear models to test how the density of wild bees was impacted by land use, the density of honey bees, sampling period (i.e. each sampling per time and plot) and the density and richness of flower species. We performed each test separately using univariate models to assess which of the potential predictors would have the largest effect.

To analyse the temporal trends in pathogen prevalence in wild bees we used logistic regression model with the logit link function with sampling period as the predictor. Variation in pathogen prevalence in honey bees along sampling periods was tested with a quasibinomial model to deal with overdispersion. Next, to find the main factor determining the prevalence of *V. ceranae* in wild bees we fitted a series of separate, univariate logistic models with the following predictors: the prevalence of V. ceranae in A. mellifera, the density of honey bees, wild bee density, flower density, flower species richness and each of the network structural metrics. We include honey bee prevalence and density as potential predictors because the honey bee is often assumed to be the main host of V. ceranae (Higes et al. 2008b). Flower density, richness and bee abundance were included because floral resources and bee abundances can shape pathogen transmission patterns (Adler et al. 2018, Piot et al. 2021, Tuerlings et al. 2022). Finally, network structural metrics were also tested because species are directly and indirectly connected to one another as a result of their interactions, and this may also lead to pathogen transmission. To test whether land use can affect pathogen prevalence in wild bees we performed logistic regression models with land use type within each site and the buffer as predictors. Again, we used a series of univariate tests to detect the most relevant scale affecting pathogen prevalence. Data from site five in the 3rd sampling period were excluded from this analysis because the site was an outlier. Excluding these data did not significantly alter the interpretation of our results. We also tested the impact of land use at different spatial scales on the pollination networks by using independent univariate linear Gaussian models.

To understand whether pathogen prevalence detected in the different bee species could be predicted from their direct and indirect interaction patterns, we analysed the correlation between the total effects of the honey bee on each species in pollination networks representing each site, and their pathogen prevalence in that site, using non-parametric Spearman correlations for each site. If honey bees are indeed the main host transmitting the pathogen to other bees, we should expect that wild bees that were indirectly connected to honey bees more strongly via shared plant usage would have a greater pathogen prevalence. Flowers have been highlighted as hubs for pathogen transmission among bee species (Graystock et al. 2015). Therefore, plant species visited by a higher number of bees positive to V. ceranae are, theoretically, more likely to host the pathogen. Thus, we also tested the correlation among the total effects of the honey bee in networks and *V. ceranae* prevalence in the bees visiting each plant species. Pathogen prevalence per plant species was calculated by dividing the number of visits received by bees positive to the pathogen by the total number of visits. Visits performed by honey bees were excluded from this analysis to prevent

bias in the results (i.e. measure the impact of the total effects of honey bees on the networks on themselves).

All statistical analyses were performed in R ver. 4.1.1 (www.r-project.org). Explanatory variables were standardised to facilitate the comparison among the different land uses and variables with different scales with the R package 'robustHD' (www.r-project.org, Alfons 2019). Residuals of all the models were checked with the R package 'DHARMa' (www.r-project.org, Hartig 2022). The absence of spatial and temporal autocorrelation in the models was also tested (Bjornstad 2020). Furthermore, we tested for overdispersion in logistic models with the R package 'performance' (www.r-project. org, Lüdecke et al. 2021). Bonferroni correction was applied to models testing the impact of land use on wild bee density, pathogen prevalence and pollination network properties, and models analysing the effect of pollination network properties on wild bee pathogen prevalence, to reduce the chances of having false significant relationships due to multiple models testing (p-value_{adi}) (Jafari and Ansari-Pour 2019). Note that the calculation of pathogen prevalence for network properties analyses only included bee individuals that interacted with a plant. Most wild bees have foraging ranges of less than 200 m (Kendall et al. 2022) and short life spans (< 30 days) and foraging periods (10–14 days) (Danforth et al. 2019). Therefore, densities of bees in each site and sampling period were considered as independent data.

Results

Plant-pollinator interactions

We sampled 816 individuals, 506 wild bees and 310 honey bees, and we recorded 705 plant–pollinator interactions (Supporting information). A total of 92 molecular operational taxonomic units of bees and 53 plant species were found in the overall sampling (Supporting information). We built nine pollination networks, one per study plot, merging the data from the four sampling periods. The size of the networks varied between 39 and 122 interactions at sites three and one, respectively. See Supporting information for network parameters. The density of wild bees varied between 0 and 0.0275 bees/m² (Supporting information) and did not show any temporal pattern (β =0.0003; p-value=0.763, n=36). Wild bee densities were explained neither by the density of flowers (β =0.0004; p-value=0.743, n=36) nor by the richness of flowering plant species (β =0.002; p-value=0.154, n=36).

Beekeeping effects on pollinators

The density of honey bees did not have any effect on the density of wild bees (β =0.032; p-value=0.514, n=36). A total of 235 bees tested positive for *V. ceranae*, of which 96 were wild bees (Supporting information). Pathogen prevalence in honey bees decreased along with the sampling period (β =-1.208; p-value < 0.001***, n=35) (Fig. 2a), while it increased in wild bees (β =0.298; p-value=0.009**, n=35) (Fig. 2b).



Figure 2. Temporal variation in *Vairimorpha ceranae* prevalence in honey bees (p-value > 0.001^{***}) (a) and wild bees (p-value = 0.009^{**}). (b) T1 = late winter; T2 = early spring; T3 = mid spring; and T4 = late spring. Boxplots show the median (thick horizontal lines), the quartiles (boxes and vertical lines) and the outliers (empty dots). Silhouettes taken from www.phylopic.org.

Pathogen prevalence in wild bees was not related to the density of bees, either managed (β =-0.119; p-value=0.427, n=35) or wild (β =-0.003; p-value=0.979, n=35). However, the occurrence of *V. ceranae* in wild bees showed a negative significant relationship with the pathogen prevalence in honey bees (β =-0.355, p-value=0.008**, n=35). Furthermore, flower density was negatively associated with pathogen prevalence in wild bees (β =-0.406, p-value=0.008**, n=35). Floral species richness did not show any impact on *V. ceranae* prevalence in wild bees (β =-0.030; p-value=0.781, n=35). Pathogen prevalence in pollination networks was negatively associated with Shannon diversity of the interactions (SD) (β =-0.269, p-value_{adj}=0.034*, n=9) and the number of plant species in the network (P) (β =-0.297, p-value_{adj}=0.018*, n=9) (original and adjusted p-values in Supporting information). *Apis mellifera* showed by far the largest total effect on the pollination networks, followed by *Eucera* sp2 and *Seladonia* species (Fig. 3a). With regard to plants, *Carduus* spp., *R. officinalis* and *A. cytisoides* exhibited the largest total effects (Fig. 3b).



Figure 3. Total effects of bees (a) and plant species (b) on the nine pollination networks. Boxplots show the median (thick horizontal lines), the quartiles (boxes and vertical lines) and the outliers (empty dots). Only plant and bee species with more than one recorded interaction are shown. Silhouettes taken from www.phylopic.org.

The total effects of honey bees on wild bees in pollination networks showed no correlation with the pathogen prevalence across bee species in the network (Fig. 4). Similarly, there was no correlation between the total effects of *A. mellifera* on plants in the networks and the pathogen prevalence in plants (Fig. 5).

Impact of land use intensity on wild pollinators

Land use composition of the study sites was calculated from the plot level up to 1000 m (Supporting information). The most representative land uses at plot level in the study sites were rainfed crops and shrublands. Anthropogenic structures and pinewoods did not have any effect on wild bee densities. However, irrigated crops had a positive impact on bee densities at all distances (Buffer 250: $\beta = 0.004$, p-value- $_{adj} = 0.025^*$; Buffer 500: $\beta = 0.004$, p-value $_{adj} = 0.014^*$; Buffer 1000: $\beta = 0.004$, p-value $_{adj} = 0.039^*$; n=36) (Supporting information) (original and adjusted p-values in Supporting information). Contrastingly, study sites with larger areas of shrublands showed lower densities of wild bees at the plot level (Plot level: $\beta = -0.005$, p-value_{adj} < 0.001^{***} ; n=36). Rainfed crops positively affected wild bee densities only at the plot level ($\beta = -0.005$, p-value_{adj} < 0.001^{***} ; n=36). There was no correlation between pathogen prevalence in wild bees and land uses at any spatial scale.

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Shrublands increased nestedness in pollination networks from 250 to 750 m, but only with a marginal statistical significance (Buffer 250: β =5.831, p-value_{adj}=0.061; Buffer 500: β =5.866, p-value_{adj}=0.054; Buffer 750: β =5.799, p-value_{adj}=0.068; n=9). There was no other significant relationship between the land uses in the surroundings of the study plots and the pollination networks. However, land uses at the plot level had an effect on the bee communities. Rainfed crop increased the Shannon diversity of the interactions (β =0.540, p-value_{adj}=0.055; n=9) and the number of bee species in the networks (β =8.021, p-value_{adj}=0.054; n=9) (original and adjusted p-values in Supporting information), both with a marginal level of significance. Conversely,

2.0 2.0 2.5 1.2 1.6 2.4 0.5 1.0 1.5 1.0 1.5 2.0 2.5 3.0 Total effects of Apis mellifera in networks Figure 4. Non-parametric Spearman correlation analyses between the total effects of the honey bee in networks and the pathogen prevalence in wild bees. Points represent the different wild bee species in the pollination networks from the different study plots. Dashed lines depict a trendline representing the relationship among total effects of the honey bees in the networks and the pathogen prevalence in wild bees. The analyses did not find any significant correlation (p-value < 0.05). Silhouettes taken from www.phylopic.org.





Figure 5. Non-parametric Spearman correlation analyses between the total effects of the honey bee in networks and the pathogen prevalence in plants (i.e. dividing the number of visits received by bees positive to the pathogen between the total number of visits, excluding the visits realized by the honey bee). Points represent the different plant species visited by wild bees in the pollination networks from the different study plots. Dashed lines depict a trendline representing the relationship among total effects of the honey bees in the networks and the pathogen prevalence in plants. The analyses did not find any significant correlation (p-value < 0.05). Silhouettes taken from www.phylopic.org.

shrubland decreased the Shannon diversity of the interactions ($\beta = -0.557$, p-value_{adj} = 0.025^{*}; n = 9) and the number of bee species ($\beta = -7.999$, p-value = 0.057; n = 9).

Discussion

Overall, we observed that the anthropogenic stressors considered in this study (beekeeping and changes in land use) had contrasting effects on wild bee communities. We assume that honey bees might have triggered pathogen spillover in wild bees as they are considered the main host of *V. ceranae* in Europe (Higes et al. 2008b) and no research to date has found a secondary host able to spread the pathogen in pollinator communities. However, we found that managed and wild bees showed opposite temporal trends in pathogen prevalence. In addition, networks with higher interaction diversity and more plant species showed lower pathogen prevalence, but species interaction patterns failed to explain pathogen spread through bee communities. In contrast, anthropogenic land uses, such as rainfed and irrigated crops, seemed to benefit pollinators by increasing wild bee densities.

Pathogen spillover from managed to wild bees has been highlighted as a major driver of the current decline of pollinators (Goulson et al. 2015). The interspecific transmission of pathogens such as *V. ceranae* from the honey bee to several wild bees has been reported in many areas worldwide (Grupe and Quandt 2020). However, seasonal patterns of this microsporidium in wild bee communities are generally unknown. Furthermore, most of the information available on the pathogen spread from managed to wild bees is restricted to a limited number of species, and only a few studies have addressed this issue at the community level (Figueroa et al. 2020, Graystock et al. 2020, Martínez-López et al. 2021). Here, we found that *V. ceranae* prevalence in wild bee communities increased over time, while it decreased in the honey

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bees for the same period. Our results on V. ceranae prevalence in honey bees are congruent with previous studies conducted in the Iberian peninsula, which also reported peaks of infection in winter (Higes et al. 2008b), although there seems to be great variability (Jabal-Uriel et al. 2022).

The honey bee is considered the main host of V. ceranae in Europe (Higes et al. 2008b). Thus, we would expect to find parallel seasonal trends of pathogen prevalence in honey bees and wild bees. On the contrary, we found that pathogen prevalence in honey bees and wild bees was negatively correlated throughout the study period. These results suggest that the pathogen may be able to remain in the landscape after its presence in the main host has declined. Vairimorpha ceranae spores can be viable for at least 18 days in the environment (Higes et al. 2008a). However, this time period seems insufficient to explain our results, as spores would need to remain viable for more than a month. Wild bees may be acting as secondary vectors of the pathogen without becoming infected; but, if so, V. ceranae prevalence in wild bees should decline together with, or shortly after, its decrease in the main host, the honey bee. On the other hand, there could be other hosts of the pathogen in pollinator communities. Some studies report wide host ranges (Martín-Hernández et al. 2018, Grupe and Quandt 2020), although others report host specificity of the pathogen (Gisder et al. 2020, Ngor et al. 2020). Therefore, there is still a great deal of controversy on the subject. Our results indicate that the mechanisms of pathogen spread may be more complex than previously assumed. Further community level studies are necessary for a better understanding of the threat this and other pathogens pose to wild bee assemblages, and to develop effective strategies to mitigate its impact on natural populations.

Previous work has found that the structure of plant-pollinator networks can predict pathogen dynamics across landscapes (Proesmans et al. 2021). We found that pathogen prevalence decreased in networks with more plant species and higher diversity of interactions. More plant species and higher diversity of interactions in networks can lead to an increase in niche partitioning, which in turn reduces the chances of individuals from different species interacting during visits and exchanging pathogens (Doublet et al. 2022). Similarly, previous studies have demonstrated that floral traits affect pathogen transmission (Adler et al. 2018, Figueroa et al. 2019) and that increasing bee and flower species richness reduces pathogen interspecific transmission (Graystock et al. 2020, Fearon and Tibbetts 2021). Furthermore, our results showed that flower density is negatively related to pathogen prevalence in wild bees, which could be explained by a diluting effect as the density of the host is reduced in the landscape (Graystock et al. 2020, Piot et al. 2021). Neither total effects of the honey bee in networks nor pathogen prevalence on plants showed any relationship with pathogen prevalence in wild bees. The temporal mismatch between pathogen prevalence in honey bees and wild bees may explain the lack of a relationship between the indirect influence of honey bees over wild bees and pathogen prevalence. The ability of flowers to host and disseminate bee pathogens varies according to the

plant species (Adler et al. 2018, Figueroa et al. 2019), which can explain why our approach, considering the entire flowering plant community, also failed to predict pathogen spread. Additionally, there may be other routes of exposure, as microsporidia spores have been found in air (Sulborska et al. 2019) and water (Izquierdo et al. 2011).

Natural and seminatural areas are critical for maintaining pollinators in agricultural landscapes (Winfree et al. 2009, Roth et al. 2023). Conversely, intensification of agricultural lands can trigger a decline in wild bee populations and the extinction of the most vulnerable species (Vanbergen and Insect Pollinators Initiative 2013). Thus, maintaining heterogeneous land use matrices that combine natural patches of vegetation and low-intensity agricultural management practices could counteract the effect of highly intensive land uses, such as intensive agriculture and urbanization, by providing a wider variety of resources to bees (Tscharntke et al. 2005, Kennedy et al. 2013). Previous studies on the effects of land use intensification on pollinator communities and plant-pollinator networks found that bees are highly resistant and only experience sharp declines in situations of extreme landscape degradation, although these responses vary according to the biogeographical regions (Winfree et al. 2009, De Palma et al. 2016, Morrison and Dirzo 2020, Millard et al. 2021). For instance, Millard et al. (2021) analysed the impact of variable levels of land-use intensity on pollinator communities worldwide. They found that low levels of land use intensity can be beneficial for pollinators, while the negative impact of agricultural intensity on pollinators seems to be restricted to tropical areas. Our results are in line with previous research, as we did not detect any negative impact of anthropogenic land uses on wild bee densities and plant-pollinator networks. Contrastingly, we found a positive impact of rainfed crops on wild bees at plot level (higher wild bee densities, more bee species in networks and more diverse interactions) and irrigated crops (higher bee densities from 250 to 1000 m), and a negative impact of shrublands (lower bee densities, lower diversity of interactions and reduced number of bee species). These findings are congruent with previous research that also reported a positive impact of low and medium/high intensity croplands on bee richness and abundance in comparison with natural vegetation areas (De Palma et al. 2016, Millard et al. 2021). This could be due to the higher offer of floral resources in agricultural patches. This trend can be particularly relevant in semiarid ecosystems, like in our study area, because drought reduces floral resources for bees (Phillips et al. 2018). Therefore, irrigated crops would provide more food resources which turn into an increase in wild bee densities and species richness. However, the attractant effect of irrigated crops can be a double-edged sword, as these crops are often associated with increased pesticide use, which could increase the exposure of wild bees to these chemical agents even when foraging on non-cultivated plants and flowers at field borders (Long and Krupke 2016, Ward et al. 2022). Pollinator transects in this study were performed in rainfed crops and shrublands, and hence we do not have data on pollinator abundance in irrigated crops, which makes it difficult to disentangle bee

preferences towards any particular land-use type. Therefore, the positive relationship between wild bee density and irrigated crops may be caused by bee preference for other land use types. Thus, future studies should assess pollinator abundances in different land use types to fully understand bee preferences at the landscape scale.

In conclusion, our results suggest that *V. ceranae* prevalence in honey bees is not a good predictor of pathogen spread in bee communities. There seems to be a temporal mismatch between the honey bee and wild bee pathogen dynamics, which highlights the importance of conducting more research on the seasonal patterns of pathogen dynamics in plant-pollinator networks (Adler et al. 2018, Tuerlings et al. 2022). The analyses of the total effects accounting for the temporal dimension could help to shed light on this issue, but would require a sampling design focusing on obtaining a good temporal characterization of the interaction networks. Furthermore, there is an urgent need to disentangle whether wild bees are just secondary vectors or can become infected and spread V. ceranae spores across environments. The land use matrix composition in our study areas seems to be suitable for pollinators. Thus, land use change drivers leading to landscape simplification might have negative consequences for pollinators. For example, land abandonment of agricultural patches is increasing in many areas of the Northern Hemisphere such as the Mediterranean basin (Cramer et al. 2008). These old fields are colonized by natural vegetation such as shrublands, which could lead to a reduction of pollinators' richness and abundance (Shinohara et al. 2019, Colom et al. 2021). Therefore, management policies should address these issues and take adequate measures in order to preserve wild bee communities.

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Vicente Martínez-López: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). Carlos Ruiz: Conceptualization (supporting); Data curation (supporting); Investigation (supporting);

Methodology (supporting); Validation (supporting); Writing – review and editing (supporting). **Mathias M. Pires:** Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Validation (supporting); Wisualization (supporting); Writing – review and editing (supporting). **Pilar De la Rúa:** Conceptualization (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5qfttdzcv (Martínez-López et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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