



Association patterns between farmland abandonment and the non-native Common Waxbill (*Estrilda astrild*) in the eastern Iberian Peninsula

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Abstract

Pet trading has led to a growing number of bird introductions worldwide, which has negatively affected recipient ecosystems and native species. Studying the seasonal and spatial distribution patterns of native and non-native bird species, such as the Common Waxbill (*Estrilda astrild*), is fundamental for understanding the ecological interactions between these two groups of species. For this purpose, we ran a year-round survey of passerine communities in two Mediterranean wetlands of the eastern Iberian Peninsula and investigated Common Waxbill's feeding preferences. We studied the Common Waxbill association with native birds and their habitat use. The cluster analysis indicated that the Common Waxbill was the most abundant species of a distinct community, with peak presence in autumn. The random forests analysis revealed that it preferred human-modified land uses. Furthermore, farmland abandonment and the presence of two invasive plants, Pampas Grass (*Cortaderia selloana*) and Giant Reed (*Arundo donax*), positively influenced Common Waxbill presence. However, when eaten plants were divided into native, non-native and invasive, the Common Waxbill did not exhibit any preference. This corroborates that the Common Waxbill has significant ecological plasticity, which allows it to exploit a wide range of feeding resources in human-modified habitats. This study enhances knowledge of the interactions between native birds and invasive plants due to farmland abandonment, and of one of the most globally widespread non-native bird species. It highlights the need to monitor both groups of species and their long-term interactions.

Keywords Farmland abandonment · Alien species · Degraded habitat · Invasive plants · Land use · Avian ecology

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Zusammenfassung

Die Stilllegung von Ackerland und der nicht einheimische Wellenastrild (*Estrilda astrild*) im Osten der Iberischen Halbinsel: Muster ihrer Wechselwirkungen

Der Handel mit Haustieren hat weltweit zu vermehrten Vogelein-schleppungen geführt, die sich negativ auf die vorhandenen Ökosysteme und ihre einheimischen Arten ausgewirkt haben. Die Untersuchung der jahreszeitlichen und räumlichen Verbreitungsmuster einheimischer und nicht einheimischer Vogelarten, wie z. B. des Wellenastrilds (*Estrilda astrild*), ist von grundlegender Bedeutung für das Verständnis der ökologischen Wechselwirkungen zwischen diesen beiden Gruppen von Arten. Zu diesem Zweck führten wir eine ganzjährige Untersuchung von Singvogelgemeinschaften in zwei mediterranen Feuchtgebieten im Osten der Iberischen Halbinsel durch, analysierten die Nahrungspräferenzen des Wellenastrilds und untersuchten, in was für einer Beziehung er zu den einheimischen Vögeln und deren Nutzung ihres Habitats stand. Eine Clusteranalyse ergab, dass der Wellenastrild innerhalb einer bestimmten Vogelgemeinschaft am häufigsten vorkam und dies vor allem im Herbst der Fall war. Eine Random-Forst-Analyse ergab, dass der Wellenastrild Bodenflächen mit einer vom Menschen veränderten Landnutzung bevorzugte. Darüber hinaus wirkten sich die Stilllegung von Ackerland und das Vorhandensein zweier invasiver Pflanzen, Pampasgras (*Cortaderia selloana*) und Riesenschilfrohr (*Arundo donax*), positiv auf das Vorkommen des Wellenastrilds aus. Bei einer Einteilung der gefressenen Pflanzen in einheimische, nicht einheimische und invasive Pflanzen zeigte der Wellenastrild allerdings keine Präferenz. Dies bestätigt, dass der Wellenastrild eine erhebliche ökologische Anpassungsfähigkeit aufweist, die es ihm ermöglicht, ein breites Spektrum an Nahrungsressourcen in vom Menschen veränderten Lebensräumen zu nutzen. Diese Untersuchung vertieft unser Wissen von den Wechselwirkungen zwischen einheimischen Vögeln und invasiven, nach der Stilllegung von Ackerland sich dort ansiedelnden Pflanzen einerseits und über eine der weltweit am weitesten verbreiteten, nicht einheimischen Vogelarten andererseits und unterstreicht die Notwendigkeit, beide Gruppen von Arten und ihre langfristigen Wechselwirkungen weiter zu beobachten.

Introduction

Pet trading has caused numerous bird introductions worldwide (Gippet and Bertelsmeier 2021), which has had deleterious effects on the recipient ecosystems and inhabiting native species (Downs and Hart 2020). Birds recently introduced into Mediterranean ecosystems, particularly in the Mediterranean Basin, have a proven significant capacity to establish self-sustaining populations (Kark and Sol 2005). This phenomenon has been favoured by a substantial human-induced alteration of landscapes with activities like agriculture, forest exploitation and urban development (Gaertner et al. 2017), which contribute to generate novel ecological resources by facilitating the successful establishment of these introduced bird species (Saâd et al. 2021; Ibañez et al. 2023).

The Common Waxbill (*Estrilda astrild*) stands out for being one of the most globally pervasive non-native bird species (Reino et al. 2009). It exhibits opportunistic reproductive behaviour and is well suited to exploit transient breeding opportunities (Beltrão et al. 2021) across its vast native sub-Saharan distribution area. The Common Waxbill's native distribution spans an extensive range of climates, from the Mediterranean climate in South Africa, to the tropical and humid climate of the Rift Valley, to the xeric Sahel with its climate of remarkable extremes. Its current non-native distribution includes, among others, many tropical and subtropical islands, such as Trinidad and Tobago, Puerto Rico, Hawaii and Bermuda, but also continental

areas like Brazil (Stiels et al. 2011). In Brazil, the Common Waxbill has demonstrated the ability to extend its ecological niche and successfully colonise new areas thanks to intrinsic factors (behaviour flexibility), but also to extrinsic factors (intentional releases, lack of predators, road infrastructures that funnel their spread, deforestation and Africanisation of substituting grassland). All this highlights this species' paramount adaptability and plasticity (Cardoso da Silva et al. 2018).

In the Iberian Peninsula, the Common Waxbill has long since been established (Clement et al. 1999). The first deliberate release in Portugal occurred in 1964 (Reino and Silva 1998), and it soon spread towards Spain to reach nearby Andalusia and Extremadura regions in the 1970s (Cardoso and Reino 2018). However, it was not recorded in eastern Spain until the late 1980s (SVO 1997; Estrada et al. 2005; Polo-Aparisi and Polo-Aparisi 2021).

In the Iberian Peninsula, the Common Waxbill breeding season goes from April to October, which is longer than it is for any native passerine (Sanz-Aguilar et al. 2015). Previous studies in the Iberian Peninsula have suggested that the Common Waxbill occupies a vacant niche in highly human-modified habitats (Batalha et al. 2013). Interactions among native, non-native and invasive species are complex (Ricciardi et al. 2013), and can be influenced by the environmental characteristics of recipient habitats (Hernández-Brito et al. 2014). This can be particularly important when recipient habitats are highly modified and have been previously occupied by other taxa (e.g. invasive plants), which can lead

to the exploitation of differentiated resources (Hernández-Brito et al. 2014). For instance, the autumn and winter diets of the Common Waxbill and the most ecologically similar native species in foraging terms, the European Serin (*Serinus serinus*), have been compared to reveal that non-native plants constitute a larger portion of the Common Waxbill's diet (Cardoso et al. 2018).

Other studies have found that the Common Waxbill is positively associated with the presence of rice fields, which are underexploited by native species, but is likely to occur across a wide range of vegetation types (Sullivan et al. 2015). The Common Waxbill feeds preferentially on rough grasses, emergent vegetation and forbs, while emergent vegetation and the invasive Giant Reed (*Arundo donax*) were strongly selected for shelter, with a comparatively weaker selection of trees and bushes (Sullivan and Franco 2018). Hence, the remarkable success of its colonisation is facilitated by a long breeding season, which serves as an exceptional phenological trait, by its opportunistic behaviour, sheltering and dietary preferences, and by adaptability to diverse ecological niches (Cardoso et al. 2018).

Invasive plants often alter habitat composition and food resource availability by creating favourable conditions for non-native bird species (Mandon-Dalger et al. 2004; Nelson et al. 2017). In the coastal wetlands and dunes of the eastern Iberian Peninsula, Giant Reed and Pampas Grass (*Cortaderia selloana*) are considered to form part of the most invasive plants in the region (Domènech et al. 2005; Aguiar and Ferreira 2013). Giant Reed already occupies large extensions in Spain (Jiménez-Ruiz et al. 2021), whereas Pampas Grass has rapidly extended, which threatens habitats of special interest (Company et al. 2019) and benefits from disturbed areas, mainly in the form of abandoned crop fields and cultivated areas (Pausas et al. 2006; Pyšek et al. 2010). In Spain, its invasion has prevented restoring wastelands back to wetlands where some rare or endemic species occur (Domènech and Vilà 2007). Thus, both species have been included in the National Spanish Catalogue of Invasive Species and are actively managed to mitigate their impact (MITECO 2018; Muñoz-Mas et al. 2021).

In general, a positive relation exists between the presence and abundance of non-native and invasive species and the degradation of recipient habitats and ecosystems (Salgado et al. 2019; Colléony and Shwartz 2020). To date, Common Waxbill's ecological preferences in the eastern Iberian Peninsula have been understudied, and include the use of degraded habitats and non-native plants as food resources. Furthermore, its species density in the region and its interactions with local passerine communities remain largely unknown. In the Valencia Region (the eastern Iberian Peninsula), where this study was conducted, the Common Waxbill population has exhibited a positive trend ever since

the first individuals were recorded (Gómez-Serrano et al. 2000; Tirado et al. 2015, 2017, 2019). This phenomenon is coupled with the massive abandonment of citrus orchards, caused by different socio-economic and climatic drivers (Morell-Monzó et al. 2021, 2023), whereas the relation linking extensive farmland abandonment, its colonisation by Giant Reed and Pampas Grass, and Common Waxbill's extension warrant further research to corroborate a potential interconnection.

Based on all this, we hypothesise that Common Waxbill presence and abundance are related to degraded and abandoned farmlands, where these two dominant invasive plant species, Giant Reed and Pampas Grass, are present. To test these hypotheses, we carried out the following analyses at two taxonomic levels. At the community level, we delineated the bird communities with which the Common Waxbill co-exists by employing a community detection algorithm on the resulting association network to test which communities have closer similarities to the Common Waxbill. Then, we related the presence of each community to several environmental factors, including geographic, botanical, climatic and land-use variables, with a random forest analysis to test whether there are association patterns among these bird communities, including those where the Common Waxbill is present, and farmland abandonment and the presence of invasive plant species. At the species level, we estimated Common Waxbill's density and seasonal abundance. We also estimated whether there is a relation between the presence of the invasive Giant Reed and Pampas Grass and Common Waxbill's presence. Finally, we identified consumed plants and investigated dietary preferences, including whether the species more frequently consumes native, non-native or invasive plants.

Methods

Study area and bird community sampling

The study was carried out in two wetlands of the Valencia Region, in the eastern Iberian Peninsula (Fig. 1), classified as sites of community importance: Marjal de la Safor (latitude 39.00°, longitude − 0.20°, area 1245 km²) and the Pego-Oliva Natural Park (latitude 38.87°, longitude − 0.06°, area 1255 km²). The sampling methodology consisted of point counts (Buckland et al. 2015) and is widely used to make inventories and to monitor bird communities (de Gabriel Hernando et al. 2022).

The ownership of most of the land in our study areas is private, and is fenced in many cases. Thus, we systematically surveyed the point counts on public paths and tracks. In all, 71 sites (37 in Marjal de la Safor, 34 in the Pego-Oliva Natural Park) were uniformly distributed

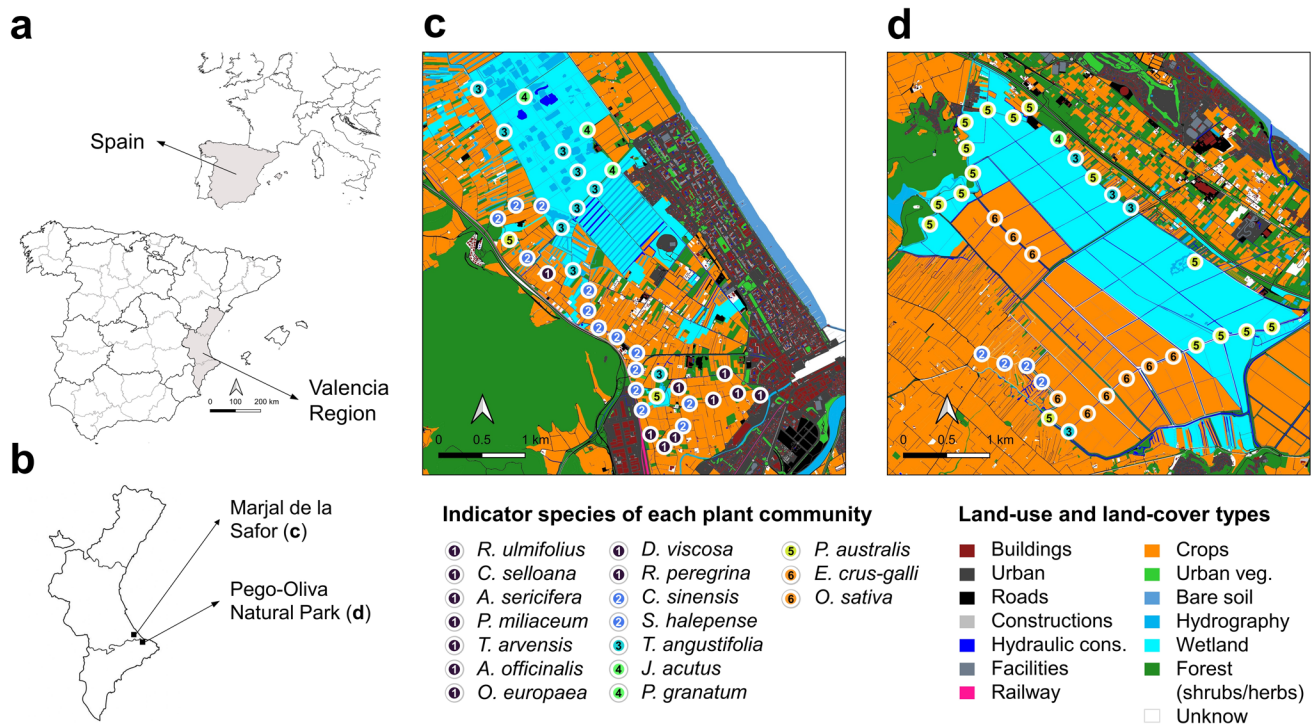


Fig. 1 Location map on the European (a) and Spain scales (b) of the two study areas, Marjal de la Safor (c) and the Pego-Oliva Natural Park (d), in the Valencia Region (E Spain). Circles represent the sites at which birds were sampled via point counts approximately every fortnight from mid-March 2022 to mid-April 2023. They are coloured and numbered with the dominant plant community. Each plant community is represented by one indicator species or more (details in

the Methods and Results sections). Land-use types are the result of human activities that modify land surface (e.g., urban areas or crop-lands), whereas land-cover types (e.g., wetlands or forests: shrubs/herbs) pertain to natural or seminatural landscapes primarily shaped by biophysical processes, but possibly with signs of modification from human activities

300 m apart, and covered all the representative habitats found in both study areas. These are composed of a mix of natural wetlands (reedbeds), cultivated farmland (including orange tree orchards and paddy fields) and abandoned orchards, primarily comprised of former orange tree orchards which have been colonised by ruderal plant species. Surveys were conducted using 5-min point counts. There was a 5-min settlement period before point counts began. We employed point transects because they are a better choice than line transects due to complex terrain, where the challenging accessibility of flooded marshes and fenced orchards reduces observers' ability to walk a line transect (Bibby et al. 2000).

At each point count, an experienced ornithologist counted all the passerine birds detected (seen and/or heard) in a circle (100 m radius), and noted the group size (flock) and the distance of the first observed position of each bird landing. Any birds detected during direct flight while crossing through the sampling area, but did not land, were not counted. Surveying started one hour after sunrise and finished within 3 h. Windy or rainy days and heat waves were avoided. Sampling was replicated approximately every fortnight from mid-March 2022 to mid-April 2023. Sample

size ranged between 20 and 23 surveys per site because some areas were temporarily flooded. We did 1564-point counts.

When the Common Waxbill was observed feeding both during the survey and in the transit between sites, we identified consumed plants. These feeding plants were classified as: rough grass, grass that is rugged and natural (mostly therophyte and hemicryptophyte grasses, e.g., *Poa annua*); forbs: herbaceous flowering plants other than grass (e.g., *Amaranthus viridis*); emerged vegetation, plants whose roots are in water (helophyte, e.g., *Phragmites australis*). We also classified these plants according to their geographic distribution, and as native, non-native (Mateo-Sanz and Crespo-Villalba 2014) and invasive following the Spanish catalogue of Invasive Exotic Species (MITECO 2023). The plants with a Palearctic and Neotropical biogeography were classified as non-native, whereas Palearctic, Mediterranean, Subcosmopolitan, Subtropical and Holarctic were classified as native (Castroviejo 1992).

Environmental data collection

A vegetation survey was carried out in spring 2022. We identified any plant with a minimum 5% coverage in the

100 m radius at each site. Vegetation cover was estimated, and plants were classified as native, non-native and invasive to Spain following the same criteria as the aforementioned feeding plants (Mateo-Sanz and Crespo-Villalba 2014; MITECO 2023). This allowed us to use the dominant plant species, and the number of species and the coverage of the native, non-native, and invasive plant species, as variables. Additionally, the percentage of the different land-use and land-cover types in the 100 m radius at each site was obtained with QGIS (QGIS.org 2023) after processing official regional land-use cartography (Institut Cartogràfic Valencià 2023). Thus, we extracted 14 land-use and land-cover categories (electronic supplementary material Table S1). However, we used only 13 categories and excluded the category named Bare soil because it expressly refers to beaches and was not present at or near our sites. The forest class in the study area on the fringes of truly forested areas refers to abandoned farmland, which has become a mixture of grassland and shrubland since pioneer species have colonised land. We renamed it forest (shrubs/herbs). We also obtained the dominant land use or land cover from each site, which gave four main categories: crops, water, wetland and forest (shrubs/herbs), including abandoned farmlands.

Meteorological data, i.e., temperature and precipitation, were obtained from the closest meteorological station to each study area (AVAMET 2023). Apart from the sampling day temperature, we used the mean temperature and the accumulated and maximum precipitations on the previous 17 days to each survey, which was the average time between visits. Additionally, the distance to the permanent water and the minimum elevation at each site were calculated with QGIS (QGIS.org 2023). Apart from incorporating the variables outlined in electronic supplementary material Tables S1 and S2, we included site and study area (Marjal de la Safor and the Pego-Oliva Natural Park) to control whether there were any differences not explained by the remaining environmental variables.

Analyses at the community level

Community delineation–cluster analyses

In order to investigate whether the Common Waxbill was scattered over different bird communities or formed a differentiated group within point counts, we delineated these communities (i.e., groups or clusters of point counts with similar species composition), and found their indicator species. Bird communities were obtained by applying a community detection algorithm to an association network (Bangal et al. 2022; Brunner et al. 2022). We used the functions implemented in the *R* (R Core Team 2021) package *igraph* (Csárdi and Nepusz

2006) to build the association network based on the Euclidean distance between point counts after Hellinger transformation (Legendre and Gallagher 2001). Once the network was created, and before applying the community detection or clustering algorithm, we sparsified the network by removing the least important connections (i.e., longest distances) between bird point counts to better reveal similarities and differences between point counts with the *lans* function implemented in the *R* package *simplifyNet* (Foti et al. 2011). This function eliminates every edge under a certain probability based on a user-defined parameter α (Kramer and Mercier 2022), which was selected by a grid search to eliminate the maximum number of connections, while keeping each network point count or vertex connected to at least another one. Then, we applied the *cluster_fast_greedy* function (Clauset et al. 2004) implemented in *igraph* because it renders a slightly inferior and more amenable number of communities and the modularity index (Newman 2006), employed to determine if the optimal communities did not markedly differ from the other community detection algorithms implemented in the *igraph* package. Finally, we used the *robinGPTest* function implemented in the *R* package *robin* (Policastro et al. 2021), which applies a Gaussian process-based approach to test whether delineated communities differed from random employing distinct stability measures (Kalaitzis and Lawrence 2011): (i) variation of information (VI) (Meilă 2007); (ii) normalised mutual information (NMI) (Danon et al. 2005); (iii) split-join distance (van Dongen 2000); (iv) adjusted rand index (ARI) (Hubert and Arabie 1985). This approach provides a single indicator (Bayes factor) per stability measure of the evidence that delineated communities differed from those communities obtained at random. Bayes factor values above 30 indicate very strong evidence, and those above 100 denote extreme evidence for being different than random communities (Jeffreys 1961; Lee and Wagenmakers 2013).

To determine the existence of indicator species in each group, we used the *multipatt* function implemented in the *R* package *indicspecies* (De Cáceres and Legendre 2009; De Cáceres et al. 2010). In this case, indicator species were defined as the most characteristic species of each group, found mostly in a single group and present at the majority of the sites belonging to that group (Dufrêne and Legendre 1997). This approach calculates indicator values that rate species specificity, abundance in each group (community) and fidelity, occurrences in each group, whereas the statistical significances (*p*-values) of the indicator values are estimated by 9999 random reassignments (permutations) of point counts across groups. When the *p*-value is significant ($p < 0.05$), the species is considered an indicator. We collapsed the network into one vertex per community and used the median number of observations of indicator species

to graphically scrutinise the similarities and composition of the delineated communities with pie charts.

We also applied this clustering and data visualisation procedure to the vegetation and land-use coverage described in the preceding section to delineate plant communities and land-use groups. Instead of Hellinger transformation, we applied isometric log-ratio transformation using the function *ilr* implemented in the *R* package *compositions* (van den Boogaart and Tolosana-Delgado 2008) because both groups of variables were compositional (i.e., sum 100) (Aitchison et al. 2002; Egozcue et al. 2003). We did not calculate the indicator species for the land-use groups, because they were meaningless. The resulting plant communities and land-use groups were utilised in subsequent analyses.

Variable effects on the probability of bird community presence

We investigated which were the most relevant uncorrelated environmental variables among those described in Sect. Environmental data collection and the electronic supplementary material (Tables S1, S2), and their effect on the delineated bird communities to elucidate when they were present in the study area and what were the most prominent characteristics of the site where they occurred more often. To achieve this, we optimised a multiclassification model by predicting the probability of each community's presence (dependent variable) using random forests (Breiman 2001). Random forest is a machine-learning ensemble technique based on the aggregation of multiple decision trees that is able to outperform other modelling approaches (Fernández-Delgado et al. 2014; Muñoz-Mas et al. 2019). This is partly due to its ability to find non-linear variable effects, detect interactions between variables (Olden et al. 2008) and reduce overfitting by randomising both training data and input variables during the development (growing) of each component decision tree (Breiman 2001). To develop random forest, we employed the *R* package *ranger* (Wright and Ziegler 2017). We calculated the correlation between variables with the *hcor* function of the *R* package *polycor* (Fox and Dusa 2022), because it allows the correlation between continuous and categorical variables to be calculated (See Fig. S1 in the electronic supplementary material for a complete depiction of the correlation matrix). To develop optimal random forests, and in addition to the uncorrelated variable subset used to create the model, several hyperparameters need to be adjusted (optimised) to control the complexity of each decision tree in the forest (Martinez-de-Pison et al. 2019). Depending on the selected input variable set, the best hyperparameters might vary and, consequently, they need to be simultaneously sought (Lucio-Puig et al. 2024).

To find the best combination of uncorrelated variables and hyperparameters, we used the genetic algorithm (Holland 1992) implemented in the *R* package *rgeoud* (Mebane and Sekhon 2011). Genetic algorithms are loosely based on Charles Darwin's theory of natural selection (Holland 1992) and, by mimicking evolutionary strategies, they allow the impracticality of evaluating every possible combination of variables and hyperparameters to be tackled. These algorithms work as follows: at the beginning, a set of solutions is evaluated by calculating the associated error through cross-validation. Each solution is a vector that encodes a combination of hyperparameters and selected variables (Muñoz-Mas et al. 2016, 2019). Then through several generations (iterations), the algorithm combines high-performing solutions and introduces random mutations to find better solutions in each generation and approximates the optimal solution. Evolution continues until the maximum number of generations is obtained or, when no better solution is found, after a given number of generations (early stop) (Muñoz-Mas et al. 2016). We did not allow pearson/polyserial/polychoric correlations above 0.66. Therefore, when the algorithm faced correlated combinations of variables, it rendered very bad performance (i.e., – 99,999) to downgrade them during evolution. In this study, the population had 925 solutions ($20 \times$ number of hyperparameters and variables) (Muñoz-Mas et al. 2016, 2019). The maximum number of generations was 3700 ($100 \times$ number of hyperparameters and variables) and the early stop was set at 370 generations without improvement ($10 \times$ number of hyperparameters and variables). The optimised hyperparameters were those that constrained the complexity of component trees (*min.bucket* and *max.depth*) (Muñoz-Mas et al. 2016) and randomness during tree growth (*mtry*) (Strobl et al. 2009). The number of trees in the forest was set at 5000, which was ten-fold the default value (Probst and Boulesteix 2018).

Multiclassification in ecology is still rare because it is a complex task with several elements that need to be considered (Bourel and Segura 2018). Like other modelling techniques (Sor et al. 2017), the multiclassification of random forests is sensitive to class imbalance and the prevalence of each delineated community, which can bias the model to predict the most frequent bird communities (Matsuzawa et al. 2023). Therefore, to prevent overfitting and to favour a good balance of the error in each community, we weighted each case by the inverse of the corresponding community's frequency by setting the parameter *case.weights*. We also used an ad hoc error function to maximise the mean sensitivity (proportion of correctly predicted cases) among communities, minus the difference between the largest and the lowest sensitivity indices. The latter term was included to not favour an optimal solution being found for some communities, which compensates for poorer performances in others. As is customary (Veza

et al. 2015; Janitza and Hornung 2018; Probst et al. 2019) sensitivity indices, calculated with the *confusionMatrix* function implemented in the *R* package *caret*, were obtained using out-of-bag predictions (i.e., repeated hold out cross-validation, carried out internally by random forests during the forest growth process) from each tested combination of hyperparameters and input variables during the optimisation process.

After identifying the best hyperparameters and the most relevant uncorrelated input variables, we scrutinised the effect of the selected input variables with a sensitivity analysis based on partial dependence plots. These plots were obtained by permuting the values of the investigated variable across each variable range and the mean probability of presence predicted for each community (Friedman 2001; Muñoz-Mas et al. 2018). Additional importance and interaction analyses among the selected variables, calculated by employing the *R* package *vip* (Greenwell and Boehmke 2020), are found in the electronic supplementary material (Fig. S2, S3).

Analyses at the species level

Common Waxbill density estimates

The relative Common Waxbill abundance for each study area (Marjal de la Safor and the Pego-Oliva Natural Park) was estimated through distance-based models for point samplings (Buckland et al. 2001). We estimated relative bird densities (i.e., number of birds/hectare) by correcting for species detectability by recording distances to birds and flocks using the *R* package *Distance* (Miller et al. 2019). We fitted models with several detection functions and adjustments: the hazard rate with no adjustments, half-normal with no adjustments, uniform with cosine adjustments, the hazard rate with cosine adjustments and polynomial adjustments, half-normal with cosine and Hermite polynomial adjustments. The best model was selected according to the Akaike Information Criterion (AIC) (Burnham and Anderson 2004). The selected model's goodness of fit was tested by Cramér von-Mises statistics. The detection distances were right-truncated. Any detections over 60 m (from the observer) were excluded from the detection model before adjusting the detection function (Miller et al. 2019). We included two potential covariates: (i) study area, which refers to all the sampled areas (Marjal de la Safor and the Pego-Oliva Natural Park); (ii) season, because we observed that species abundance increased significantly towards autumn. Density estimates were calculated as the number of individuals per hectare (ha), expressed as the density estimate $\pm$ standard error (SE).

To detect temporal trends, we performed a non-parametric Kruskal–Wallis test using the *R* package *car* (Fox and Weisberg 2019) to assess the seasonality of

Common Waxbill abundance because our data did not meet normal distribution. Subsequently, and only when the Kruskal–Wallis test was significant, we performed Dunn's test (Dinno 2015), which is a non-parametric pairwise multiple comparisons procedure to identify significant differences between pairs of seasons.

Relations between Common Waxbill abundance with plant communities and land-use groups

In order to assess whether relative Common Waxbill abundance was statistically related to the plant communities delineated in Section [Analyses at the community level](#) or the land-use types and dominant land-use groups, we also applied the previously described non-parametric Kruskal–Wallis test. Subsequently, we ran Dunn's test (Dinno 2015) among plant communities, land-use groups and the dominant land uses when the Kruskal–Wallis test was statistically significant ($p < 0.05$).

Common Waxbill, Giant Reed and Pampas Grass co-occurrence, and Common Waxbill's feeding preferences

We tested the co-occurrence of the Common Waxbill, Giant Reed and Pampas Grass at each point count with chi-square tests to investigate whether they were related. To test feeding preferences, we firstly corrected each feeding event by the relative abundance/availability of plants per point count (1/percent coverage). When observations were made in transit between sites, we averaged the coverages from the preceding and subsequent sites to correct the feeding event. Then, we used Kruskal–Wallis and the pairwise comparisons of Dunn's tests to analyse whether the Common Waxbill had a preference for native, non-native or invasive plants, and for the following vegetation types: forbs, rough grass and emerged vegetation, as described in Sect. [Study area and bird community sampling](#).

Results

Results at the community level

Bird abundances (point counts)

We documented 50 distinct passerine species (electronic supplementary material Table S3), totalling 9716 individual birds. The House Sparrow (*Passer domesticus*) was the most abundant and widely distributed with 1860 individuals present at 69 of the 71 sites. The next commonest was the Sardinian Warbler (*Curruca melanocephala*) with 753 sightings across 58 sites, followed by the European

Goldfinch (*Carduelis carduelis*) observed at 59 sites with 720 individuals.

The Common Waxbill was noted at 45 of the 71 sites, and accounted for 129 sightings (84 in Marjal de la Safor and 45 in the Pego-Oliva Natural Park). This gave a total of 441 birds, which made them the sixth commonest species in our study with a total of 264 and 177 individuals recorded in Marjal de la Safor and the Pego-Oliva Natural Park, respectively.

Bird community delineation–cluster analysis

The community detection algorithm applied to the association network revealed the existence of eight groups of point counts or communities (Fig. 2a), which were extremely unlikely to be casual because Bayes factor ranged between 145.4 and 193.8. Anticipating the results obtained in the subsequent analysis, delineated communities exhibited marked temporal dissimilarity. The Common Waxbill was the indicator and the most abundant species of Community 1 (Fig. 2b). Community 2 was represented by wintering species, such as the European Robin (*Erithacus rubecula*), but also residents like the Sardinian Warbler, which typically

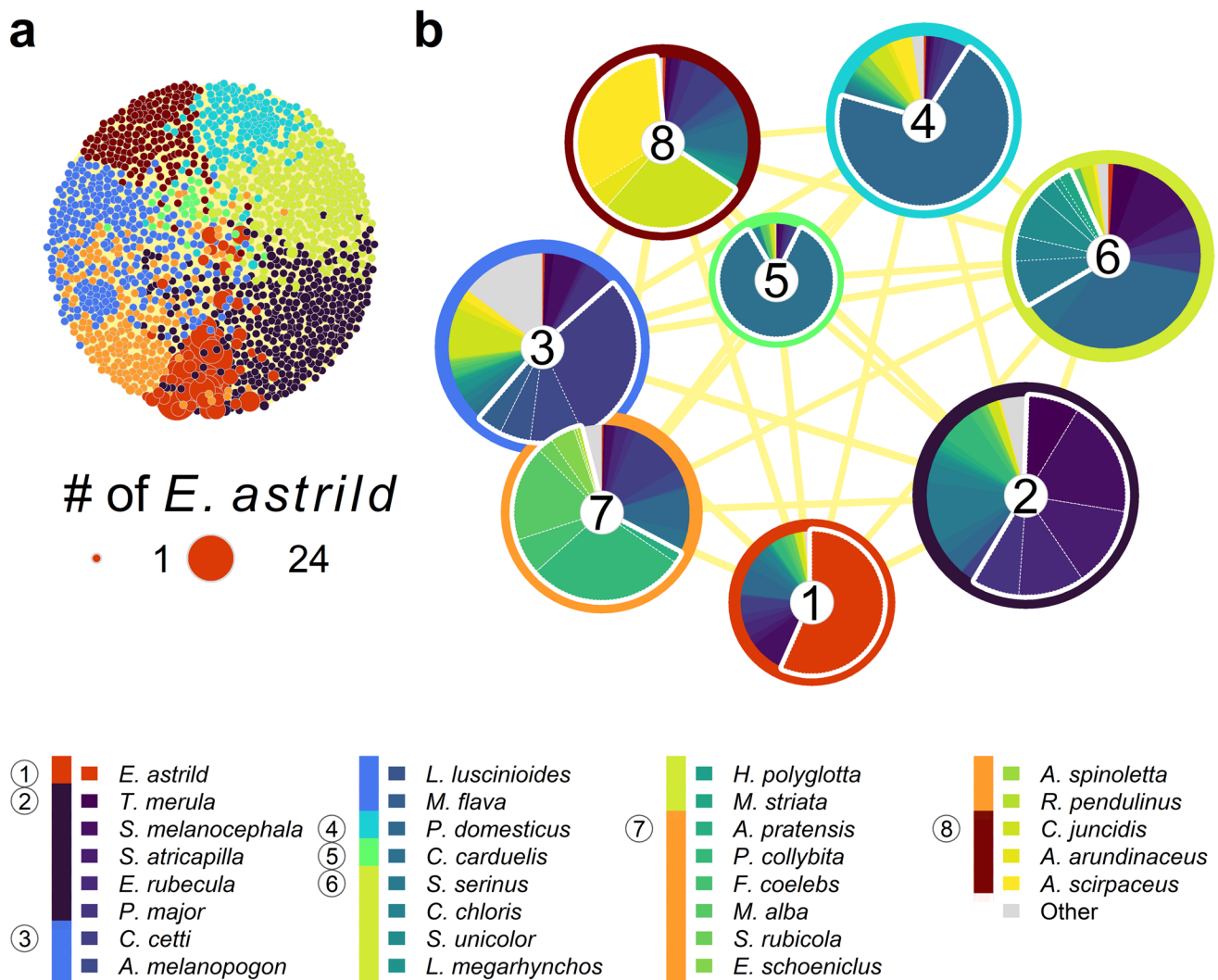


Fig. 2 Bird community clustering. **a** Sparsified association network based on the similarity (Euclidean distance) between the observed bird assemblages (point counts). Vertex size is proportional to the number of observed Common Waxbills (*Estrilda astrild*) in Community 1. The colour code refers to delineated communities and is common to the outer circles in **b** and the legend. **b** The collapsed network in one vertex per community depicts the median number of observa-

tions of the indicator species. The white frame highlights the indicator species of each community, which are listed in the figure legend and specified by the number and colour bar next to the corresponding species. The Other category encompasses non-indicator species. An interactive version of **a** can be downloaded from <https://doi.org/10.6084/m9.figshare.25998928>

occur in cultivated orchards. Community 3 encompassed marsh passerines with restricted habitat requirements, such as the resident Moustached Warbler (*Acrocephalus melanopogon*), but also summer visitors like the Western Yellow Wagtail (*Motacilla flava*) and Savi's Warbler (*Locustella luscinoides*). The House Sparrow was the indicator, and was by far the most abundant species of Community 4, while the European Goldfinch was the indicator and the most abundant species of Community 5.

Community 6 was characterised not only by resident species, such as the European Serin, but also by summer visitors like the Spotted Flycatcher (*Muscicapa striata*), which typically occur in orchards. Community 7 was characterised by wintering species. The most abundant indicator species was the Common Chiffchaff (*Phylloscopus collybita*), followed by the White Wagtail (*Motacilla alba*). Finally, Community 8 was characterised by summer reedbed species, such as the Great Reed Warbler (*Acrocephalus arundinaceus*). The other category encompassed non-indicator species, the most abundant of which were the Common Starling (*Sturnus vulgaris*), the Eurasian Tree Sparrow (*Passer montanus*) and the Song Thrush (*Turdus philomelos*). A complete list of the indicator bird species can be seen in electronic supplementary material Table S4.

The cluster analysis indicated that the communities compositionally closer to the Common Waxbill (Community 1) corresponded to two communities that encompassed wintering species: Community 2, which typically occurred in orchards, and Community 7, which encompassed wintering wetland species (Fig. 2). On the contrary, the most distant group was summer reedbed specialists (Community 8). The Common Waxbill occurred almost exclusively in a differentiated community (Community 1) and was the most abundant species. It was poorly represented in the remaining communities, but was absent only from Community 5, whose composition was dominated by the European Goldfinch (Fig. 2b).

The wintering (Community 2) and summer (Community 6) communities that usually inhabited orchards were closely related because the Sardinian Warbler was also abundant in Community 2. Community 6 and Community 4 were closely related because the House Sparrow was also abundant in Community 6. Community 7, which encompassed wintering species inhabiting wetlands, overlapped somewhat with the reedbed specialist of Community 3 because they shared some resident species, such as Cetti's Warbler (*Cettia cetti*) and Moustached Warbler.

Relevant variables and effects on the probability of bird community presence

The optimal random forest included nine variables, but excluded site and sampling area (Fig. 3). The mean

sensitivity of the final model was 0.61 ± 0.16 , whereas it was 0.41 ± 0.05 during the cross-validation based on out-of-bag predictions. Additional general performance criteria (also for each community) can be found in electronic supplementary material Tables S5–S10. Overall, month was the most important variable to predict the probability of delineated communities' presence and the hydrography percentage (i.e., water bodies) was the least relevant one.

The probability of community presence for which the Common Waxbill was the indicator and the most abundant species (Community 1) markedly increased towards autumn and peaked in November. Both elevation and presence of hydraulic constructions had a minor negative effect on its probability of presence. In contrast, an increase in the percentage of roads and tracks, especially the cover of invasive plants, had a positive effect on the probability of this community's presence. The effect of the non-native plant cover percentage was almost constant, except when these percentages exceeded 80%. Then the probability of Community 1's presence decreased. The number of native plant species had no clear effect on this community. Conversely, the presence of water (i.e., hydrography) and forest (shrubs/herbs) had a strong positive effect. Forest (shrubs/herbs) presence, which included mainly abandoned fields and orchards, was one of the most important variables for Community 1.

As expected, the summer communities (Communities 6 and 8) showed an inverse temporal trend compared to the wintering communities (Communities 2 and 7). A higher percentage of cover of both non-native and invasive plants favoured the probability of orchard communities' presence (Communities 2 and 6), while non-native and invasive plant cover (%) negatively affected reedbed specialist communities presence (Communities 3 and 8). The cover of non-native plants seemed to slightly reduce the probability of presence of the community characterised by the House Sparrow (Community 4). A higher percentage of abandoned farmland, forest (shrubs/herbs) land-cover type, reduced the probability of presence of the community characterised by the European Goldfinch (Community 5), and the community encompassing the wintering wetland bird species (Community 7) and the summer reedbed specialists (Community 8). However, this effect was not so pronounced in the reedbed specialist community that included the migrant Western Yellow Wagtail or the resident Moustached Warbler (Community 3).

Results at the species level

Common Waxbill density

Model selection indicated that the best model to estimate Common Waxbill density was the uniform with cosine

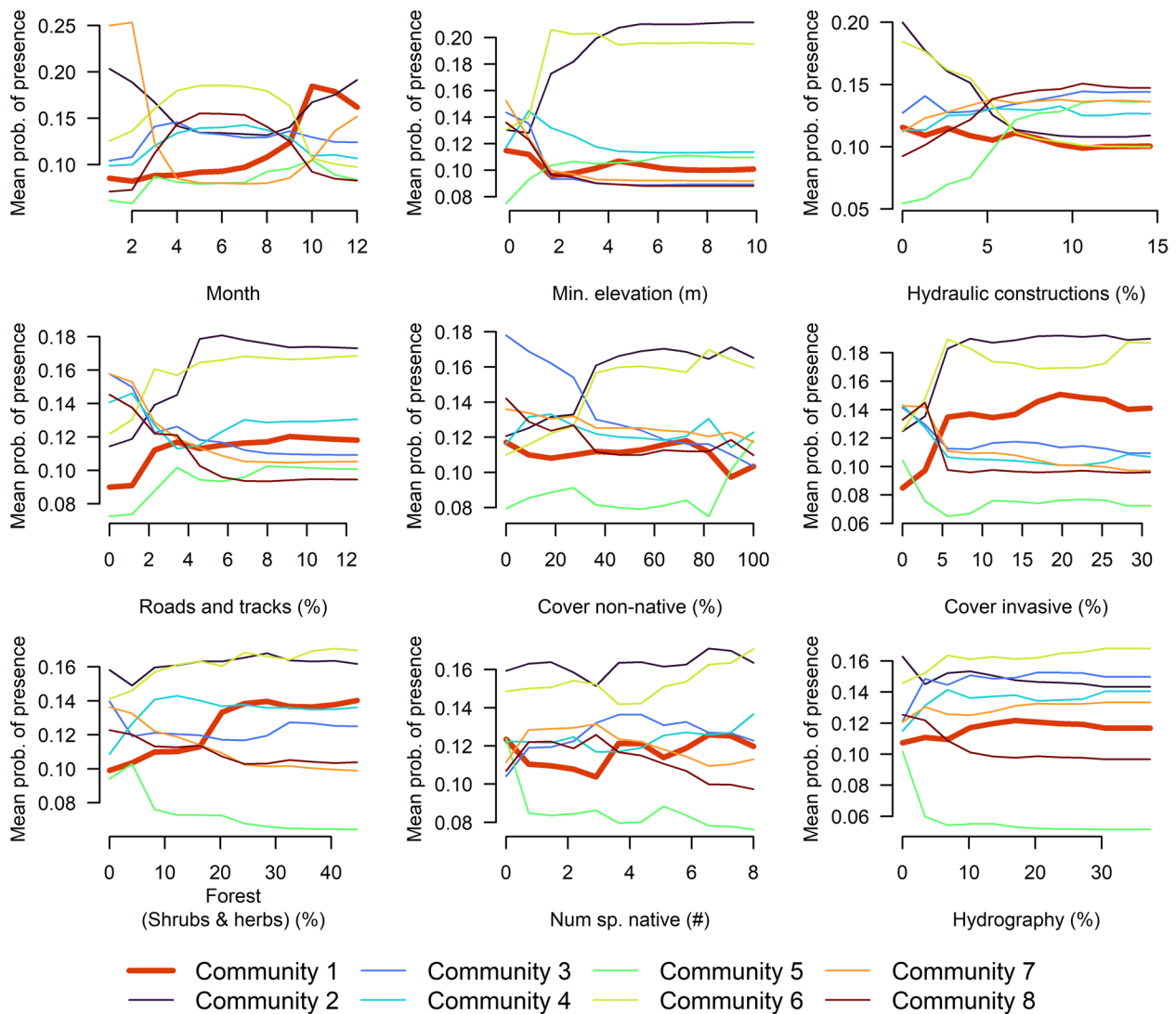


Fig. 3 Sensitivity analysis (partial dependence plots) depicting the mean effect of the selected variables on the probability of presence of the eight bird communities. The thicker line highlights the commu-

nity dominated by the Common Waxbill (i.e., Community 1). Variables are sorted in decreasing order by their importance from top left (month), to bottom right (hydrography/water bodies)

Table 1 Average detection probability (Avg p) and standard error (SE) of the best-rated distance sampling models based on ΔAIC in Marjal de la Safor and the Pego-Oliva Natural Park

Key function	Covariate	Avg p	SE	C-vM	AIC	ΔAIC
Uniform with cosine adjustment order 1	NA	0.314	0.011	0.839	966.854	0.000
Half-normal	Null	0.266	0.028	0.846	967.642	0.787
Hazard-rate	Area	0.288	0.043	0.906	968.524	1.669
Half-normal	Area	0.265	0.028	0.873	968.726	1.871
Half-normal	Area + season	0.257	0.029	0.927	970.51	3.658
Hazard-rate with cosine adjustment order 1	Null	0.254	0.049	0.933	970.896	4.042

Cramér-von Mises p (C-vM); and study area (Area)

adjustment of order 1. This finding indicates that the detection probability did not improve when either study area or season were included as covariates (Table 1). The Cramér-von Mises test had a $p=0.840$, and the plot indicated that the model fitted the data (electronic supplementary material Fig. S4). Therefore, we used the uniform with cosine adjustment of order 1 to estimate annual densities, which resulted in 0.257 ± 0.052 (SE) birds/ha for Marjal de la Safor and 0.161 ± 0.036 (SE) birds/ha for the Pego-Oliva Natural Park. The combined density of both study areas was 0.209 ± 0.032 (SE) birds/ha.

Seasonality of Common Waxbill abundance

The Common Waxbill occurred all year round. However, more sightings of them started as from summer, peaked in mid-autumn, and declined towards winter and spring (Fig. 4, date). The boxplot reveals a larger number of birds recorded per point count in winter and autumn, with a maximum number of 24 birds seen at a point count. This contrasts with the smaller groups observed in spring and summer (Fig. 4, season).

The non-parametric Kruskal–Wallis test indicated a significant variation in Common Waxbill abundance among seasons ($p < 0.001$). The subsequent Dunn's test corroborated that Common Waxbill abundance varied among seasons, except between spring and winter, when its abundance remained low ($p = 0.389$) (Table 2).

Relation between Common Waxbill abundance and plant communities

In all, 64 plant species were identified at the sites of the two study areas (electronic supplementary material Table S11) which, after clustering, were confidently divided into six plant communities because Bayes factor ranged between 89.2 and 102.8 (unlikely to be random) (Fig. 5). Community 1 had nine representative species and included plants that are indicators of wet ruderal soils (e.g., Elmleaf Blackberry *Rubus ulmifolius* and Pampas Grass). Community 2 encompassed orange tree orchards (the indicator species included cultivars of Orange Tree *Citrus sinensis*). Community 3 was associated with permanently flooded areas because the Narrowleaf Cattail (*Typha angustifolia*) was the indicator species. Community 4 was represented by the Sharp Rush (*Juncus acutus*) and Pomegranate (*Punica granatum*), which indicate drier soils and farmed areas in marshes. Common Reed (*Phragmites australis*) was the indicator of Community 5, and Rice (*Oryza sativa*) characterised the surveyed paddy fields (Community 6). See electronic supplementary material Table S12 for the indicator species of each plant community.

Table 2 Significance (p -value) of the Dunn's test for comparing Common Waxbill abundance among seasons

Seasons	Autumn	Spring	Summer
Spring	0.0000	–	–
Summer	0.0001	0.0024	–
Winter	0.0000	0.3896	0.0009

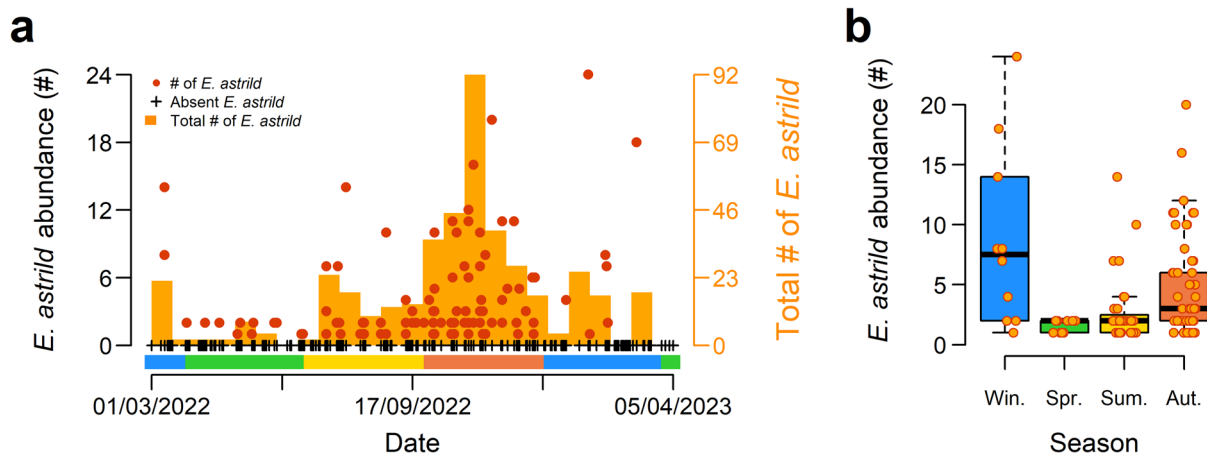


Fig. 4 Common Waxbill abundance across seasons (a). On a, the left y-axis indicates the number of birds (abundance; with red dots) recorded at each point count. The orange right y-axis refers to the accumulated number of birds seen on particular sampling date i.e., multiple point counts (background orange polygon). Boxplot indicat-

ing the number of birds recorded per season (b). For both plots, dots denote the number of birds (abundance) recorded at each point count other than zero. Plots including zero values can be found in electronic supplementary material Fig. S5. Zero values were not removed for the statistical analyses

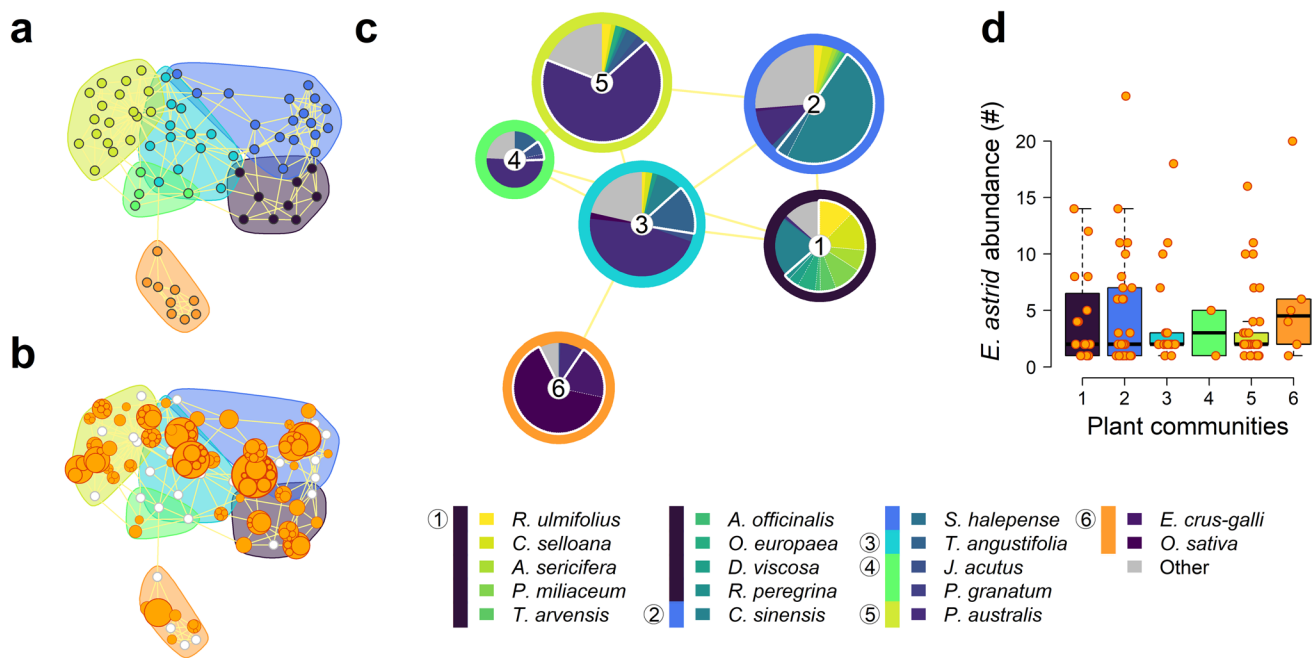


Fig. 5 Plant community clustering aggregating sites with similar plant species. **a** Clusters of sites associated with each plant community. Colour code refers to delineated communities and is common to **b** and **d**, the outer circles in **c**, and the legend. **b** Common Waxbill abundance at each site throughout the study period (size of the outer orange circles is proportional to the total number of Common Waxbills seen at that site; small orange circles refer to the number of birds seen during a particular visit; white dots indicate those sites with no Common Waxbill sightings). **c** Collapsed network into one vertex per plant community depicting the median coverage of indicator species. The white frame highlights the indicator species of each community,

which are listed in the figure legend and specified by the number and colour bar next to the corresponding species. The Other category encompasses non-indicator species. **d** Boxplot with the Common Waxbill abundance seen in each plant community during a particular visit. Dots indicate the number of birds (abundance) recorded in each sighting other than zero, which were not removed in the statistical tests. Plots including zero values can be found in electronic supplementary material Fig. S6. An interactive version of the **a** can be downloaded from <https://doi.org/10.6084/m9.figshare.25998928>

Table 3 Significance (p -value) of Dunn's test when comparing the Common Waxbill's feeding preferences between vegetation classes

Vegetation classes	Forbs	Emerging vegetation
Emerging vegetation	0.000	–
Rough grass	0.365	0.000

Common Waxbill sightings were recorded in every plant community with varied abundances (Fig. 5b, d). The Kruskal–Wallis test indicated no significant variation in Common Waxbill abundance among plant communities ($\chi^2 = 8.935$, $df = 5$, $p = 0.112$). In contrast, the chi-squared tests showed a positive association between Common Waxbill and Pampas Grass ($\chi^2 = 38.034$, $df = 1$, $p < 0.001$) and Giant Reed ($\chi^2 = 4.935$, $df = 1$, $p = 0.026$) presence.

Feeding preferences of the Common Waxbill

We observed 56 feeding events, which encompassed 15 plant species, including forbs, rough grasses and emergent

vegetation (electronic supplementary material Table S13). Once corrected by their abundances (coverage), the Kruskal–Wallis test indicated that there were significant differences ($\chi^2 = 32.281$, $df = 2$, $p < 0.001$) in their feeding preferences. Dunn's test showed that the Common Waxbill significantly preferred forbs and rough grasses, and avoided emerging vegetation ($p = 0.365$) (Table 3).

At the species level, Common Reed (8 observations), Indian Goosegrass (*Eleusine indica*) (7 observations) and Bermuda Grass (*Cynodon dactylon*) (6 observations) were the most consumed plants (37.5% of the total). Seven out of 15 consumed species were non-native with the Paletropical (*Sorghum halepense*, *Eleusine indica*, *Setaria adhaerens*, *Echinochloa crus-galli*, and *Oryza sativa*) and Neotropical (*Eleusine tritachya* and *Amaranthus viridis*) distributions, and was one invasive, the *Cortaderia selloana*, with the Neotropical distribution. Regarding species origin (i.e., native versus non-native and invasive), 26 of the 56 feeding observations (46.4%) corresponded to non-native plants, 26 of the 56 feeding observations to native plants and 0.07% to invasive plants. However, the Kruskal–Wallis test indicated no clear preference for any of these groups ($\chi^2 = 3.616$, $df = 2$, $p = 0.164$).

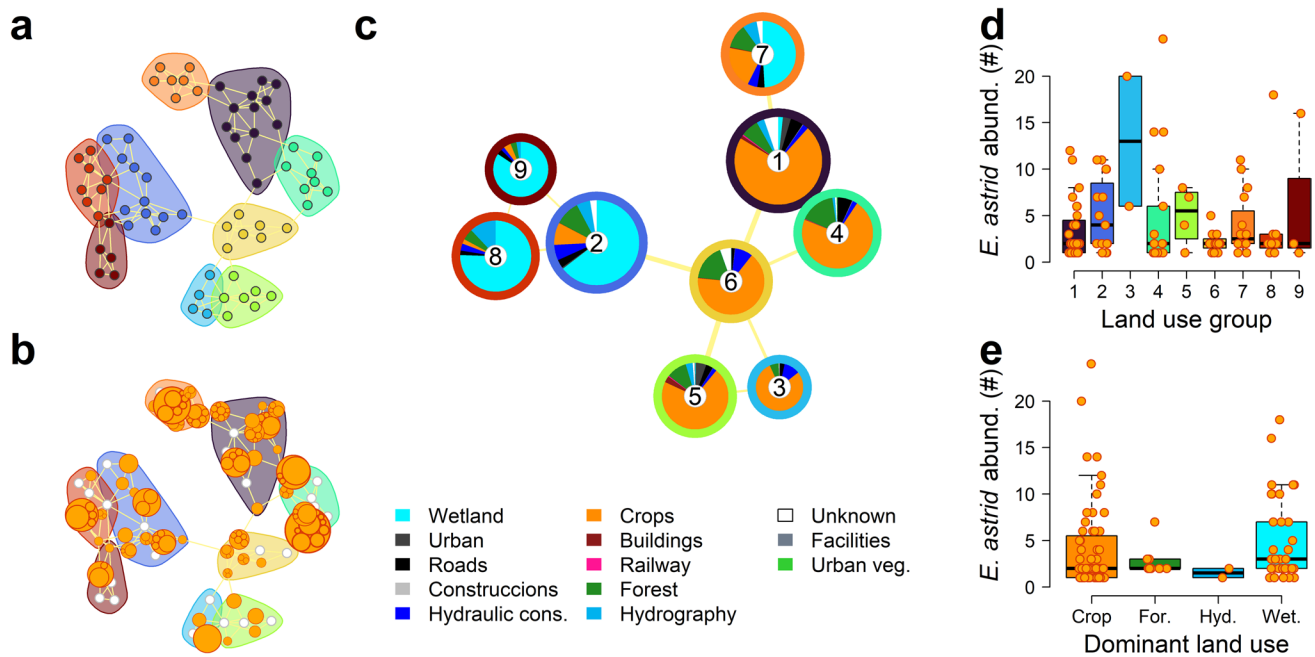


Fig. 6 Land-use group clusters aggregating sites with similar land-use and land-cover types. **a** Clusters of sites associated with each land-use group. Colour code refers to delineated groups and is common to b, the outer circles in c, d, and e. **b** Common Waxbill abundance at each site throughout the study period (size of the outer orange circles is proportional to the total number of Common Waxbills seen at that site; small orange circles refer to the number of birds seen during a particular visit; white dots indicate those sites with no Common Waxbill sightings). **c** Collapsed network into one vertex

Relation between Common Waxbill abundance and land-use groups and dominant land uses

The 71 sampling sites were aggregated into nine clusters or groups (Fig. 6a). Bayes factor ranged between 118.3 and 126.0. Common Waxbill sightings occurred in every group (Fig. 6b, d). The Kruskal–Wallis test indicated that Common Waxbill abundance varied for at least one land-use cluster ($\chi^2 = 21.204$, $df = 8$, $p = 0.006$). However, Dunn’s test did not reveal differences between pairs of land-use and land-cover type groups ($p > 0.05$).

Wetlands or crops were the dominant land uses in every group (Fig. 6c), with most Common Waxbill sightings in these two dominant groups (Fig. 6e). However, from a strictly statistical viewpoint, the Kruskal–Wallis test indicated that Common Waxbill abundance was not clearly related to any particular dominant land use ($\chi^2 = 7.597$, $df = 3$, $p = 0.055$).

Discussion

Common Waxbill was the sixth commonest species in our two study areas and the indicator species of a single specific community, Community 1, where it was the most

per group depicting the median coverage of land-use types. **d** Boxplot with the Common Waxbill abundance seen in each group during a particular visit. **e** Boxplot with the Common Waxbill abundance seen during each visit by dominant land use. In d and e, dots indicate the number of birds (abundance) recorded in each sighting other than zero. Plots including zero values can be found in electronic supplementary material Fig. S7 and Fig S8. An interactive version of the **a** can be downloaded from <https://doi.org/10.6084/m9.figshare.25998928>

abundant species, was scarcely represented in the other bird communities. Common Waxbill was recorded at 45 of the 71 sites, and the estimated annual density for the global study area was 0.209 ± 0.032 (SE) birds/ha. This density is lower than that observed by Sullivan et al. (2015) in Portugal and western Spain (i.e., 2.1 birds/ha). However, we acknowledge that this difference could be temporal and not be caused by lower habitat suitability and/or climatic mismatch (Reino 2005) between both regions. Thus, additional data on multiple geographic and temporal scales would be needed to properly compare the densities of both areas. The Common Waxbill was more abundant in autumn and winter after their typical lengthy breeding season (April to October) (Sanz-Aguilar et al. 2015). Therefore, the closer groups of birds to the community where the Common Waxbill was the most abundant species encompassed wintering communities that either inhabited orchards (Community 2) or wetlands (Community 7). The most important variable in random forests was month, which underscores how seasons, followed by habitat, explain the temporal occurrence of the delineated bird communities from both study areas.

This notable increase in the number of Common Waxbill sightings in autumn has been previously observed in wetlands (Sanz-Aguilar et al. 2015), and might be due

to vagrant movements and this species' tendency to form larger flocks in autumn, which might reduce their densities in other habitats at this time of year (Beltrão et al. 2021). The Common Waxbill is considered a non-territorial species (Catry et al. 2010) and has never been reported to act aggressively with other bird species (Catry et al. 2010; Cardoso and Reino 2018), which reduces the possibility of having an impact on other co-occurring bird species.

Species rearrangement can occur when food preferences and requirements overlap those of natives, which implies competition, or there can be minor effects when non-native and invasive species capitalise underutilised resource opportunities (Hernández-Brito et al. 2014). Cardoso et al. (2018) found in autumn and winter that the Common Waxbill did not compete for food resources with an ecologically similar native species, the European Serin. We did not find a clear association with any specific plant community, and the Kruskal–Wallis test indicated no clear preference for a native, non-native or invasive plant-based diet, which might indicate barely any interference with native birds.

The presence of water bodies (hydrography) had a positive effect on the probability of Common Waxbill presence because they primarily breed in mesic habitats and wetlands (Barnard 1997; Reino and Silva 1998; Murgui 2001). These results corroborate that the Common Waxbill requires the proximity of riparian or wetland vegetation for roosting, nesting and foraging in open areas that lie adjacent to wetlands or close to agricultural fields (Batalha et al. 2013). This underscores its position between Communities 2 and 7, which respectively inhabit orchards and wetlands.

In contrast, as described for other non-native bird species (Fujisaki et al. 2010), an increase in the percentage of roads and tracks and, especially in the cover of invasive plant species, had a positive effect on the probability of Common Waxbill presence. Moreover, the percentage of forest (shrubs/herbs) at the sampling site, which included mainly abandoned fields and orchards, had some of the strongest positive effects on the probability of presence of the community where the Common Waxbill was the most abundant species (i.e., Community 1). This could be related to the positive effect of habitat modification and degradation, which have been described for other invasive bird species (Sol et al. 2002). This line of reasoning, which aligns with the positive relation among the presence of Common Waxbill, Pampas Grass and Giant Reed, generally suggests that the species takes advantage of the vacant niches created by human activities and their discontinuance (Sirami et al. 2008).

The Common Waxbill preferred feeding on rough grasses and forbs rather than on the emerged vegetation (Sullivan et al. 2015) that dominated orchards and rice field margins, which corroborates previous work on this species (Cramp et al. 1994; Sullivan et al. 2015; Cardoso et al. 2018). We recorded 15 different plant species on which the Common

Waxbill fed, three of which were Hairy Crabgrass (*Digitaria sanguinalis*), annual Meadow Grass (*Poa annua*) and Cockspur Grass (*Echinochloa crus-galli*). These three plant species have been previously recorded in Portugal by Cardoso et al. (2018) who, in turn, have reported overconsumption of non-native plants. The results of Cardoso et al. (2018) cannot be completely compared to those of our study because the sampled study area encompassed mostly horticulture (onion, cabbage, carrot, etc.) and irrigated corn fields. Our results indicated that Common Reed, an emergent wetland plant species, was an important feeding resource for the Common Waxbill, as were the rough grasses and forbs associated with agricultural practices. This is consistent with opportunistic behaviour and the ability to exploit different feeding resources as and when they become available (Cardoso da Silva et al. 2018).

Our observations revealed a noteworthy prevalence for the Common Waxbill of invasive Pampas Grass and Giant Reed presence. Giant Reed has been previously documented for providing both shelter and food (Sullivan and Franco 2018). Our observations also indicated that Pampas Grass offered shelter and occasional sustenance. Such positive interactions between non-native species have been widely documented elsewhere (Bourgeois et al. 2005; Thibault et al. 2018). Moreover, both Pampas Grass and Giant Reed fruit in autumn (Mateo-Sanz and Crespo-Villalba 2014), when Common Waxbill abundance peaked, which could imply that they provide additional food resources.

Our results confirmed the Common Waxbill's habitat preferences and its versatile nature for adapting to different available food resources. These characteristics have contributed to its success in spreading to an array of different regions (Stiels et al. 2011). This research revealed Common Waxbill's temporal distribution patterns in the region. It also contributed to providing a deeper understanding of the dynamics between invasive plants that result from farmland abandonment, particularly aggressive Pampa Grass and Giant Reed, and a widespread non-native bird species, the Common Waxbill. Our study confirmed this species' plasticity and its ability to exploit human-modified spaces.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-025-02257-5>.

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Author contributions PLP and RMM contributed to the study conception and design. PLP and JG collected the field data. PLP and RMM analysed the data and wrote the first draft. All authors contributed to

the interpretation of data and revised critically previous versions of the manuscript. All the authors read and approved the final manuscript.

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Data availability The datasets generated and analysed in the present study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval This is a field study. No animal handling or collection was involved.

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