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Contrasting effects of agriculture and urbanisation on bird and reptile communities in a Mediterranean delta (Gediz Delta, Türkiye)

Dilara Arslan[1,2,3*], Elie Gaget[1,4], Kerim Çiçek[5], Anthony Olivier[1], Thomas Galewski[1], Ömer Döndüren[6], Anis Guelmami[1], Lisa Ernoul[1] and Arnaud Béchet[1]

Abstract

Background Wetlands have been some of the most destroyed ecosystems over the last century, with important land-use changes resulting from agricultural, industrial, and urban development. Gediz Delta is a large wetland on the Aegean coast of Western Türkiye with natural areas affected by conversion to agriculture and urban developments from the Izmir metropolis. We assessed the effects of landscape type (natural, agricultural, and urban) on the composition of breeding bird (90 species) and reptile (14 species) communities in the Gediz Delta between 2019 and 2021. We used generalized linear models to estimate the effect of landscape types on community indexes and joint species distribution models to assess how species-specific habitat preferences explained their responses to landscape type.

Results Our results show that bird and reptile community compositions were impacted differently depending on landscape type. Landscape type significantly affected bird abundance and Shannon equality indices but had no significant effect on bird and reptile species richness. Natural landscapes accommodated higher bird abundance and lower diversity indexes than the other two landscapes. On the other hand, we found that urban and agricultural landscapes accommodated more *generalist* species than natural ones. Natural landscapes were preferred by *Marine & Coastal* and *Inland wetland* bird specialists and reptiles relying on *Mediterranean Habitats*. Overall, these results suggest that community composition encountered in different landscape types is explained by species' habitat specializations.

Conclusions We highlight the critical importance of natural landscapes for conserving specialist species within the Delta while showing the potential of agricultural areas for a few freshwater reptile species. These results imply that the Gediz Delta would benefit from biodiversity conservation planning to enhance the protection of natural habitats and mitigate the negative impacts of agricultural and urban development on bird and reptile populations.

Keywords Joint species distribution modeling, HMSC, Community assemblages, Community structure, Reptiles and birds

*Correspondence:
Dilara Arslan
arslan@fzp.czu.cz; kizildilara@gmail.com

Full list of author information is available at the end of the article

Background

Land use and land cover changes (LULCC) have been the most important forces driving changes in species composition in the last century [1, 2]. Communities have been reshaped by LULCC with winners (species that have benefited due to the changes) and losers (species that have declined or become extirpated). Generalists or opportunistic species generally do better in newly human-altered landscapes (e.g., agricultural or urban areas) than do specialist species [3, 4]. In turn, the decrease of specialist species results in increased biological homogenization across human-altered communities, with a concentration of mostly generalist species [5]. Many studies have focused on the negative effects of LULCC on a single taxonomic group (e.g. birds), while the combined effect of LULCC on multiple groups with contrasting behavioural ecology and physiology has not been well studied. Understanding the processes underlying changes in communities following LULCC requires wide documentation of patterns across taxa and ecosystems because they may not occur similarly everywhere. Besides, there is still considerable uncertainty on the responses of different taxonomic groups to LULCC. In this regard, joint species distribution models (JSDM) are a useful tool to help quantify how the environmental drivers shape the species community assemblies [6–10]. JSDM is a method for quantifying the ecological communities which are assembled through a hierarchical filtering process in which species' relationships with each other, their traits, phylogenetically relatedness, and relationships to other environmental variables all influence the assemblage [6, 7].

Wetlands are important habitats for biodiversity, and many species depend on them to complete their life cycle [11]. Among natural ecosystems, wetlands are the most converted terrestrial habitats worldwide, with most of the destruction caused by agricultural expansion or urbanization [12]. As a result, 87% of wetland areas have been lost since the beginning of the 19th century [13, 14]. Mediterranean wetland surface area has declined by 45–51% since 1970, with important associated losses of ecological, economic, and social values [15, 16]. Despite the accumulating evidence that LULCC affects wetland's biodiversity negatively [1, 17–20], there is little documentation of the geographical variations of this impact, in particular outside European and North American countries [21, 22]. Assessing the effect of LULCC on different taxa in poorly studied wetland regions is required to improve our understanding of how wetland biodiversity will change in the future [23–25].

Gediz Delta (Aegean coast, Western Türkiye) is a Mediterranean wetland with intense urbanization and agricultural expansion [26–28]. The Delta is located along the northern edge of İzmir, a metropolis of >4 million inhabitants [29]. It is composed of a mosaic of salt and freshwater marshes along its coasts and a large agricultural and newly urbanized landscape inland [29, 30]. The Delta hosts significant biodiversity consisting of over 400 species of plants, 299 species of birds, and 35 species of reptiles and amphibians [31–33]. Significant parts of the Delta's natural areas have been converted over the last century to accommodate the growth of the city. The most considerable transformation was the translocation of the Gediz riverbed 50 km to the north through a system of dikes and canals at the beginning of the 19th century to reduce flooding risks in İzmir Bay and the margins of the delta were urbanized in the early 2000s [26, 34, 35]. Most of the actual urban and agricultural landscapes of the delta have been reclaimed from previously natural wetlands [28]. A large part of the Gediz Delta (20,400 ha) has been under strict national protection since 1985 and listed as a Ramsar site since 1998 [31]. Specific conservation efforts have been focused on waterbirds, such as the Greater flamingos (*Phoenicopterus roseus*) or the Dalmatian pelican (*Pelecanus crispus*) [36, 37], while other species did not benefit from such conservation efforts, like the Spur-thighed tortoise (*Testudo graeca)*, or farmland bird species [37, 38].

The Gediz Delta offers the opportunity to better understand how agriculture and urbanization affect biodiversity in the Mediterranean region, where many deltas face similar threats [16]. The Gediz Delta is known as one of the most important key biodiversity areas among the Mediterranean wetlands [15, 39, 40]. The delta is experiencing rapid changes due to urbanization and expansion of agriculture, but very little is known regarding the biodiversity impact of these alterations [27, 28, 41]. In particular, the impact of LULC changes on biodiversity has been focused only on a specific taxonomic group in a very limited number of studies due to of the scarcity of quantitative data, making inter-taxon comparison very difficult [37, 41]. Besides, there is a significant under-representation of the impacts of LULC research across the globe, since most studies focus on Europe and North America [16, 42]. Our study helps fill this geographic gap by addressing this question in a wetland from the east of the Mediterranean.

Here, we investigated how landscape types affect bird and reptile community composition and abundance in a study area covering the natural, agricultural, and urban areas of the Gediz Delta. Differences in dispersal ability between reptile and bird species will provide an understanding of how flexible a species is in colonising different parts of the delta. We tested the following hypotheses: (1) the landscape type (natural, urban, and agricultural) has an effect on the community composition of birds and reptiles by influencing species richness, abundance and evenness; (2) species habitat preference drive variations in species occurrence and community structure in different landscape types. We predicted that specialist species would have the highest occurrence and abundance in natural landscapes, moderate representation in agricultural landscapes, and the lowest occurrence in urban landscapes. On the other hand, we expected generalist species to show the opposite trend, i.e. higher occurrence and abundance in urban and agricultural landscapes and lower representation in natural landscapes. These predictions are consistent with the hypothesis that species with wider ecological tolerances are more common in human-modified landscapes.

We first explored variations of species richness and evenness across landscapes using generalized linear models. We predicted that these community indices are higher in natural than agricultural or urban landscapes. Second, we used joint species distribution models (JSDM) to assess how species habitat preference explain community patterns and species co-occurrence while controlling for phylogenetic relatedness [6, 7].

Methods

Study area and sampling design

Gediz Delta (38˚ 30'N, 26˚ 55'E) is located in the eastern Mediterranean basin (İzmir, Türkiye) on the coast of the Aegean Sea (Fig. 1). It comprises a mosaic of freshwater and saltwater ecosystems made up of Mediterranean scrubland, salt meadows, reed beds, marshes, lagoons, saltpans, beaches, farmlands, and urban landscapes [31]. The study area (ca. 80,000 ha) is located between the present and past tributaries of the Gediz River and includes the immediate surroundings of İzmir (Fig. 1).

Land cover data were obtained by the analysis of 2020 satellite images by Guelmami [28] and habitats were classified according to the classification system adopted by the Mediterranean Wetlands Observatory, combining CORINE Land Cover (CLC) classes with the Ramsar habitat definitions [43, 44].

The study area was divided into 200 2 × 2 km cells. Three landscape types were defined by the most common habitat within the same cell: natural, agricultural, and urban (Fig. 1, Table SM1). We then randomly selected 10 cells per landscape type (5 cells sampled in 2019 and 5

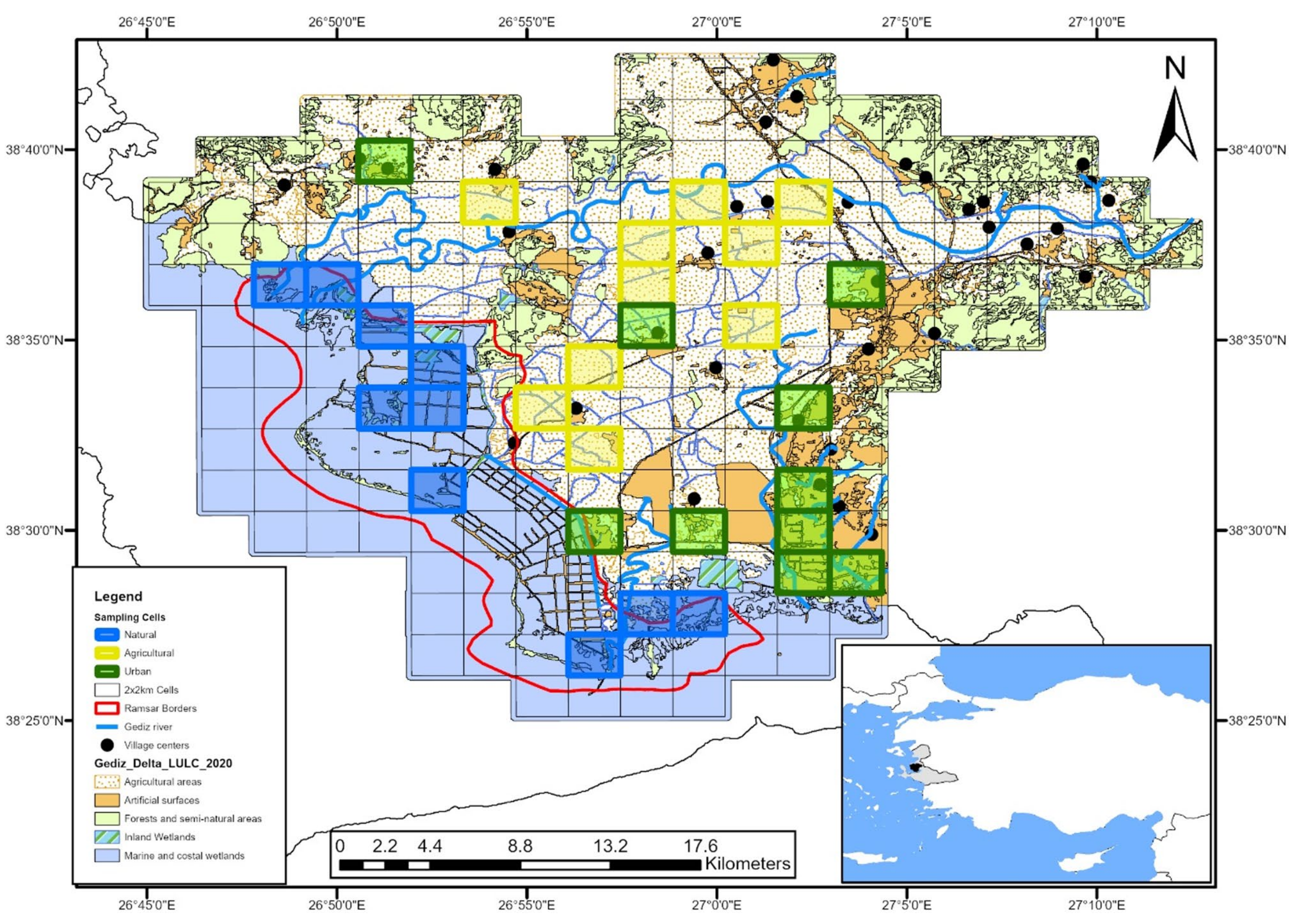

Fig. 1 Study area with landscape types (Agricultural, Natural and Urban) and other ecosystems of the Gediz Delta (Western Türkiye). Squares locate cells that were samples for Birds and Reptiles in each landscape type.(adapted from Arslan et al. 2021)

cells in 2021), totalling 30 sampling cells where we collected biodiversity data (see Biodiversity data collection below). Natural landscape cells were composed on average of 95% natural habitats, including wetlands, along a gradient of management from low to no hydrological management (e.g., coastal lagoons) to intensive hydrological management (e.g., saltpans). To ensure that the selected natural cells were predominantly composed of homogeneous natural wetland habitats, and to avoid potential confounding effects due to habitat heterogeneity within landscape types, we did not sample the other natural habitat types, such as Mediterranean maquis, arborescent matorral and olives forests in the delta. Agricultural landscape cells were made up of an average of 90% intensive farmland areas. The main crops in 6 out of 10 sampled agricultural cells were wheat, cotton, and some vegetables (e.g., tomatoes, cucumbers), and the 4 other cells consisted of a mix of fruit orchards (olives, plum, or grapes). Urban landscapes cells were composed of an average of 50% of urban areas. Thus, the 10 selected urban landscape cells contained an average of 56% human settlements, 28% intensive farmland areas, and 16% natural landscapes (Table SM1). The natural landscape cells were located along the coastline in the protected zone of the delta, and 6 of them included saltpans (out of 10 cells); 4 of them included coastal lagoons, salt marches and sand beaches. The agricultural cells were located in the interior of the delta. Among the urban landscape cells, 6 were located on the periphery of the delta, and 4 in the villages generally surrounded by the agricultural landscape. Four out of 6 urban cells in the periphery were developed through wetland drainage and building on a coastal lagoon, so they still include some remnant coastal wetlands habitats. All sampling sites shared a similar elevation (between 0 and 10 m) and included the presence of at least one water body (e.g., temporary ponds, ditches, or channels).

Bird and reptile data collection

Bird and reptile counts were carried out by the same observer (DA) in 2019 and 2021 over the 30 selected sampling cells. Each cell was sampled twice a year (for a total of 60 days of fieldwork), once in April-May and once in May-June, for both birds and reptiles.

Birds were monitored by a point count framework, with 5-point counts selected within each cell and located a minimum of 500 m from each other. Bird surveys of a given cell/day lasted from sunrise to 11 am. Birds were only monitored on non-windy days (wind speed below 25 km per hour) without rainfall and with temperatures averaging 14.8 °C ± 6.4 (SD). At each point, birds were identified and counted for 15 min within a 50 m-radius circle, recording all individual birds or flocks of each species seen or heard. Birds flying and located more than 50 m from the cell were excluded from the analyses. We summed the abundance of bird species observed or heard at the same point and date; then, we used the maximum abundance over the sampling period. For practical reasons, a small number of bird visits in urban areas were done in the afternoon ($N = 10$ over 2 cells). Because we suspected that this timing may affect bird abundance and richness, we tested for an effect of time since sunrise on these parameters (SM2). The results of this sensitivity analysis did not show any effect of time since sunrise on bird abundance and richness (Table SM2.1), so we kept these visits in the dataset. Finally, we retained only the bird species known to breed in the Gediz Delta [41], thus excluding non-breeding species. We excluded non-breeding bird data because breeding bird species have higher habitat requirements and are more sensitive to habitat changes [45]. Furthermore, the recent study conducted by Arslan et al. [38] has shown little temporal variation in non-breeding bird populations in the Delta over the last 100 years.

Reptiles were surveyed by walking along 3 transects 200 m long and 5 m wide, randomly set up within the 30 selected cells. In agricultural landscapes, the transects were generally located along the field edges, in urban landscapes transects were located along streets or across public areas like parks or wastelands avoiding private properties, while in natural landscapes, transects were located randomly. Reptiles were counted by walking and checking under rocks or flat surface debris (e.g. garbage in urban zones). Surveys occurred from 8:30 am to 5:00 pm on non-windy days (wind speed below 25 km per hour) and temperatures averaging 23.4 °C ± 6.1. The transects were walked slowly, with on average 14 ± 6 min allocated to each transect. Variation in transect duration was due to handling and identification time, while walk speed was maintained as constant as possible. The presence of all species that were seen or captured was recorded. We considered a reptile species present at a transect location when it had been observed at least once over the two visits. We did not record reptile abundance because some species had low detectability and cryptic behaviours, which could affect abundance estimations [46].

The sampling effort resulted in 150-point counts for birds (presence/absence and abundance) and 90 transects for reptiles (presence/absence) over the 30 sampling cells.

Statistical analyses

We used two approaches to assess the relationship of landscape type (agricultural, natural, urban) with bird and reptile communities.

The first approach **(Approach 1)** estimated the effect of the landscape on biodiversity metrics. For birds, we used species richness, abundance, and Shannon equitability index assessed as the Shannon index divided by the log of species richness. The Shannon equitability index was used to compare species evenness [47]. For reptiles, we used only the species richness due to the lack of robust abundance data (see methods). To assess the relationship between biodiversity metrics and landscape types, we run one generalized linear mixed model per biodiversity metric with the glmmTMB package of R [48]. Such models can deal with the nested structure of our sampling scheme [49]. Biodiversity metrics were the response variable, landscape types were the fixed effect and the 2×2 km cell were set as random factors because several points and transects were set inside each cell. We used a negative binomial error distribution for abundance and Gaussian error distribution for species richness (bird and reptile models) and Shannon equitability index. Model quality was assessed using the R package DHARMa [50].

The second approach **(Approach 2)** evaluated community composition in birds and reptiles across the three landscape types using Joint species distribution modelling with the Hierarchical Models of Species Communities (HMSC) package of R to assess species occurrence or abundance changes in response to environmental variables, and to quantify the importance of habitat preference and phylogeny to shape species responses to environmental variables [7, 51]. A species habitat preference matrix was created for each taxon. We used the bird habitat classification provided by the European Breeding Bird Atlas 2 [52] to associate each species to one of seven habitats preference categories. Following this classification, specialists were the species associated with one specific habitat, and generalist species were the species not associated with a unique habitat. Based on this classification, the species in our dataset were grouped into six habitat categories: *Agricultural & Grassland*, *Forest*, *Inland Wetlands*, *Marine & Coastal*, *Mediterranean Habitats* and *Generalist* (Table SM3a). This habitat preference classification allows direct comparisons between different geographical regions and facilitates meta-analyses of habitat associations across Europe. Habitat preferences of reptile species were assigned by the reptile experts of this study (DA, AO and KC), relying upon the works of [53, 54]. These reference books provide habitat descriptions for each reptile species, including information on primary habitat types and associated environments. In conclusion, reptiles were assigned to either one of two habitat preference categories: *Inland Wetlands* and *Mediterranean Habitats* (Table SM3b). Species assigned to two habitats are considered habitat generalists.

As recommended in this type of approach, we used phylogenetic trees to assess the residual variation in species occurrence not explained by species habitat preferences. Phylogenetic trees were obtained from Vertlife for birds (www.vertlife.org/, accessed on 08/01/2024) and Time Tree for reptiles (www.timetree.org/, 08/01/2024). We included sampling locations of the counts in both bird and reptile models as a spatially structured random effect to account for spatial autocorrelation among sampling sites (sampling points of birds or middle points of the reptile transects).

For the bird community, we performed two HMSC, one on presence/absence data and one on the abundance conditional on presence (Abundance COP). To avoid unnecessary computing time for species with limited information [55], we excluded 11 species with only one occurrence (Table SM3a). We used a binomial error distribution to model species presence/absence and a Gaussian error distribution for the log of Abundance COP. For the reptile community, we performed only one HMSC using presence/absence data as response variables (binomial error distribution) and landscape types as explanatory variables. We ran the model on 12 reptile species, excluding 2 species with only one occurrence (Table SM3b).

We assumed a default prior distribution [7] and sampled the posterior distribution with four Monte Carlo Markov Chains (MCMC). Each presence/absence model was run for 37,500 iterations, of which the first 12,500 were removed as burn-in, and we thinned the remaining iterations by 100, returning 1000 posterior samples. For the bird abundance COP, the model ran for 750,000 iterations, of which the first 250,000 were removed as burn-in, and we thinned the remaining iterations by 2,000, returning 1,000 posterior samples. We assessed MCMC convergence by examining the model parameters' potential scale reduction factors [56]. The explanatory power corresponds to the variance explained by the model on data used in the model. The predictive power is a measure of the variance explained by the model, on data not used in the model. We quantified the predictive power by a two-fold cross validation in which half of the data were randomly selected to assess the Tjur R^2 and AUC for presence-absence models and R^2 for abundance models [55]. The statistical program used for all the statistical analyses was R version 4.2.1, and the R package *Hmsc* was used for fitting Joint species distribution models [51, 57].

Results

Species occurrence patterns in three landscapes

Bird species

A total of 143 bird species from 45 families were recorded across the Gediz Delta (Table SM3a) with only 90 breeding species retained for the analyses. The most abundant bird species were Greater flamingos, Barn swallows *(Hirundo rustica)*, and Yellow-legged gulls (*Larus michahellis*). The most frequent bird species were Eurasian magpies (*Pica pica*), Barn swallows, and Crested larks (*Galerida cristata*). We observed 27.8% of the bird species (25 species) only in natural landscapes, 5.6% (5 species) only in agricultural landscapes, and 3.3% (3 species) only in urban landscapes (Fig. 2A). *Generalist* species accounted for 28.9% of the observed species. In comparison, 28.9% were specialists of *Agricultural & Grassland* habitats, 24.4% specialists of *Inland Wetlands*, 12.2% specialists of *Marine & Coastal* habitats, 3.3% specialists of *Mediterranean habitats* and 2.2% specialists of *Forest habitats* (Table SM3).

Reptile species

A total of 14 reptile species were observed across the Gediz Delta (Table SM3b). Nine species were evaluated as specialists of *Mediterranean habitats* and five as specialists of *Inland Wetlands*. The most frequent reptile species were Snake-eyed lizards *(Ophisops elegans)*, western Caspian turtles (*Mauremys rivulata*), and Mediterranean Spur-thighed tortoises. Five reptile species were found in the three landscape types, three species were present only in natural landscapes, one was found only in agricultural landscapes, while zero species were found only in urban landscapes (Fig. 2B).

Community structure patterns as a function of landscape type

Bird community

The generalized mixed effect models fitted to 90 bird species (**Approach 1**) showed that natural landscape accommodated higher bird abundance than agricultural and urban landscapes ($\beta = 0.20 \pm 0.06$ (SE), $p < 0.001$; $\beta = 3.57 \pm 1.11$, $p < 0.001$; respectively, Table 1). Indeed, natural landscape hosted on average 231 birds [150; 356 (95%CI)], compared to 45 birds [29; 69] in agricultural and 65 birds [42; 100] in urban landscapes (Fig. 3). Species richness was not significantly different between landscape types (Table 1; Fig. 3). Shannon equitability index was lower in natural landscapes than in agricultural and urban landscapes ($\beta = -0.21 \pm 0.53$, $p < 0.001$; $\beta = -0.20 \pm 0.53$, $p < 0.001$; respectively, Table 1; Fig. 3). Higher abundance and lower equitability suggested uneven bird abundance in natural landscapes, with a few of them being highly abundant.

HMSC (**Approach 2**, performed on 79 bird species) based on bird presence/absence demonstrated a moderate explanatory power (AUC mean = 0.84 ± 0.10 (SD); range = 0.64–0.99) but a lower predictive power (AUC mean = 0.67 ± 0.17) (Fig. SM4.1). Habitat preference explained most of the presence/absence model variation

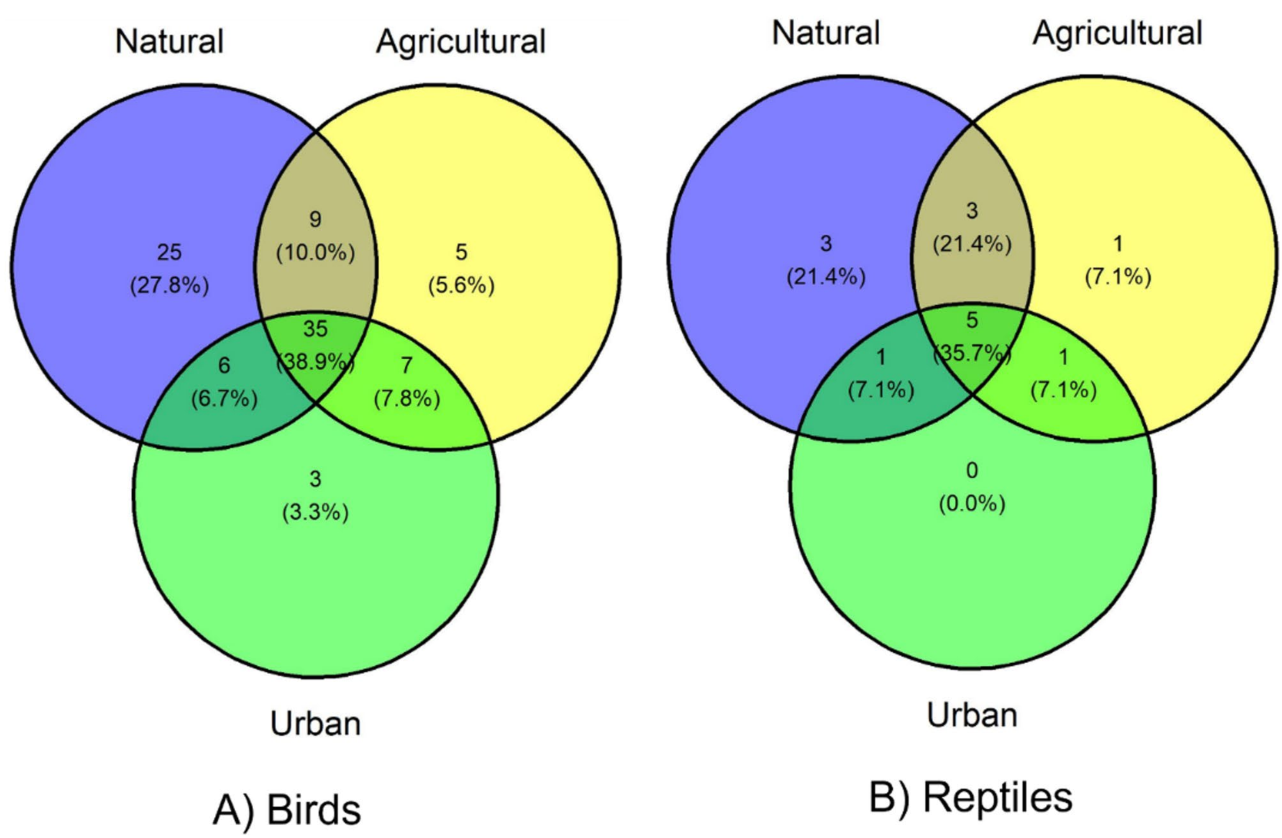

Fig. 2 Venn diagram of bird (**A**) and reptile (**B**) species number (and percentage) occurring over the three landscape types (Agricultural, Natural and Urban) in the Gediz Delta

Table 1 Results of the generalized linear mixed effect models on birds and reptiles, presenting the pairwise differences between landscape types (natural, agricultural and urban). Significant differences ($p < 0.05$) in abundance, species richness and Shannon equitability are in bold

Taxon	Variables	Pairwise	Estimate	SE	Df	z	*P*-value
Birds	**Abundance**	**Agricultural-Natural**	**0.195**	**0.061**	**145**	**-5.263**	**< 0.001**
Birds	Abundance	Agricultural-Urban	0.694	0.215	145	-1.180	0.465
Birds	**Abundance**	**Natural-Urban**	**3.566**	**1.108**	**145**	**4.091**	**< 0.001**
Birds	Richness	Agricultural-Natural	-1.200	0.793	145	-1.513	0.288
Birds	Richness	Agricultural-Urban	-0.260	0.793	145	-0.328	0.943
Birds	Richness	Natural-Urban	0.940	0.793	145	1.185	0.464
Birds	**Equitability**	**Agricultural-Natural**	**0.205**	**0.053**	**145**	**3.888**	**< 0.001**
Birds	Equitability	Agricultural-Urban	0.008	0.053	145	0.144	0.989
Birds	**Equitability**	**Natural-Urban**	**-0.198**	**0.053**	**145**	**-3.744**	**< 0.001**
Reptiles	Richness	Agricultural-Natural	0.976	0.234	90	-0.102	0.9943
Reptiles	**Richness**	**Agricultural-Urban**	**2.153**	**0.628**	**90**	**2.631**	**0.0231**
Reptiles	**Richness**	**Natural-Urban**	**2.207**	**0.641**	**90**	**2.723**	**0.0178**

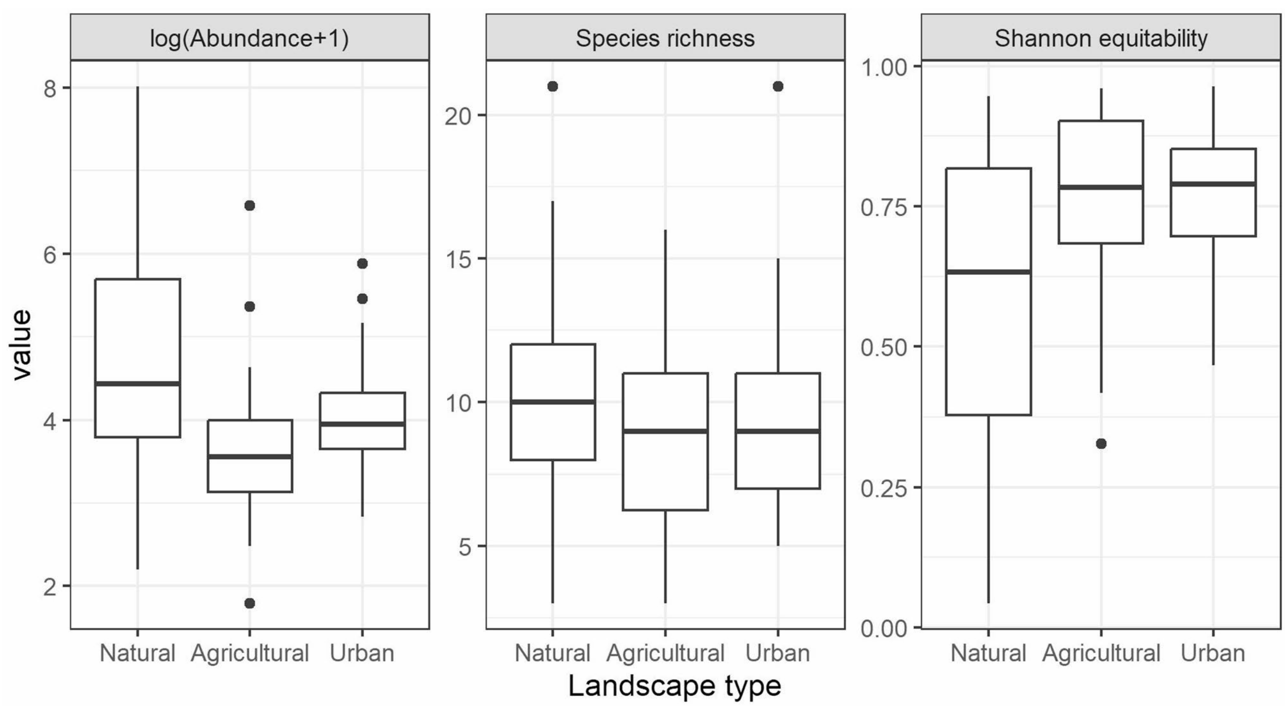

Fig. 3 Bird abundance (log), species richness and Shannon equitability per landscape types (Agricultural, Natural and Urban). Each landscape type was sampled by 10 sampling grids

(mean = 77.6 ± 23.19%). On the other hand, the second HMSC based on bird abundance COP had a low explanatory power (measured by the mean $R^2 = 0.61 \pm 0.32$; range = 0.04–1) and a null predictive power (-0.15 ± 0.33; Fig. SM4.2). Because of the poor performance of the abundance COP model (i.e., low explanatory and predictive power) we do not present these results.

From the presence/absence HMSC, we identified effects statistically supported (95% credible interval) for at least one landscape type on 57 species (72%), two landscape types on 33 species (42%), and three landscape types on 14 species (18%) (Fig. 5, see detailed results in Table SM5.1).

The variation of occurrence between agricultural and natural landscapes was statistically supported for 40 species (Fig. 5a). Among them, 29 species were more likely to occur in natural landscapes than in agricultural landscapes, and those species were typical from *Marine & Coastal* (11 species), *Inland Wetlands* (7 species), *Agricultural & Grasslands* (5 species), *Generalist* (5 species) and one *Mediterranean habitats* species. These species were mainly waterbirds (20 out of 29 species). In contrast, the 11 species with a higher occurrence probability in agricultural landscapes than in natural landscapes mainly consisted of *Generalist* (6) and *Agricultural & Grassland* species (4), and only one *Forest* species. None of these species were waterbirds.

The contrast between agricultural and urban landscapes was statistically supported for only 32 species. For 18 species, the occurrence probability was lower in urban landscapes compared to agricultural landscapes (Fig. 4b). These species mainly consisted of *Agricultural & Grassland* (13) species, but also included three *Inland wetlands* and one *Forest* species. The 13 species with higher occurrence probability in urban landscapes mainly consisted of *Generalists* (11 species) with only one *Agricultural & Grassland* and one *Marine & Coastal* species.

The contrast between natural and urban landscapes was statistically supported for 51 species. In particular, 36 species have a higher occurrence probability in natural landscapes than in urban ones (Fig. 4c). These consisted mainly of *Agricultural & Grassland* (11 species), *Marine & Coastal* (10 species) and *Inland Wetlands* (9) species, with a few *Generalist* (5) and one *Mediterranean habitat* species. The 15 species occurring more in urban than natural landscapes are mainly *Generalist* (11), a few *Agricultural & Grassland* (3) and one *Forest* species.

Overall, *Marine & Coastal* specialist species occurred more frequently (i.e. statistically supported at 95%) in natural than agricultural landscapes. Conversely, *Generalist* species occurred more frequently in urban landscapes than in agricultural (β = 1.09) and natural (β = 1.14) landscapes (Fig. 4). The *Agricultural & Grassland* species occurred less in urban than agricultural (β = -0.62) and natural (β = -0.71) landscapes. No statistically supported effect was detected for *Forest*, *Inland Wetlands* and *Mediterranean habitat* species in community-level responses.

Model output showed a poor phylogenetic signal (95%CI; [0.00;0.43]) meaning that residual variations of the model, after taking into account for species habitat preferences, are not phylogenetically structured.

Reptiles community

Reptile species richness was significantly lower in urban compared to natural and agricultural landscapes (β = -2.21 ± 0.64 (SE), $p = 0.02$; β = -2.15 ± 0.63, $p = 0.02$; respectively, Table 1) (**Approach 1**). Indeed, natural (1.4 species [1.0; 2.0 (95%CI)]) and agricultural landscapes (1.4 [1.0; 2.0]) hosted about two times more species than urban landscape (0.7 [0.4; 1.0]) (Fig. 5). Species richness was not significantly different between natural and agricultural landscapes ($p > 0.05$, Table 1).

HMSC (**Approach 2**, performed on 12 reptile species) showed a high explanatory power as measured by AUC (mean = 0.91 ± 0.05 (SD); range = 0.84-1.00) but a lower predictive power of 0.58 ± 0.16 (Fig. SM4.3). Habitat classification explained 80.4% ± 9.9 of the model variation. Landscape types resulted in effects statistically supported for nine species (Fig. 5, see detailed results in Table SM5.2).

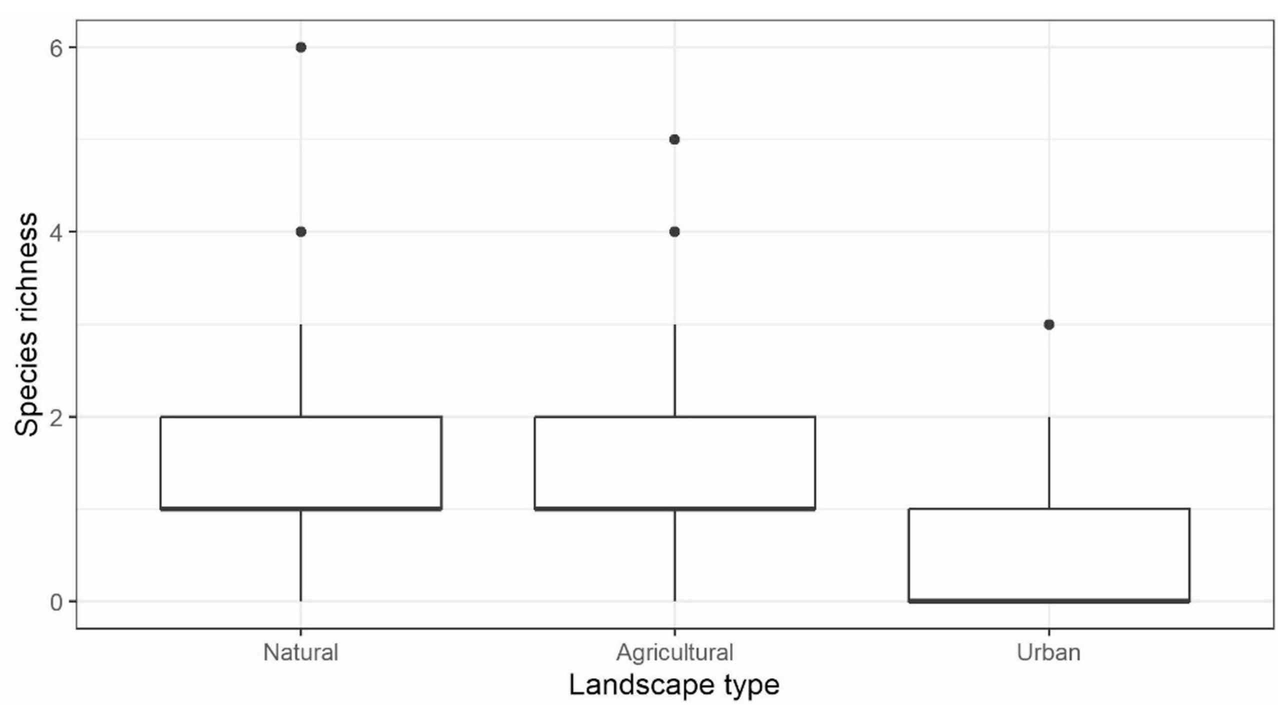

Fig. 4 Reptile species richness per landscape type (Agricultural, Natural and Urban). Each landscape type sampled was sampled by 10 sampling grids

Fig. 5 Pie charts summarizing HMSC estimated differences (95% credible interval) in bird ($n = 79$ species) and reptile ($n = 12$ species) occurrences between (**a**, **d**) natural and agricultural landscapes, (**b**, **e**) natural and urban, and (**c**, **f**) agricultural and urban landscapes. The species are grouped by habitat preference (Inland Wetlands, Agricultural & Grasslands, Generalist, Marine & Coastal, Mediterranean habitats, Forest)

The contrast between agricultural and natural landscapes was supported for seven species (Fig. 5d) with occurrence probability higher in natural than agricultural landscapes for four species, namely the Snake-eyed lizard, Rough-tail agama (*Stellagama stellio*), Caspian whipsnake (*Dolichophis caspius*) and Spur-thighed tortoise. Conversely, three species occurred more in agricultural than natural landscapes: European pond turtle (*Emys orbicularis*), Western Caspian turtle, and Grass snake (*Natrix natrix*). They are all *Inland wetland* species.

The contrast between agricultural and urban landscapes was supported for five species (Fig. 4e). All five species occurred more in agricultural than urban landscapes: Blotched snake (*Elaphe sauromates*), European pond turtle, Balkan terrapin, Grass snake and Dice snake (*Natrix tessellata*).

The contrast between natural and urban landscapes was supported for five species (Fig. 4f). The Caspian whipsnake, Blotched snake, Snake-eyed lizard, Rough-tail agama, and Spur-thighed tortoise occurred more in natural than urban landscapes, while no species occurred more in urban than natural landscapes.

Overall, the occurrence probability of the *Mediterranean habitat* reptile species was higher in natural ($\beta = 0.99$), and urban ($\beta = 0.84$) landscapes compared to agricultural landscapes. The *Inland wetland* reptile species occurrence probability was lower in urban landscapes compared to agricultural landscapes (β = -1.03). The species responses to environmental covariates showed a low phylogenetic signal 95%CI; [0.00; 0.78] in the presence-absence model, which means that missing residual variation is not phylogenetically structured.

Discussion

Our results show how agricultural and urban into the natural landscapes of the Gediz Delta shape bird and reptile community composition in contrast with natural landscapes. Generalist bird species dominate in urban areas while natural landscapes are of prime importance to the conservation of specialist bird and reptile species. Despite the general negative effect of agriculture landscapes on bird and reptile communities, our results highlight the potential importance of agricultural areas for reptile species associated with wetland habitats. This later effect however was not found not for waterbirds or reedbed passerines, a result that contrasts with what could be found in other Mediterranean deltas, where such birds can be found in agricultural areas (e.g., the Camargue [58]).

The natural landscapes of the delta appear to be much more favorable for both birds and reptiles in terms of abundance and species richness, especially for habitat specialist species. The lower evenness of bird diversity in natural landscapes of the Delta is likely due to the high abundance of some colonial waterbird species, such as the Greater flamingos that often congregate in large numbers when habitats are favorable. Natural landscapes are related to higher occurrences of *Marine & Coastal* and *Inland wetland* bird species, which is mainly driven by waterbirds and reedbed passerines. In turn, our results suggest that in the Gediz Delta, *Marine & Coastal* bird species do not seem to find alternatives in the agricultural habitats. This contrasts with other regions of the Mediterranean basin where ricefields offer alternative foraging habitats for Herons, Gulls, or the Common Shelduck (*Tadorna tadorna*) [58]. The mostly dry crops (e.g. cotton) cultivated in the Gediz delta are likely to explain the poor attractivity of agricultural habitats for these species. However, it should be noted that these species may have benefited to some extent from the transformation of certain natural and semi-natural habitats. The creation of large areas of salt pans - considered in this study as "natural" habitats - may strongly benefit some waterbird species, particularly the Greater flamingo [41]. Despite the limited remaining freshwater habitats in natural landscapes, the high occurrence probability of several *Inland Wetland* species in natural landscapes could be attributed to recent conservation efforts made in the delta (such as building artificial islands or pumping freshwater into the delta for Mute Swans (*Cygnus olor*), Dalmatian pelicans or Ruddy Shelducks (*Tadorna ferruginea*) [41]). Both the restoration of freshwater marshes and creation of salt pans may also have benefited a number of *Generalist* waterbird species that we found better represented in natural landscapes than elsewhere (e.g. Common Tern (*Sterna hirundo*), Common redshank (*Tringa tetanus*) or Collared pratincole (*Glareola pratincola*)). Among them, there are several bird species without strong ecological requirements (e.g., water salinity or depth) but which need aquatic habitats that are seldom found within agricultural and urban landscapes.

The pool of *Agricultural & Grassland* species breeding in the Gediz Delta is dominated by species adapted to open grassy habitats (e.g. Isabelline wheatear (*Oenanthe isabellina*), Crested lark or Calandra lark (*Melanocorypha calandra*)) with a few species that appreciate open or linear woodlands such as orchards or hedgerows (e.g. Woodchat shrike (*Lanius senator*) or European turtle dove (*Streptopelia turtur*)). Agricultural landscapes appear to be more favorable than natural and urban landscapes for these species. Yet a few of them, mostly birds with steppe affinity (e.g. Eurasian stone-curlew (*Burhinus oedicnemus*), Crested Lark, Calandra Lark or Corn Bunting (*Miliaria calandra*)) are more frequent in natural habitats. This likely results from the fact that intensive crops (primarily cotton) of the delta are not suitable for birds because of low landscape heterogeneity (monoculture, absence of permanent pasture or set aside fields, low percentage of uncultivated areas at the edge of parcels), high use of synthetic pesticides and fertilizers, and mechanization, which are the main drivers of bird population decline in farmlands elsewhere [59, 60]. Previous studies also indicated that several species typical of the *Agricultural & Grassland* bird guild decreased or even disappeared from the Gediz Delta following the decrease in wet pastures and grasslands habitats [41]. These bird species need short natural vegetation, often maintained by extensive sheep or cattle grazing, for breeding or foraging [52]. The destruction of such habitats is likely to have a negative impact on those birds. Similar negative impacts of agricultural intensification have been observed elsewhere in the Mediterranean basin [1, 8, 20, 61] and Europe [62]. Some of these farmland birds still find acceptable conditions in natural landscapes, in grazed scrubland or in brackish marshes, dry in summer and dominated by low shrub vegetation. The persistence of these species thanks to the presence of large areas of wetlands is observed in other Mediterranean deltas such as the Camargue [1].

Interestingly, *Inland wetland* aquatic reptile species - the European Pond turtle, the Western Caspian turtle, and the Grass snake – are more widespread in agricultural landscapes than in natural ones. This could be explained by the fact that freshwater habitats are very limited in the natural landscapes of the delta [26, 28, 34, 35] whereas the network of irrigation and drainage channels that surround cultivated fields provide good alternative habitats. One of these three species (the Caspian turtles) was the most common species observed during sampling. However, it is worth noting that these species are also observed in unnatural habitats such as cemented canals and that in these environments, it is easier to detect these species compared to more natural environments such as reedbed canals or marshes. Furthermore, only a fraction of the *Inland wetland* species community is able to adapt to these linear habitats, as it was also demonstrated in the Rhone Delta for birds [20].

Regarding *Generalist* bird species, as predicted, we found that they have a higher occurrence probability in urban landscapes than in agricultural and natural landscapes. These *Generalist* bird species have a large ecological niche that allows them to nest and forage in highly anthropized habitats like plantations of exotic trees or even on the roofs of houses [5, 17, 63]. There is a higher presence of trees planted in parks and urban areas whereas trees are less common in natural and agricultural landscapes of Gediz Delta. This can explain why *Generalist* species such as the Great tit (*Parus major*) are found to be linked to urban settlements in this delta. This results is similar to what has been found in other coastal Mediterranean wetlands [1, 64].

Our results contrast with prior research showing that remnant wetlands in urban landscapes are positively related to some aquatic reptile species [65]. The low species richness in urban landscapes could be related to the lack of substitute habitats, such as ponds or scrubland patches in urban parks, and to the low number of anthropophilic species observed during our survey. We also showed that *Mediterranean Habitat* reptile species occurrence probability of at least three species (Spur-thighed tortoise, snake-eyed lizards, and Rough-tail agama) was higher in natural landscapes compared to agricultural landscapes. One possible explanation is that the probability of occurrence of these species is higher due to the greater diversity of habitats present in the natural areas compared with the highly simplified and intensive agricultural habitats present in the Gediz Delta. These species are known to live in traditional agricultural landscapes in Türkiye.

Birds and reptiles are both used as bioindicators because of their specific ecological requirements (trophic levels, dispersal ability, and degree of habitat specialization). However, birds have generally received more attention due to their higher detectability in various habitats [1, 66–71]. Our results suggest that the lower detectability of reptiles makes them less suitable than birds to assess the effects of land use change on a territory like the Gediz Delta. Indeed, during this study, we observed only 50% of the species (14/28) of the reptile species known in the delta [33]. However, it should be noted here that the atlas study carried out by Arslan et al. 2018 [38] covered all delta habitats including the hills. In contrast, our study was developed over wetlands embedded into landscape types (natural, agricultural and urban) so that the biodiversity patterns relevant to each landscape could be analysed. Hence, we did not expect to contact reptile species linked to arborescent matorral and Mediterranean maquis habitats, even if they occur in the delta. Moreover, Arslan et al. (2018) [38] found that 11 to 15 herptiles species on average occurred per grid, with greater total species numbers recorded in the northern delta regions. Based on this, the number of species recorded in our study is representative, comforting the ecological validity of the study.

Community composition varies in response to LULCC through different mechanisms sometimes difficult to elucidate [24, 57, 72]. JSDM have allowed us to clarify how species habitat preferences affected species co-occurrence providing an efficient tool to assess functional change induced by LULCC. In contrast we did not find a strong signal for an effect of phylogeny relatedness on species assemblage, both in birds and reptiles. This may result from the small number of species considered with low number of closely-related species.

A first limitation of the approach in our case was the poor fit of the model for bird abundance conditional on presence so that it did not provide meaningful results. Because abundance models are suggested to be more useful for conservation purposes than occurrence models [73] further effort should be made to improve data quantity and quality. This could be done for instance by refining the spatial and thematic resolution of the environmental variables, as well as implementing national breeding bird monitoring. Compared to birds, limited reptile observations with low detectability and high ecological requirements may be less efficient indicators in places like the Gediz Delta [46, 66]. Among the 28 reptile species known to occur in the area (Arslan et al., 2018), four are recognized as primarily nocturnal: Mediterranean House Gecko (*Hemydactylus turcicus*), Kotschy's Gecko (*Mediodactylus kotschyi*), Javelin Sand Boa (*Eryx jaculus*), and Cat snake (*Telescopus fallax*). Although these species may occasionally be observed during the day (e.g., Mediterranean House Gecko was recorded in this study), their nocturnal activity patterns may have participated to their low detectability in our daytime surveys.The second limitation of the study is that the sampling cells of both agricultural and urban areas included a few remnant natural habitats, such as marshes, which may positively impact the presence of specialized species in these cells [20, 74–77]. A possible research development would be to investigate the effect of remnant-habitat types on the community changes following urbanization and agricultural conversion.

Conclusions

Our study shows that the community composition in different taxa is impacted by LULCC in different dimensions, with winner and loser species in every studied landscape type. Here, intensive farming is likely causing negative effects on many species in both taxa compared to natural habitats, but agricultural habitats retain more species and more specialized species than urban landscapes. The agro-ecological transition of the local agricultural sector could be a lever to promote farmland and inland wetland species. For instance, in an intensive agricultural context, proper management of open channels surrounded by reeds can provide alternative habitats for several reedbed species [20].

The lower levels of biodiversity observed in urban environments, particularly for specialist species, suggest that they do not represent alternative habitats for the species originally present in the delta. Therefore, our results call for stopping the urbanization of the delta and for the ecological restoration, where possible, of the natural habitats originally present. A significant proportion of freshwater and grassland habitats (such as ponds or reedbeds), are located outside the strict protection area of the delta and are largely threatened by human impacts [27, 28, 78]. In addition, the coastal zone of the Delta is facing increasing salinity due to limited freshwater resources [31, 79], leading to a decline in freshwater habitats. Protecting and restoring these diminishing habitats is crucial for sustaining regional biodiversity. In order to reduce the negative impacts of urbanisation and agriculture in the delta, there is a need to extend conservation activities beyond the strictly protected areas and develop appropriate restoration activities in these two landscape types. In urban areas, it would be interesting to increasing the number of ponds and parks and to plant natural vegetation to increase their connectivity with natural areas. In agricultural landscapes, concrete agricultural irrigation channels could be restored using natural materials, and water management could be improved to preseve freshwater resources.

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

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Author contributions

DA was responsible for the conceptualization, data collection, and analysis, creation of the figures and tables, drafting the first manuscript, and coordinating the drafts of the manuscript. EG was responsible for data analysis and editing of the drafts of the article. KÇ, AO, TG, and ÖD were responsible for conceptualization, data interpretation, and editing of the drafts of the article. AG was responsible for LULCC data production and editing of the drafts. LE and AB were responsible for conceptualization, editing of the drafts of the article, project administration, and funding.

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Data availability

All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declarations

Ethics approval and consent to participate

This study was conducted under the Turkish Ministry of Agriculture and Forestry (permission number: 21264211-288.04-E.574004) and the ethical permit of Ege University (number: 2019-012).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details
[1]Tour du Valat, Institut de Recherche pour la Conservation des Zones Humides Méditerranéennes, Le Sambuc, Arles 13200, France
[2]Institut Méditerranéen de Biodiversité et d'Ecologie Marine et Continentale 3(IMBE), UMR CNRS IRD Aix Marseille Université, IUT Site Agroparc, Avignon Université, BP 61207, Avignon CEDEX 09, 84911, France
[3]Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Prague 6 CZ- 165 00, Czech Republic
[4]Department of Biology, University of Turku, Turku, Finland
[5]Zoology Section, Department of Biology, Faculty of Science, Ege University, Izmir, 35100, Türkiye
[6]İzmir Büyükşehir Belediyesi, İzmir 35250, Türkiye

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