Protecting a heterogeneous landscape supports avian diversity across seasons on a Mediterranean island

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ABSTRACT

Conservation efforts commonly target the protection of specific threatened species and habitats, with the value of heterogeneous landscapes often overlooked. Areas with small fragments of habitat tend to receive little attention, but the overall habitat mosaic may support substantial biodiversity. In this work, we investigated seasonal bird-habitat associations on Akrotiri Peninsula, Cyprus, a well-known migration bottleneck site. The area comprises a heterogeneous landscape of diverse but fragmented habitats, with extensive wetlands rich in bird species. We mapped habitat types across the study area, and performed 388 point counts to record bird species richness and abundance in each season for one year. A total of 6,255 individuals of 115 species were recorded. The study revealed that species were clustered within and around freshwater bodies, and taller and structurally more complex habitats. Seasonal patterns showed that winter and spring seasons supported greater richness of species and numbers of individuals compared to summer and autumn. Overall, we show that water availability and structural complexity of habitat types are positively correlated with both species richness and abundance. Our comprehensive seasonal bird-habitat association study in a protected, designated site, highlights the value of protecting a heterogeneous landscape in its entirety because of the overall diversity it can support across seasons.

Keywords: bird abundance, species richness, habitat heterogeneity, point counts, NMDS, Cyprus

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INTRODUCTION

Habitat heterogeneity is an important contributor to biodiversity, providing niches to different species, thus satisfying their diverse ecological needs (Hurlbert and Haskell 2003; Veech and Crist 2007; Elsen et al 2021). Furthermore, structural complexity of each habitat within a mosaic further enhances species diversity (Tews et al 2004; Loke et al 2015). Thus, protection of habitat diversity regardless of the conservation value of each habitat individually is beneficial (László et al 2018), enhancing the degree of community variability (β-diversity) (Whittaker 1960). It may also enhance overall species richness of a study area (γ-diversity).

Because of their detectability, birds are extensively used as indicators of habitat quality (Robledano et al. 2010; Jarrett et al 2020; Panda et al 2021). The structure of the vegetation in a habitat is of fundamental importance to birds, providing them with feeding, nesting, roosting, foraging and shelter, and is what drives birds to select a specific area (Sutherland et al. 2004; Seoane et al. 2004). Indeed, even over a small area, habitat heterogeneity can result in the presence of large numbers of species (Girma et al 2016). Yet, because bird species are typically adapted to specific landscapes, conservation of natural habitats with specific composition is vital for their survival (Fuller et al. 2007), while changes in vegetation composition, might be followed by bird community changes in response (Isacch et al. 2005; Stagoll et al. 2010). Then again, the presence of certain species in a specific habitat does not necessarily mean that they prefer that habitat. Presence could be related to abundance of the specific habitat, the scarcity of a preferred habitat, or the proximity of the habitat to a preferred one, with both obligate and facultative species occupying each habitat type (Sutherland et al. 2004; Azpiroz and Blake 2016). The spatial extent of each habitat may also influence the presence of some area sensitive species (Herkert 1994). Furthermore, the mobility and migratory nature of birds affects seasonal species richness, especially across migratory corridors where resident and migrant breeders, passage migrants and winter visitors may comprise the mix (Hurlbert and Haskell 2003; Hovick et al 2014; Girma et al 2016). Moreover, especially in wetlands where water presence may vary dramatically through the year, seasonality plays an important role in bird diversity (Panda et al 2021).

Despite the high ornithological value of the Mediterranean basin, relatively few studies have focused on bird-habitat associations using a quantitative approach. Indeed, most ornithological surveys in the region have provided little information about habitat types (Katsimanis et al. 2006; Fuller et al. 2007; Bergner et al. 2015). Nevertheless, targeted bird species studies in association with habitats have been performed on the island of Cyprus (e.g. Ieronymidou et al. 2012; Papanikolas et al. 2021~~unpublished ms~~), but multi-species bird habitat associations have seldom been undertaken, except in the context of farming practices (Hellicar et al. 2019).

We carried out a bird-habitat association study for the Akrotiri Peninsula, at the southern tip of Cyprus, the easternmost island in the Mediterranean. The Akrotiri Peninsula is topographically a predominantly flat area. Altitudes range from 2.7 m below sea level at the lowest point of the Salt Lake, to 60 m above sea level on the southern coastal cliffs (Charilaou et al. 2012, Hadjikyriakou et al. 2020). Protected status designations include a Ramsar Wetland of International Importance (Ramsar Convention on Wetlands 2010), as well as a Special Protection Area (SPA) and a Special Area of Conservation (SAC) under local legislation (SBAA 2010~~1~~; SBAA 2015).

The study site comprises a mix of habitats with an extensive Salt Lake at its centre (Fig. 1). ~~Despite~~Although the peninsula overall has a ~~the~~ high ornithological value~~ of the site~~, with 363 bird species recorded thus far (Hadjikyriakou 2021), the landscape is heterogeneous and it is not known which habitat types across the Peninsula ~~are fragmented within a heterogeneous landscape~~support which communities of birds and in which seasons.

Thus far, 363 species of birds have been recorded at Akrotiri (Hadjikyriakou 2021). As a result, assessment of the value of each different habitat, and its contribution to the overall ornithological importance of the Peninsula is challenging. We hypothesized that some habitats, such as the relatively extensive saline lagoons, may play a predominant role on bird diversity, but a detailed assessment is missing. Through this studyOur we aim was ed at mappingto map mapped the habitat types of the Akrotiri Peninsula at a suitable level to facilitate bird-habitat associations. This allowedDoing so, would allow us to target and assess each habitat separately but also determine how the heterogeneous nature of the peninsula may support avian communities. To that end, wWe performed habitat specific , and performed bird surveys in summer during the breeding season, over winter, and during autumn and spring migration, aiming atso we could . We then determined species richness and abundance by habitat type, habitat area and season, and produced a non-metric multidimensional scaling ordination to determineing e associations of species with habitats across seasons. Bird-habitat association studies are important for conservation because they inform management decisions regarding the importance of habitats in supporting birds, while also creating a baseline for future ecological monitoring work (Stirnemann et al 20154).

METHODS

Habitat mapping

The European Nature Information System (EUNIS) habitat classification (European Environment Agency 2010) was used to map habitats at a suitable level for bird-habitat associations. The EUNIS system clusters habitats hierarchically, facilitating grouping and consolidation of fragmented habitats within the study area (Cox et al. 2009) to more ecologically meaningful habitats in relation to birds (Fuller et al. 2007). We used a previous

Akrotiri Peninsula habitat map (Cox et al. 2009) prepared with the EUNIS system as a starting point, and filled in gaps and discrepancies using a satellite image (Digital Globe 2011) and GPS-based ground truthing in the field (Sutherland et al. 2004). We then grouped habitats at higher hierarchical levels to render them suitable for bird-habitat associations, as per recommendations in Bibby et al. (2000).

Bird counts

We used point counts to determine species richness and abundance (Bibby et al. 2000; Huff et al. 2000; Sutherland et al. 2004; Hostetler and Main 2008), with one point per 100 hectares of each habitat type (Fuller et al. 2007), and a minimum of five points per habitat type following recommendations in Huff et al. (2000). Point count locations were selected using regular grids (Sutherland et al. 2004) in ArcGIS, with at least 250 m distance between each point count (Ralph et al. 1995; Katsimanis et al. 2006), resulting in 97 point counts in total. A fixed point count radius was preferred over an unlimited radius to allow comparisons between point counts within and between habitats (Ralph et al. 1995). Because vegetation density and height was variable between habitat types, we considered a 50 m radius most appropriate across habitat types, allowing for standardisation of our surveys (Ralph et al. 1995; Karl et al. 2000; Stagoll et al. 2010). Different habitats may require different count times to record a sufficient percentage of the birds present, but standardization is necessary (Karl et al. 2000; Stagoll et al. 2010). To that end, for dense habitats it has been suggested that at least nine minutes are necessary to detect a minimum of 80 % of the species and individuals present (Shiu and Lee 2003), thus a ten-minute point count duration was implemented for all types of habitats. All birds seen or heard were recorded including flying individuals in zones of 0 – 20 m and 20 – 200 m above ground as long as their activity was related to the specific habitat type, e.g. hovering, feeding on the wing or thermalling (Karl et al. 2000; Huff et al. 2000; Hostetler and Main 2008; Oneal and

Rotenberry 2009). We did not record flying individuals over 200 m above ground passing over the point count; we deemed such overflights unrelated to the habitat type. The recorded species status (i.e. resident, migrant breeder, migrant wintering and passage migrant) was based on the BirdLife Cyprus (2021~~11~~) checklist of Cyprus birds.

Point counts were performed four times, once in each season (following Sutherland et al. 2004), with a total of 388 over the study year. Counts were performed during the breeding season (16 May – 29 June 2010); autumn migration (30 August – 20 October 2010); winter (22 – 31 December 2010); and spring migration (8 –23 March 2011). All observations were undertaken within the first four hours of daylight, when bird activity is at its peak (Huff et al. 2000; Shwartz et al. 2008; Flaspohler et al. 2010; Stagoll et al. 2010). The observation locations were approached as quietly as possible and any birds flushed from the survey area were recorded (Ralph et al. 1995). Counts were cancelled during extremely windy conditions or when it was raining heavily as this could result in poor detection ability (Hostetler and Main 2008; Huff et al. 2000; Stagoll et al. 2010). The coastal open habitats were quite windy on many occasions; however the survey proceeded as long as the wind did not affect detection ability (Ralph et al. 1995). Distances within the point count were measured with a rangefinder (Leica Rangemaster 1600) to visually establish the point count perimeter (Shwartz et al. 2008; Alldredge et al. 2007; Bibby et al. 2000). An audio recorder (Olympus LS10) was used to record songs and calls, to ~~aid~~ double check and confirm identification ~~of~~ of some individuals~~, not identified visually~~ especially of cryptic species not verified visually in the field (Sutherland et al. 2004). The same observer performed all the counts to avoid observer-related bias (Bergner et al. 2015).

Data analysis

The number of point counts varied between habitat types because it was determined by the size of the habitat in the study area. Thus, for the calculation of the bird abundance in each habitat a factor was used, which was calculated by dividing the total number of individuals recorded in each habitat with the number of point counts therein and the number of visits undertaken during the study period (Shwartz et al. 2008; Hovick et al 2014; Azpiroz and Blake 2015). We tested for the effect of habitat type and season on species richness and abundance using Generalised Linear Mixed Models (GLMM), with a Poisson distribution, with point count as random factor. A separate GLMMs was run with a Poisson distribution to test for the effect of habitat area on species richness and abundance. Because the effect of area may vary by season, season was again included in the model, with habitat type as a random factor. Moran's autocorrelation index was calculated in ArcGIS, annually and seasonally, to identify any clustering patterns of species and individuals around specific point counts. Non-metric multidimensional scaling (NMDS) was used to examine differences and similarities in species composition among habitat types in each season and for all seasons combined (Alonso et al. 2013; Hovick et al. 2014). Species with fewer than 3 records throughout the study period were excluded from the ordination (Leveau et al. 2018). The Bray-Curtis distance metric was selected because of its sensitivity to the most abundant bird species over those less abundant (Pillsburry et al. 2011). GLMMs were performed using the GLMMTMB package (Brooks et al. 2017), while for the NMDS ordination the vegan package was used (Oksanen et al. 2020), both in R 4.0.1 (R Core Team 2020). We checked that models had not deviated from expectations and passed Kolmogorov-Smirnov tests ($P > 0.05$), with all residuals fitting model predictions in DHARMa (Harting 2019). All habitat and bird data were entered in ArcGIS 10.3 (ESRI 2014) and linked to the point count and to the habitat type they belong, facilitating visualisation and spatial analysis.

RESULTS

Habitat mapping

Thirty-seven previously mapped EUNIS habitat types, along with mapping gaps identified and filled via field work, were consolidated into thirteen habitat types across Akrotiri Peninsula~~.~~ (Fig. 2 and Table 1). Most extensive habitats with over one thousand hectares each were the saline lagoons, which included the ~~(mostly represented by the salt lake~~Salt Lake~~)~~, the surrounding salt meadows, and the cultivated areas primarily north and south of the ~~salt lake~~Salt Lake. These are followed by mostly fragmented ~~j~~J*uniperus* maquis and phryganas / grasslands, as well as built-up areas, predominantly within the southern half of the Peninsula. The ~~rest of the~~remaining habitats ~~were relatively~~comprised smaller exten~~d~~ts of pine forest~~s~~, eucalyptus plantations, reed beds, and coastal stretches of cliffs and sand / gravel. ~~Least represented~~ Smallest in size were the freshwater wetlands at~~, with~~ just seventeen hectares.

Bird counts

Within the 13 habitat types (Fig.2 and Table 1) 388 point counts were performed. In total, 6255 individuals were recorded from 115 bird species, including 997 flying individuals which were judged to be associated with the habitat they flew over (Huff et al. 2000). Some of the species were generalists found in several habitat types, while other species were only found in specific habitats or groups of habitats. Generalists included *Corvus cornix*, *Cisticola juncidis*, *Falco tinnunculus, Galerida cristata* and *Hirund*o~~a~~ *rustica*, *Carduelis carduelis* and *Passer domesticus,* all were recorded in at least ten habitat types. The remainder were recorded in fewer than ten habitats, with 48 species found in a single habitat type. The five most abundantly recorded species were *Passer domesticus* (1183 individuals recorded), *Corvus cornix* (499), *Hirundo rustica* (421), *Fulica atra* (334), and *Phoenicopterus roseus* (293). For the remaining species, fewer than 200 individuals were recorded, with fewer than five individuals recorded for 41 species (Online Resource 1 - Table S1).

Species richness

Species richness was highest in the freshwater habitat with 58 species, and lowest in the coastal habitats of sea cliffs and sand / gravel shores with 13 species each (Fig. 3). Nevertheless, ~~, though~~based on the GLMM analysis, ~~all~~ ~~most~~all habitats,~~, except~~ ~~apart~~ except ~~from~~ sea cliffs, sand / gravel shores, ~~the latter two and~~ salt meadows and phryganas / grasslands, had significantly higher species richness than the reference habitat, saline lagoons (Table 2). Species richness of breeding birds in the study site was highest in cultivations, freshwater, phryganas / grasslands and maquis, and lowest in coastal habitats (Fig. 3). No significant effect of season on species richness (Fig. 4) after controlling for the effects of habitat and variation by point count was found (Table 2). In addition no significant effects of available habitat area on species richness (z = 0.96, P = 0.34) were found. In fact, the habitat with the smallest area, freshwater wetlands, had the highest species richness (Table 1).

Bird abundance

The freshwater habitat also maintained the highest bird abundances, with a mean of 61.1 individuals per point count per visit, and along with built-up areas and cultivations had significantly higher abundances than saline lagoons. The lowest abundances were in sand / gravel shores with a mean of 3.4 individuals per point count per visit (Fig. 3 and Table 1), and along with grasslands were the two habitats with significantly lower abundances than saline lagoons (Table 3). Abundances were higher in winter compared to spring, but they were significantly lower in summer and autumn (Table 3). Contrary to species richness, available habitat area had a significant effect on abundance (z = 2.15, P = 0.03), with greater number of individuals recorded as available habitat area increases.

Spatial analysis

Spatial autocorrelation (Moran's index) (Table 4 and Online Resource 1 - Fig. S1 – S10), indicated that species distribution in the point counts was clustered around freshwater bodies and structurally taller, and more complex habitats such as maquis and cultivated areas with plantations. By contrast, there were fewer species in structurally simpler habitats such as the salt meadows and the salt marshes. Although migrant species recorded (i.e. breeding, wintering and passage migrants) comprised more species overall, the majority of records were of resident species, present all year around in the study area (Table 5). The NMDS ordination for all seasons together indicated that there was variation among point counts within the same habitat, as well as between the different habitats, while a number of species were associated with multiple habitats. Species composition followed a gradient from the saline lagoons, salt meadows, freshwater and grasslands towards the drier habitats such as pine forest and maquis, while all other habitat types had overlap with those “extremes” in relation to wetness (Fig. 5). In spring, apart from some specialists such as *Phalacrocorax aristotelis* and *Larus michahellis* breeding on coastal areas on sea cliffs, or *Phoenicopterus roseus* and *Tadorna ferruginea* which compulsively feed within the Salt Lake, no conclusive results could be obtained from the ordination. In summer, although ordination stress values did not allow for robust conclusions, it seems that birds were converging across their preferred breeding habitats, for example *Charadri~~o~~us alexandrinus* which nested within the drying Salt Lake and the remaining *Phoenicopterus roseus* which concentrated within the core of the Salt Lake where there was still water. During the southbound migration season in autumn, as in spring, there was much variation among point counts within the same habitat. Finally, during winter, the ordination was more explanatory compared to the other seasons, with waterbirds assembling within the fully inundated Salt Lake and freshwater wetlands. Nevertheless, many other species were scattered across different habitat types (Fig. 6).

DISCUSSION

Species richness and abundance

The clustering of some species within and around their preferred habitats revealed their ecological requirements, but the fragmentation and proximity of different habitat types in the study area, and the migratory ~~status~~ importance of the Akrotiri Peninsula, ~~highlights~~ emphasises the ~~importance~~ value of the area at a landscape level over the importance of specific habitat types. Species are selective in habitat types and those that are highly selective, such as waterbirds (e.g. *Phoenicopterus roseus* and *Fulica atra*),~~,~~ ~~are~~ drivinge the pattern ~~towards~~ of a clustered species distribution. In addition, some species, although not waterbirds as such, spend time within or adjacent to wetland habitats (e.g. *Cettia cetti* and *Cisticola juncidis* (Panda et al 2021). Nevertheless, as the wetness of a habitat is critical for the presence of some specialist species, such as waders, the phenomenon of a habitat being completely dry during summer and autumn and inundated during winter and spring further perplexes the situation (Ramírez et al 2018).

Although freshwater habitat occupied the smallest area at the study site, the expected outcome of high avian species richness and abundance in this habitat (Malavasi et al. 2009) emphasizes the importance of wetland areas in such dry landscapes like Akrotiri, and in Cyprus more generally. Wetlands are increasingly recognised as biodiversity hotspots, especially those in arid regions, where they are key landscape components supporting biodiversity and core ecological functions (Robledano et al. 2010). The proximity of an area to water sources is important for species presence (Shwartz et al. 2008), and our finding of clustering of species around freshwater bodies supports this assertion. Cultivated areas were also species rich, presumably because most of them were irrigated, with Cyprus farmland areas found to have high species richness and overall bird abundance, especially those considered of High Nature Value (Hellicar et al. 2019). Our results are consistent with Kailis (2002), who found that the agricultural zone had higher bird species richness and abundance than the Eucalyptus forest and the Salt Lake within the Akrotiri Peninsula. Although Eucalyptus forests support a diversity of bird species in Australia where they are indigenous, in the Mediterranean where they are non-native, they are comparatively species poor, possibly because they fail to attract the local insect fauna and thus do not provide abundant food resources for birds (Cody 1985).

Yet, the poorest habitats in terms of species richness and abundance were the coastal habitats of sea cliffs and sand / gravel shores, which tend to contain species that are ecologically specialised, such as those nesting on the sea cliffs, including *Falco eleonorae* (Hadjikyriakou and Kirschel 2016, Hadjikyriakou et al. 2020). Structurally taller habitats typically support larger numbers of species compared to structurally simpler ones (Stagoll et al. 2010), with trees attracting more species because they provide birds with more diverse feeding opportunities, perches, shelter and nest sites (Isacch et al. 2005). Therefore, the structural complexity of a habitat is positively correlated with bird diversity by providing a higher number of possible niches (Isacch et al. 2005; Katsimanis et al. 2006; Stagoll et al. 2010). Non-native Eucalyptus forests may however be an exception, as such plantations are poor in plant species, and provide limited feeding opportunities to birds.

During the breeding season, we found that most species bred in cultivations, freshwater, phryganas / grasslands and maquis, highlighting the importance of these habitats at a critical stage of the life cycle of birds (Katsimanis et al. 2006). Although seasonal variations might affect species abundance (Isacch et al. 2005), in this study there was no significant difference in species richness between the seasons. The identified higher bird abundance in winter and spring, compared to summer and autumn, likely reflects the presence of water in the local wetlands in winter and spring which attracts large numbers of waterbirds overwintering in the Akrotiri wetlands, thus highlighting the area’s importance as a wintering destination.

Local implications

Despite the peninsula’s importance for biodiversity, its management is challenging because of land use pressures from different sources including housing development, recreation, agriculture, and military installations and activities (Charilaou et al. 2012). The pressure for development, along with consecutive changes in land use, can have a continuous negative effect on bird presence by reducing and fragmenting the available habitats (Charilaou 2012; Panda et al 2021). In addition, the uncontrolled and dense vehicle access paths across many habitat types such as the salt meadows and maquis~~,~~ can have negative effects on birds, especially on breeding species (Giosa et al 2018). ~~In particular~~Conservation efforts need to focus on key habitats, such as the freshwater habitats, which despite ~~of~~ their ~~relatively low representation across the~~ small comparative size in the Peninsula, were found to host the largest numbers of species and individuals, ~~need to form the core of conservation efforts,~~ and the ~~ir~~ hydrological balance of freshwater habitats needs to be ~~sus~~maintained. Moreover, ~~the importance of~~ cultivations ~~ought not to be overlooked, and their ability to~~ host ~~such~~ an extensive number of species ~~and individuals~~in high abundances, and any ~~needs to be maintained by avoiding~~ dramatic changes in land use should be avoided.

The location of Akrotiri Peninsula as the closest point on Cyprus to Africa, together with its extensive wetland cover enhances its migratory value, but overall its core diversity value is its habitat heterogeneity, enhancing species richness, despite it being a predominantly flat area and with its habitats of a fragmented nature (Girma et al 2016). Indeed some species, rather than the individual size of a habitat patch in a fragmented mosaic, consider the total available habitat size in a given area, thus even small habitat patches can be significant (Hogg and Nilon 2015), as long they remain free of disturbance.

Conclusions

The knowledge of bird-habitat associations is valuable for bird conservation planning, and it is often not readily available (Stagoll et al. 2010) hindering species conservation efforts (Cherkaoui et al. 2017). Furthermore, seasonality significantly determines the presence of species in habitats especially across migratory corridors (Hurlbert and Haskell 2003). Thus, bird-habitat associations, especially on a seasonal basis, are important to inform the decision-making process, and to provide managers with the necessary knowledge to take informed decisions (Hovick et al 2014; Girma et al 2016). Nevertheless, in relatively small areas such as the Akrotiri Peninsula, species distributions may overlap habitats, emphasizing the importance of landscape scale conservation efforts over individual habitat type conservation.

REFERENCES

Alldredge MW, Simons TR, Pollock KH (2007) A field evaluation of distance measurement error in auditory avian point count survey. J Wildlife Manage 71:2759-2766. https://doi.org/10.2193/2006-161

Alonso JA, Metz MR, Fine PVA (2013) Habitat specialization by birds in western Amazonian White-sand forests. Biotropica 45:365-372. https://doi.org/10.1111/btp.12020

Azpiroz AB, Blake JK (2016) Associations of grassland birds with vegetation structure in the Northern Campos of Uruguay. Condor 118:12-23. https://doi.org/10.1650/CONDOR-15-49.1

Bergner A, Avci M, Eryiğit H, Jansson N, Niklasson M, Westerberg L, Milberg P (2015) Influences of forest type and habitat structure on bird assemblages of oak (Quercus spp.) and Pine (Pinus spp.) stands in southwestern Turkey. Forest Ecol Manag 336:137-147. https://doi.org/10.1016/j.foreco.2014.10.025

Bibby CJ, Burgess ND, Hill DA, Mustoe SH (2000) Bird census techniques (2nd edition). Academic Press, London.

Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS (2020) Birds of the World. Cornell Lab of Ornithology, Ithaca

BirdLife Cyprus (20121~~1~~) Birds of Cyprus c~~C~~hecklist, monthly sightings and yearly occurrences 2016 – 2020. BirdLife Cyprus, Nicosia~~ of Cyprus Birds.~~ ~~http://www.birdlifecyprus.org. Accessed 17 October 2011~~

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. R J 9:378-400

Charilaou P, Perdiou A, Hadjistyllis C, Hadjikyriakou T, Colvill M (2012) Akrotiri Peninsula environmental management plan Ver. 2.0. SBAA, Episkopi

Cherkaoui SI, Selmi S, Hanane S (2017) Ecological factors affecting wetland occupancy by breeding Anatidae in the southwestern Mediterranean. Ecol Res 32:259-269. https://doi.org/10.1007/s11284-017-1436-5

Cody ML (1985) An introduction to habitat selection in birds. In: Cody ML (ed) Habitat selection in birds. Academic Press, California, pp 3-56

Cox J, Byfield A, Davison-Watts D, King D (2009) Botanical surveys of Natura 2000 sites in Cyprus: Volume One: Akrotiri. Jonathan Cox Associates, Hampshire

DigitalGlobe (2011) Satellite image of Akrotiri Peninsula, Cyprus. DigitalGlobe Incorporated, Logmont

Elsen PR, Farwell LS, Pidgeon AM, Radeloff VC (2021) Contrasting seasonal patterns of relative temperature and thermal heterogeneity and their influence on breeding and winter bird richness patterns across the conterminous United States. Ecography 44:1-13. https://doi.org/10.1111/ecog.05520

ESRI (2014) ArcGIS, version 10.3. ESRI Inc., Redlands

European Environment Agency (2010) EUNIS biodiversity database http://eunis.eea.europa.eu/index.jsp. Accessed 17 March 2010

Eurostat (2015) Administrative units. European Commission. http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/countries#countries14. Accessed 15 December 2015

Flaspohler DJ, Giardina CP, Asner GP, Hart P, Price J, Lyons CK, Castaneda X (2010) Long-term effects of fragmentation and fragment properties on bird species richness in Hawaiian forests. Biol Conserv 143:280-288. https://doi.org/10.1016/j.biocon.2009.10.009

Fuller RM, Devereux BJ, Gillings S, Hill RA, Amable GS (2007) Bird distributions relative to remotely sensed habitats in Great Britain: Towards a framework for national modelling. J Environ Manage 84:586-605. https://doi.org/10.1016/j.jenvman.2006.07.001

Giosa E, Mammides C, Zotos S (2018) The importance of artificial wetlands for birds: A case study from Cyprus. PLoS ONE 13:e0197286. https://doi.org/10.1371/journal.pone.0197286

Girma Z, Mamo Y, Mrngesha G, Verma A, Asfaw T (2016). Seasonal abundance and habitat use of bird species in and around Wondo Genet Forest, south-central Ethiopia. Ecol Evol 7:3397-3405. https://doi.org/10.1002/ece3.2926

Hadjikyriakou T (2021) Spatio-temporal Akrotiri bird checklist (SPABC). Akrotiri Environmental Education Centre, Akrotiri

Hadjikyriakou TG, Kirschel ANG (2016) Video evidence confirms cannibalism in Eleonora’s falcon. J Raptor Res 50:220-223. https://doi.org/10.3356/0892-1016-50.2.220

Hadjikyriakou TG, Kassinis N, Skarlatos D, Charilaou P, Kirschel ANG (2020) Breeding success of Eleonora's falcon in Cyprus revisited using survey techniques for cliff-nesting species. Condor 122:duaa045. https://doi.org/10.1093/condor/duaa045

Harting F (2019) DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. https://CRAN.R-project.org/package=DHARMa. Accessed 10 May 2021

Hellicar M, Honold J, Kirschel ANG (2019) Comparison of land cover and farming intensity-based models for mapping High Nature Value farmland in Cyprus. Bird Study 66:317-328. https://doi.org/10.1080/00063657.2019.1684875

Herkert JR (1994) The effects of habitat fragmentation on Midwestern grassland bird communities. Ecol Appl 4:461-471. https://doi.org/10.2307/1941950

Hogg JR, Nilon CH (2015) Habitat associations of birds of prey in urban business parks. Urban Ecosyst 18:267-284. https://doi.org/10.1007/s11252-014-0394-8

Hostetler ME, Main MB (2008) Florida monitoring program: Point count method to survey birds. University of Florida, Florida

Hovick TJ, Elmore RD, Fuhlendorf SD (2014) Structural heterogeneity increases diversity of non-breeding grassland birds. Ecosphere 5:1-13. https://doi.org/10.1890/ES14-00062.1

Huff MH, Bettinger KA, Ferguson HL, Brown MJ, Altman B (2000) A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon. Gen. Tech, Repo. PNW-GTR-501. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland

Hurlbert AH, Haskell JP (2003) The effect of energy and seasonality on avian species richness and community composition. Am Nat 161:83-97

Ieronymidou C, Collar NJ, Dolman PM (2012) Endemic Cyprus warbler *Sylvia melanothorax* and colonizing Sardinian *warbler Sylvia melanocephala* show differential habitat associations. Ibis. https://doi.org/10.1111/j.1474-919x.2011.01211.x

Isacch JP, Maceira NO, Bo MS, Demaria MR, Peluc S (2005) Bird-habitat relationship in semi-arid natural grasslands and exotic pastures in the west pampas of Argentina. J Arid Environ 65:267-283. https://doi.org/10.1016/j.jaridenv.2004.11.008

Jarrett C, Smith TB, Claire TT, Ferreira DF, Tchoumbou M, Elikwo MNF, Wolfe J, Brzeski K, Welch AJ, Hanna R, Powell LL (2020) Bird communities in African cocoa agroforestry are diverse but luck specialized insectivores. J Appl Ecol. https://doi.org/10.1111/1365-2664.13864

Kailis MK (2002) The effects of eucalyptus plantations on the songbird biodiversity of Akrotiri forest, Cyprus. Dissertation, University of Central Lancashire

Karl JW, Heglund PJ, Garton EO, Scott JM, Wright NM, Hutto RL (2000) Sensitivity of species habitat-relationship model performance to factors of scale. Ecol Appl 10:1690-1705

Katsimanis N, Dretakis M, Akriotis T, Mylonas M (2006) Breeding bird assemblages of eastern Mediterranean shrublands: composition, organisation and patterns of diversity. J Ornithol 147:419-427. https://doi.org/10.1007/s10336-005-0024-6

László E, György K, Zoltán B, Bence K, Csaba N, János KP, Csaba T (2018) Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. Biol Conserv 226:72-80. https://doi.org/10.1016/j.biocon.2018.07.029

Leveau LM, Isla FI, Bellocq MI (2018) Predicting the seasonal dynamics of bird communities along an urban-rural gradient using NDVI. Landscape Urban Plan 177:103-113. https://doi.org/10.1016/j.landurbplan.2018.04.007

Loke LHL, Ladle RJ, Bouma TJ, Todd PA (2015) Creating complex habitats for restoration and reconciliation. Ecol Eng 77:307-313. https://doi.org/10.1016/j.ecoleng.2015.01.037

Malavasi R, Battisti C, Carpaneto GM (2009) Seasonal bird assemblages in a Mediterranean patchy wetland: corroborating the intermediate disturbance hypothesis. Pol J Ecol 57:171-179

Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2020) Community ecology package: ordination, diversity and dissimilarities – vegan-package. https://github.com/vegandevs/vegan. Accessed 10 May 2021

Oneal AS, Rotenberry JT (2009) Scale-dependent habitat relations of birds in riparian corridors in an urbanizing landscape. Landscape Urban Plan 92:264-275. https://doi.org/10.1016/j.landurbplan.2009.05.005

Panda BP, Das AK, Jena SK, Mahapatra B, Dash AK, Pradhan A, Parida SP (2021) Habitat heterogeneity and seasonal variations influencing avian community structure in wetlands. J Asia-Pac Biodiversity 14:23-32. https://doi.org/10.1016/j.japb.2020.10.001

Papanikolas N, Hadjikyriakou TG, Sebastianelli M, Kirschel ANG (2021) Habitat selection and interspecific competition between Sylvia Warblers in Cyprus following the rapid expansion of a recent colonizer. Avian Cons Ecol 16:11. https://doi.org/10.5751/ACE-01937-160211.~~Accepted manuscript~~

Pillsbury FC, Miller JR, Debinski DM, Engle DM (2011) Another tool in the toolbox? Using fire and grazing to promote bird diversity in highly fragmented landscapes. Ecosphere 2:1-14. https://doi.org/10.1890/ES10-00154.1

R Core Team (2020) R: a language and environment for statistical computing, computer program, ver. 4.0.1 – R Foundation for Statistical Computing, Vienna. https://www.r-project.org. Accessed 23 December 2020

Ralph CJ, Droege S, Sauer JR (1995) Managing and monitoring birds using point counts: Standards and applications. In: Ralph CJ, Sauer JR, Droege S (eds) Monitoring bird populations by point counts Gen. Tech, Rep. PSW-GTR-149, USDA, Albany, pp 161-169

Ramírez F, Rodríguez C, Seoane J, Figuerola J, Bustamande J (2018) How will climate change affect endangered Mediterranean waterbirds? PLoS ONE 13:e0192702. https://doi.org/10.1371/journal.pone.0192702

Ramsar Convention on Wetlands (2010) List of Ramsar sites. http://www.ramsar.org/pdf/sitelist.pdf. Accessed 11 May 2010

Robledano F, Esteve MA, Farinos P, Carreno MF, Martinez-Fernandez J (2010) Terrestrial birds as indicators of agricultural-indiced changes and associated loss in conservation values of Mediterranean wetlands. Ecol Indic 10: 274-286. https://doi.org/10.1016/j.ecolind.2009.05.006

SBAA (2010) Game and wild birds (Special Protection Areas) Order 2010. Gazette No. 1578. Sovereign Base Areas Administration, Episkopi

SBAA (2015) Protection and nanagement of nature and wildlife (Special Areas of Conservation) Order 2015. Gazette No. 1795. Sovereign Base Areas Administration, Episkopi

Seoane J, Bustamante J, Diaz-Delgado R (2004) Are existing vegetation maps adequate to predict bird distributions? Ecol Model 175:137-149. https://doi.org/10.1016/j.ecolmodel.2003.10.011

Shiu H, Lee P (2003) Assessing avian point-count duration and sample size using species accumulation functions. Zool Stud 42:357-367

Shwartz A, Shirley S, Kark S (2008) How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park? Landscape Urban Plan 84:219-229. https://doi.org/10.1016/j.landurbplan.2007.08.003

Stagoll K, Manning AD, Knight E, Fischer J, Lindenmayer DB (2010) Using bird-habitat relationships to inform urban planning. Landscape Urban Plan 98:13-25. https://doi.org/10.1016/j.landurbplan.2010.07.006

Stirnemann IA, Ikin K, Gibbons P, Blanchard W, Lindenmayer DB (2015) Measuring habitat heterogeneity reveals new insights into bird community composition. Oecologia 177:733-746. https://doi.org/10.1007/s00442-014-3134-0

Sutherland WJ, Newton I, Green RE (2004) Bird ecology and conservation, a handbook of techniques. Oxford University Press, Oxford

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79-92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Tuomisto H (2010) A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164:853-860. https://doi.org/10.1007/s00442-010-1812-0

Veech JA, Crist TO (2007) Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. Global Ecol Biogegr 16:650-656. https://doi.org/10.1111/j.1466-8238.2007.00315.x

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30:280-338. https://doi.org/10.2307/1943563

Fig. 1 Study site at Akrotiri Peninsula, Cyprus (map outline from Eurostat (2015); image from ESRI (2014)

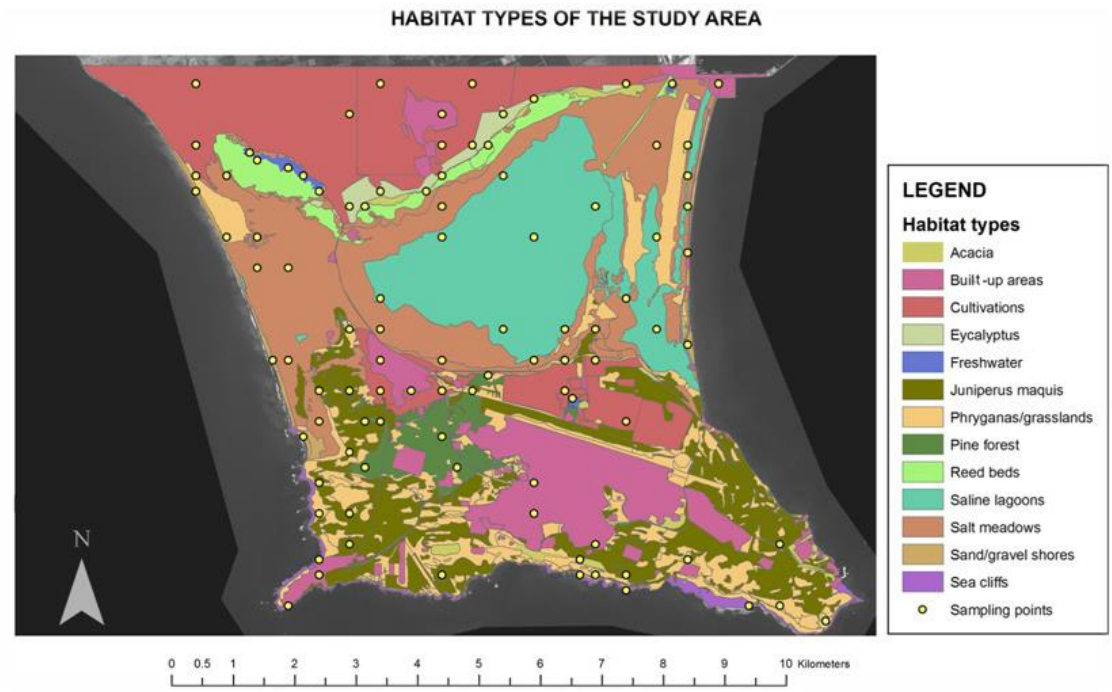
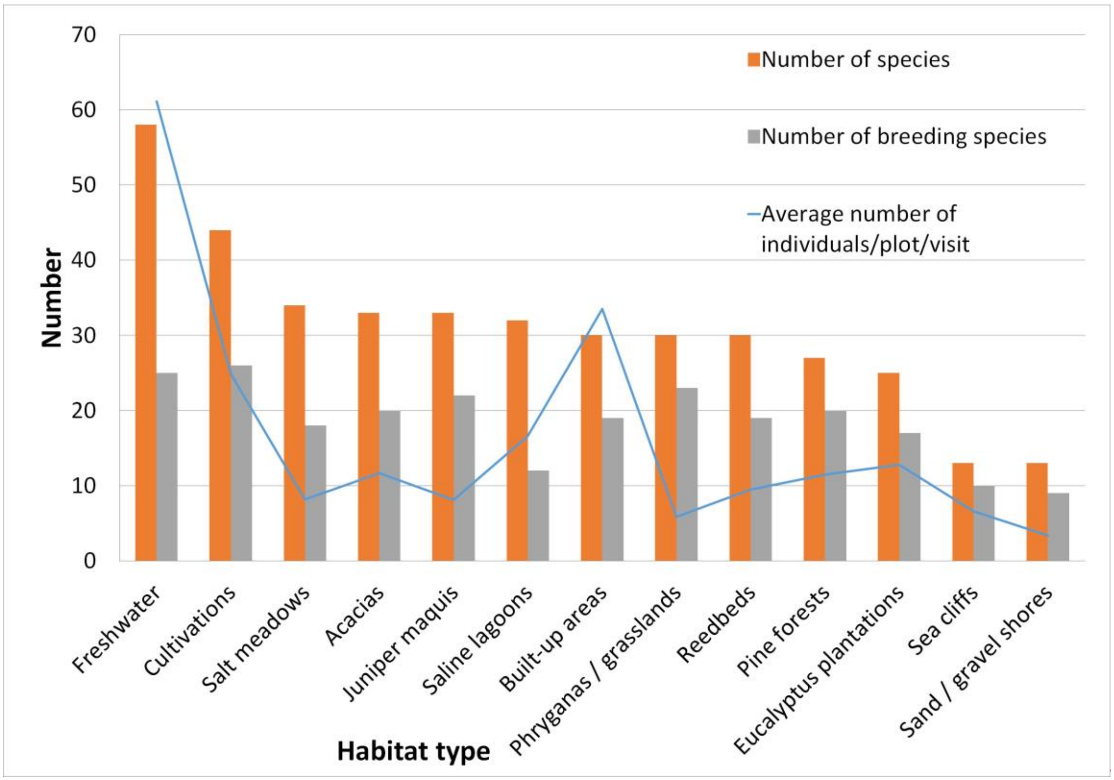


Fig. 2 Map of habitat types illustrating the location of the 97 point counts (yellow dots)



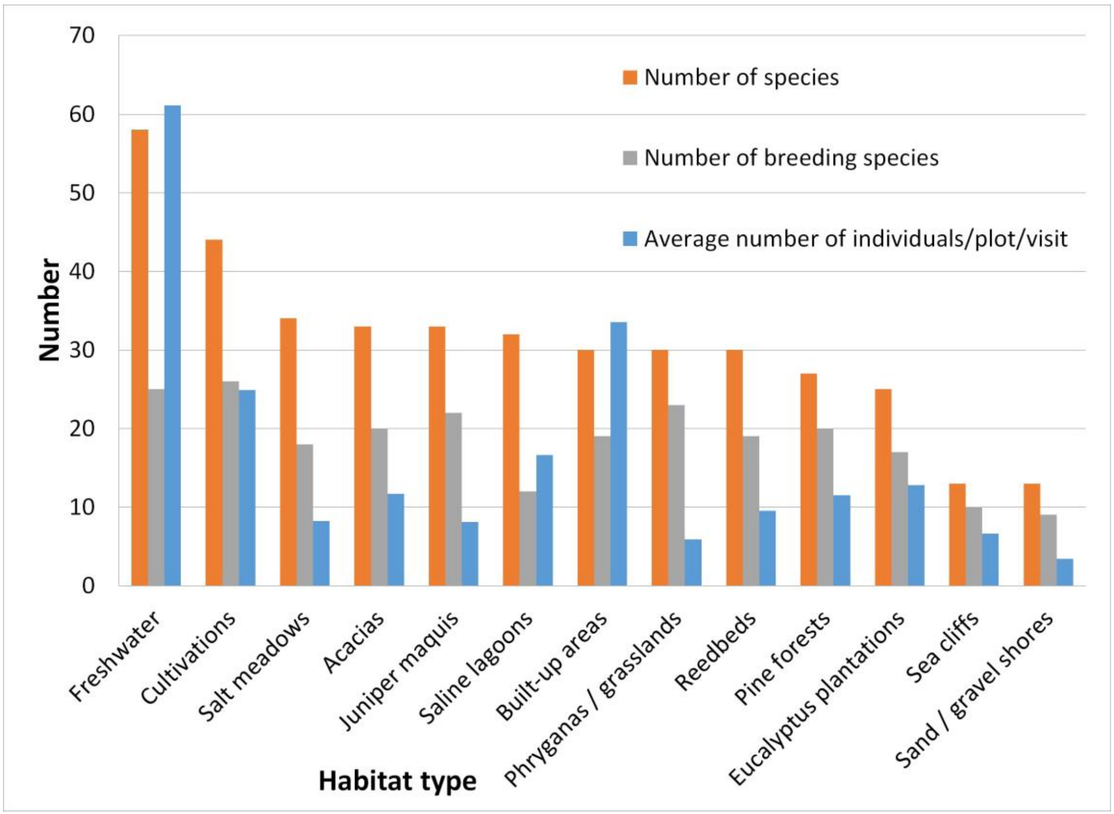


Fig. 3 Number of species overall (α-diversity), number of breeding species (resident species and migrant breeders) per habitat type, and mean number of individuals per point count per visit per habitat as an indicator of bird abundance

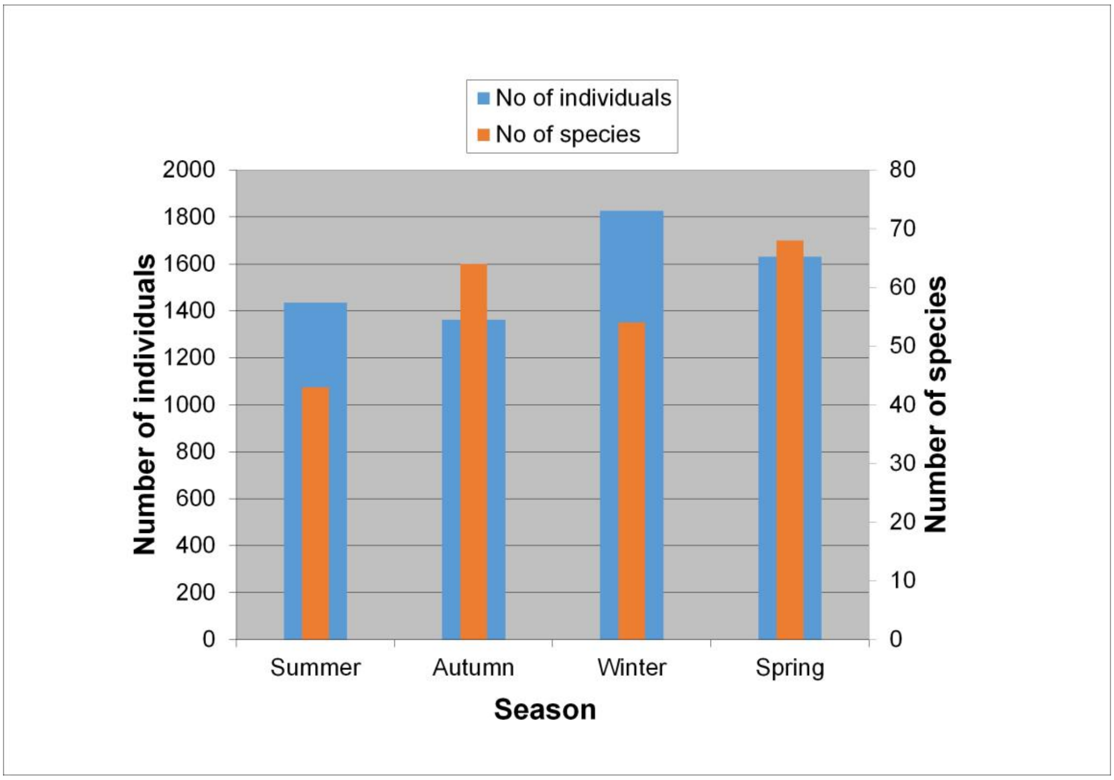


Fig. 4 Number of individuals and number of species per season showing that species richness does not imply equivalent abundance

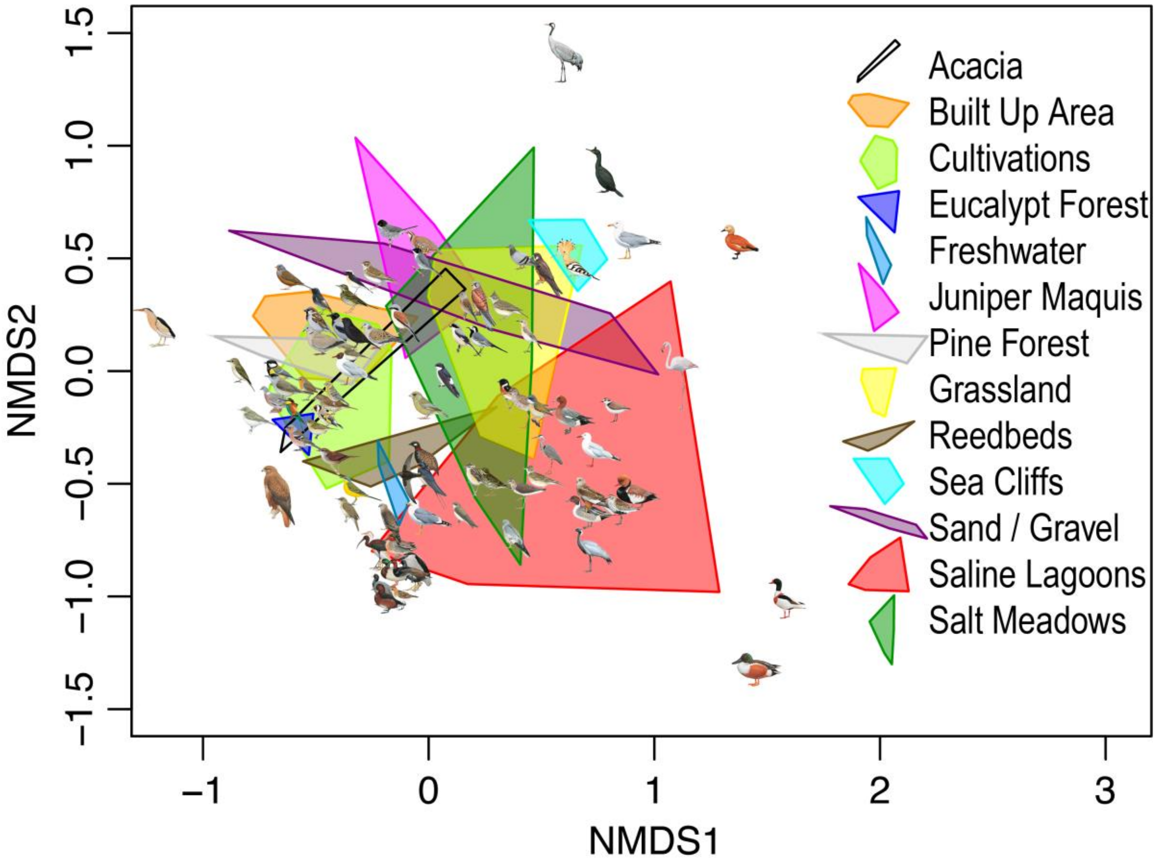


Fig. 5 NMDS ordination illustrating species associations with habitat at Akrotiri for species with 3 or more records over the study period (stress value 0.2234086). Point count numbers not shown here for illustrative purposes; see instead Fig. S11 in Online Resource 1). There is much variation among point counts within habitats as well as between habitats, while some species are associated with multiple habitats. Bird illustrations courtesy of Billerman et al. (2020), for legend see Table S2 in Online Resource 1)

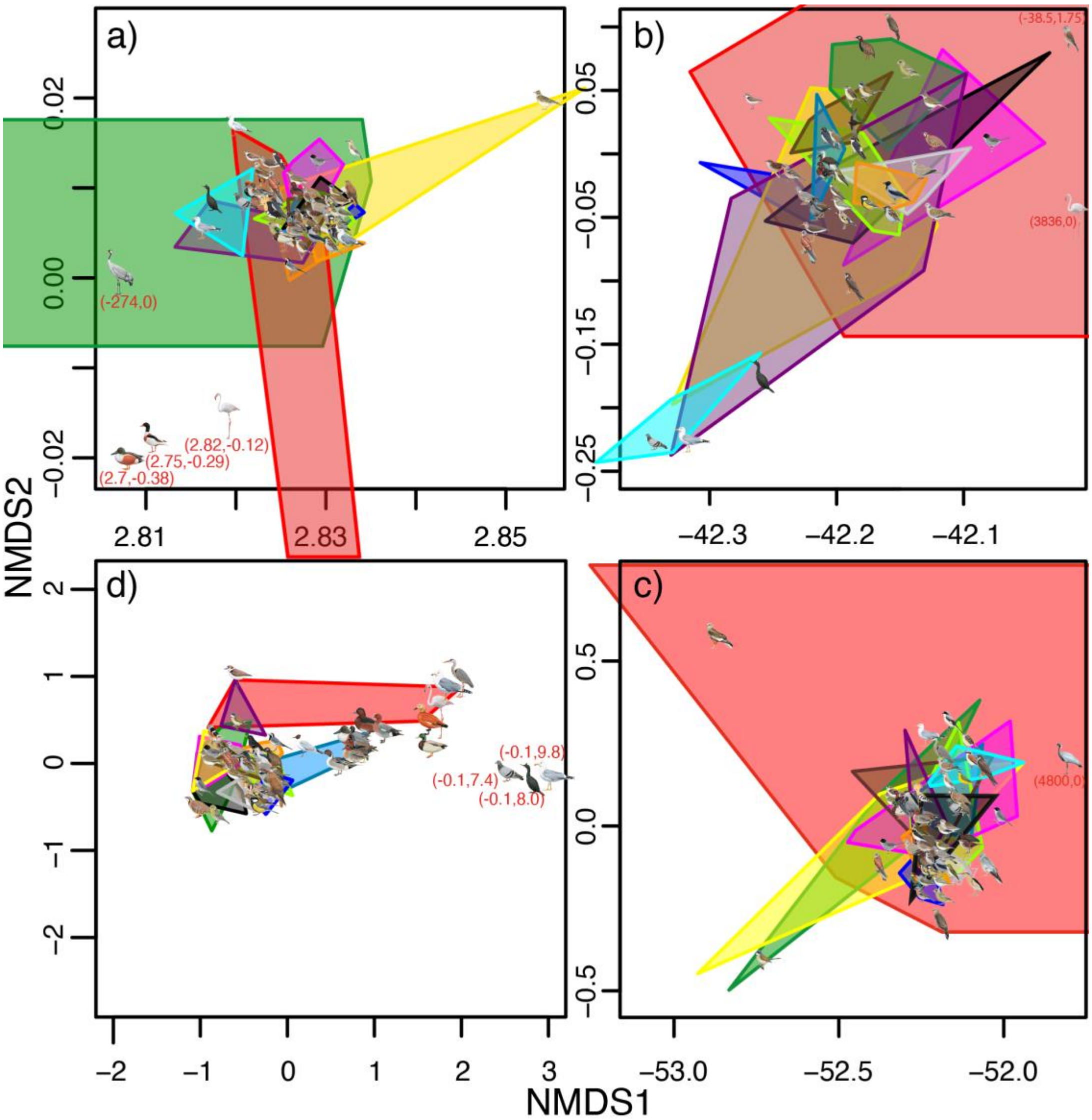


Fig. 6 NMDS ordination illustrating species associations with habitat at Akrotiri for species with 3 or more records over the study period (arranged clockwise). a) Spring: no conclusive results could be obtained from the ordination (stress value 0.0001193228). b) Summer: some species were converging towards their preferred breeding habitats (stress value 8.843405e-05). c) Autumn: there was much variation among point counts within the same habitat (stress value 7.062331e-05). d) Winter: the ordination was more explanatory compared to the other seasons, with waterbirds assembling along inundated wetlands (stress value 0.06798791. Point count numbers not shown here for illustrative purposes. Polygon shades according to legend in Fig. 5. Outliers illustrated in direction of location with

accompanying NDMS coordinates of actual position in ordination. Bird illustrations courtesy of Billerman et al. (2020), for legend see Table S2 in Online Resource 1

Table 1 Habitat types with the area of each and the number of point counts selected (1 point count every 100 hectares with a minimum of 5 points for each habitat type). Species richness and bird abundance index (mean number of individuals per point count per visit in each habitat) are also presented here to illustrate that available habitat type area is not linearly related with species richness and bird abundance

s/n	**Habitat type**	**Area (Hectares)**	**Number of point counts**	**Species richness**	**Bird abundance (Number of individuals per point count per visit)**
1.	Acacia	82	5	33	11.7
2.	Built-up areas	772	8	30	33.5
3.	Cultivations	1248	12	44	24.9
4.	Eucalyptus	87	5	25	12.8
5.	Freshwater	17	5	58	61.1
6.	Juniperus maquis	874	9	33	8.1
7.	Phryganas / grasslands	835	9	31	5.9
8.	Pine forest	178	5	27	11.5
9.	Reed beds	192	5	30	9.5
10.	Saline lagoons	1060	11	32	16.6
11.	Salt meadows	1265	13	34	8.2
12.	Sand / gravel shores	54	5	13	3.4
13.	Sea cliffs	67	5	13	6.6
	TOTAL	**6731**	**97**		

Table 2 GLMM results for the effect of habitat type and season on species richness. Species richness was highest in freshwater habitat and lowest in the coastal habitats of sea cliffs and sand / gravel shores, though all habitats except the latter two, ~~and~~ salt meadows and phryganas / grasslands had significantly higher species richness than the reference habitat, saline lagoons

	Estimate	**SE**	**z**	**P**
Intercept	0.51	0.14	3.64	< 0.001
Summer	-0.12	0.08	-1.49	0.14
Autumn	-0.09	0.08	-1.17	0.24
Winter	-0.12	0.08	-1.55	0.12
Acacia	0.82	0.20	4.13	< 0.001
Built-up	0.92	0.17	5.26	< 0.001
Cultivations	1.07	0.16	6.70	< 0.001
Eucalyptus	1.07	0.19	5.63	< 0.001
Freshwater	1.64	0.18	9.26	< 0.001
Juniperus maquis	0.69	0.18	3.95	< 0.001
Phryganas / grasslands	0.29	0.19	1.52	0.13
Pine forest	1.00	0.19	5.23	< 0.001
Reedbeds	0.96	0.19	4.99	< 0.001
Salt meadows	0.29	0.17	1.67	0.09

Sand / gravel	-0.05	0.24	-0.19	0.85
Sea cliffs	0.32	0.22	1.44	0.15

Table 3 GLMM results for the effect of habitat type and season on bird abundance. The freshwater habitat maintained the highest bird abundances, and along with built-up areas and cultivations had significantly higher abundances than saline lagoons. The lowest abundances were in sand/gravel beaches and along with grasslands were the two habitats with significantly lower abundances than saline lagoons. Abundances did not differ significantly between spring and winter, but they were lower in summer and autumn

	Estimate	**SE**	**z**	**P**
Intercept	2.32	0.21	10.80	< 0.001
Summer	-0.13	0.04	-3.52	< 0.001
Autumn	-0.18	0.04	-4.91	< 0.001
Winter	0.11	0.03	3.36	< 0.001
Acacia	0.12	0.38	0.31	0.76
Built-up	1.16	0.32	3.61	< 0.001
Cultivations	0.77	0.29	2.65	< 0.01
Eucalyptus	0.22	0.38	0.58	0.56
Freshwater	1.48	0.37	3.96	< 0.001
Juniperus maquis	-0.39	0.32	-1.22	0.22
Phryganas / grasslands	-0.69	0.32	-2.14	< 0.05
Pine forest	0.01	0.38	0.03	0.97
Reedbeds	-0.09	0.38	-0.23	0.82

Salt meadows	-0.37	0.29	-1.28	0.20
Sand / gravel	-1.28	0.40	-3.22	< 0.01
Sea cliffs	-0.59	0.38	-1.54	0.12

Table 4 Spatial clustering of individuals and species in total for all seasons, and per season, after the calculation of Moran's autocorrelation index. Species show a clustering pattern while individuals are more randomly distributed. For maps see Fig. S1 – S10 in Online Resource 1

Season / target	**Moran's index**	**z**	**P**	**Pattern Description**
All seasons / number of individuals	0.09	2.18	< 0.05	Clustered
All seasons / number of species	0.22	4.69	< 0.001	Clustered
Summer / number of individuals	0.05	1.29	0.20	Random
Summer / number of species	0.14	3.02	< 0.01	Clustered
Autumn / number of individuals	0.07	1.80	0.07	Random
Autumn / number of species	0.15	3.18	< 0.01	Clustered
Winter / number of individuals	0.04	1.12	0.27	Random
Winter / number of species	0.22	4.45	< 0.001	Clustered
Spring / number of individuals	0.10	2.20	< 0.05	Clustered
Spring / number of species	0.21	4.33	< 0.001	Clustered

Table 5 Species richness and overall abundance by status in the study area

Status	**Description**	**Number of species**	**Number of individuals**
Breeding Resident	Resident breeders that are in the area all year around, not migrating	30	4055
Migrant Breeder	Migrant breeders, which arrive in the area in spring to breed and leave in autumn	14	811
Winter visitor	Winter migrants which arrive at the area in autumn for wintering and leave in spring	37	1035
Passage Migrant	Passage migrants in autumn and/or spring	34	354
Total		**115**	**6255**