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Assessing short and long-term variations in diversity, timing and body condition of frugivorous birds

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Seed dispersal by frugivorous bird species involves a fine temporal tuning between fruiting plants and birds. However, this interaction may be severely threatened by anthropogenic climate and land-use change, which may result in phenological mismatches and pervasive ecological consequences for avian communities. In this study, we evaluate changes at long (~40 years) and short-time (seasonal) spans in an avian frugivore community using a snapshot resampling. Particularly, we focus on changes in composition, abundance, migratory timing (i.e. phenology) and physical condition in relation to variations in fruit supply. We used bird and fruit data collected during 1981–1983 and 2019–2021 in a Mediterranean scrubland site in Doñana Natural Area, SW Spain. Our findings indicate a profound transformation of species composition, bird phenology and body condition: in ~40 years, the avian community showed a 66% and 18.4% decrease of the abundance of wintering and seed-disperser species, respectively. Seasonal abundance peaks were advanced for at least one month in the 9 out of 11 frugivorous bird species included in the analyses. Avian body condition during the migratory passage has worsened, with fewer individuals showing a high-fat percentage now than in the past. Finally, we report a fruit production decrease of almost half in 2019–2021 compared to 1981–1983, probably linked to habitat encroachment by pine trees and replacement of fleshy-fruited shrubs. Vegetation encroachment and climate change are the most plausible explanations for the observed changes in the avian community, but the relative importance of these factors is yet unknown. Our results at a local scale mirror the dramatic consequences of global change affecting the diversity, phenology and physical condition of frugivorous bird species reported in multiple studies across the globe. The loss of frugivores may trigger feedback mechanisms in which seed dispersal is disrupted, leading to impaired recruitment of fruiting plants and hence less food availability for the avian community.

Keywords: avian community, avian diet, frugivory, Mediterranean, migration, phenology, seasonality, seed dispersal

Introduction

Global change drivers (such as land use change and climate change) are profoundly altering Earth's biodiversity not only in terms of species abundance or community composition, but also in the timing of organisms' life cycles, phenology and physical condition (Hansen et al. 2001, Bellard et al. 2014, Pachauri et al. 2014). Although understanding how land-use and climate change are affecting the diversity, migratory timing and body condition of avian communities has been already addressed (Zurell et al. 2018, Nowak et al. 2019), the scarcity of long-term data limits our knowledge of the extent of these impacts. This is especially relevant for frugivorous birds that feed on fruits given the ecosystem service they provide: seed dispersal. Birds are expected to respond more severely to changes in land use than to climate change, especially in the tropics (Jetz et al. 2007), given that species loss generally increases with land degradation. In addition, frugivorous bird species are shown to be less likely to occur in more intensively used habitats than insectivorous species (Newbold et al. 2013). A current challenge is to evidence the occurrence and magnitude of such changes in avian populations. When continuous monitoring has not been carried out, the resampling of historical datasets offers an alternative for testing the impact of global change, also known as snapshot resampling (Stuble et al. 2021). In this study, we test how changes in vegetation and climate have affected avian communities and their implications for seed dispersal, taking advantage of a historical dataset of plant–frugivorous birds interactions collected during 1981–1983 (Jordano 1984).

Probably the most overlooked response to global change is related to species' phenological mismatches (Kharouba and Wolkovich 2020), which occur when there is a temporal uncoupling of interacting organisms. A striking example is fruit-dependent birds and their food plants (Snow and Snow 1988), as frugivorous birds rely on fleshy fruits for acquiring the nutritional and energetic resources needed for breeding and/or building up fat reserves necessary for migration (Jordano 2014). Concurrently, plants benefit by completing their reproductive cycles by having their seeds dispersed effectively (Burns 2002, Blendinger et al. 2016). Therefore, the timing of bird arrival or fattening needs to match the timing of fruit crops ripening. Yet, global change is profoundly altering species phenology, resulting in temporal uncouplings (Visser et al. 1998, Saino et al. 2011, Nowak et al. 2019). Gaining more insight into the consequences of land-use and climate change to frugivorous species is therefore key for predicting probable shifts of the phenophases between frugivores and the fruits they rely on.

Bird species have been reported to be in decline since the 1980s; however, the trend has accelerated in the last couple of decades (Inger et al. 2015, Studds et al. 2017, IPBES 2019). One of the most reliable proxies of phenological change is bird migration, since birds show high fidelity to breeding grounds and need to tune their timing with available resources in order to succeed. As a result, migratory timing is highly susceptible to ecosystem perturbations

and changes in resource availability, which may compromise return flights to breeding grounds or the effective tracking of resources (Cuadrado 1992, Winger et al. 2019, Howard et al. 2020). There is ample evidence that birds' phenology changes due to the direct and indirect effects of global change. For example, of particular importance to migratory birds is the potential mismatch between resource availability and breeding seasons (van Schaik et al. 1993, Haest et al. 2020, Koleček et al. 2020). Nevertheless, few studies have the opportunity to test seasonal variations replicating a standardised methodology over the long-term, and this can be particularly useful in snapshot resampling when the two contrasted periods are also sampled in a replicated way within each period (Stuble et al. 2021), such that interannual 'background' fluctuations can be taken into account.

Besides phenology, global change may affect birds' physical condition. Body condition of frugivorous birds relies mainly on the availability of appropriate fruit resources (in both quantity and quality) to support the energetic demands of their life cycles. In the case of migrant species, fruit availability is critical for the timing of migration and route choice, which are related with breeding success and the probability of surviving the migratory journey (Bairlein and Gwinner 1994, Parrish 1997, Duijns et al. 2017). Concurrently, body condition changes according to fruit availability (Jordano 1988, Quintero et al. 2020, González-Varo et al. 2022). Hence, variations in body condition due to fruit availability may be used as a proxy of fitness consequences.

In this study, we aim to gain insight on how climate and land-use changes might lead to long-term changes in abundance, diversity, phenological timing and body condition of frugivorous bird assemblages. For this, we took advantage of a dataset of bird abundance and body condition sampled during 1981–1983 (Jordano 1984) in a Mediterranean sclerophyllous scrubland community and resampled using the same procedure in 2019–2021 according to a replicated snapshot resampling scheme (Stuble et al. 2021), spanning two consecutive fruiting seasons across three years.

We aimed at establishing the following:

1) Community changes in abundance, as well as species turnover in different migratory, trophic and functional avian frugivore groups.
2) Phenological changes in frugivorous bird abundance.
3) The relationship between avian frugivores body condition and fruit availability, and whether this relationship has changed between the 1981–1983 and the 2019–2021 period.

Our specific predictions are:

1) Higher mean winter temperatures alongside vegetation shifts (e.g. encroachment), whereby fleshy-fruited species are replaced by pine trees, will change avian communities, particularly decreasing migrant and frugivorous species and increasing resident and insectivorous ones.

2) We expect phenological advances in bird migration related to warmer mean winter temperatures, which likely will result in phenological uncoupling with fruit production.
3) Diminished fruit availability or phenological uncoupling between arrival time and peak fruit abundance will worsen body condition in fruit-eating bird species at both short and long-term scales.

Material and methods

Study site

The study area was located in Hato Ratón, in Doñana's Natural Area, close to Villamanrique de la Condesa, Sevilla province, southern Spain (37°10′26.4″N, 6°20′17.4″W, 11 m a.s.l.). Doñana's Natural Area (~122 500 ha) is a natural open space situated at one of Europe's most southerly points and is a common breeding and wintering area for bird species that migrate between Europe and North Africa. Its abundance of fleshy-fruited shrubs attracts a particularly high number of frugivorous bird species, each with different migratory behaviours, which makes it a prime location for this study. The site's vegetation is characterised by tall and sclerophyllous scrubland on sandy soils. Dominant plant species are fleshy fruited intermingled with pine trees (Supporting information).

The climate of the study area is typically Mediterranean, with hot, dry periods in the summer that contrast with concentrated rainy months in the spring and early autumn. Extreme rainfall events (severe drought or heavy rainfall) are also common. Average values of annual mean temperature and cumulative rainfall in 1980–1990 were 16.7°C and 547 mm respectively, whilst between 2010 and 2019, these values were 17.6°C and 497 mm (Supporting information; 1980–2020 series, data from a weather station in the Doñana Biological Reserve, 20 km from the study area). Although mean and minimum temperatures suggest a slow increasing trend, cumulative rainfall is much more variable between years and decades. It is remarkable that 1981–1983 were exceptionally dry years within the decade, with cumulative rainfall per month ~350 mm (35% lower than the mean value for the decade; Supporting information). In addition, the mean monthly minimum temperature was also the coldest in 1981–1983 from the series 1980–2020. Rainfall in 2019–2021 was about 10% lower than in the rest of the decade (Supporting information).

Data collection

Data on fruiting phenology, estimates of fleshy-fruit crop production, bird community composition, bird morphometry and body condition were collected weekly by PJ between January 1981 and October 1983 (Jordano 1984, 1985, 1987, 1988 for more details), and fortnightly between July 2019 to mid-March 2020 by CGE, JRG and IM. As we did not sample from April to June in 2019 or 2020, these months were removed from the 1981–1983 period in our analyses so that both periods were fully comparable (Supporting information). Additionally, in 2020–2021 we were only able to collect data from November to March, as a consequence of restrictions due to the COVID-19 pandemic.

Bird abundance estimates

Bird abundance was estimated using 1-km linear transects to calculate the kilometric abundance index. These were conducted 2–5 times per month. For each individual that was seen or heard, we recorded its species and the time it was seen (Jordano 1984, 1985). Bird sampling started one hour after sunrise and was carried out when weather conditions were not extreme (in absence of rain or strong wind). Censuses were conducted in 1981–1983 by PJ and in 2019–2021 by CGE and JRG, with limited samplings also by PJ. We used the census data in 2019–2021 carried out by authors PJ, CGE and JRG to test for repeatability between observers. The consistency between census estimates for abundance data carried out in 2020 by different observers was highly significantly correlated (Supporting information), indicating limited observer bias for a robust comparison between the 1981–1983 and 2019–2021 datasets.

Bird trapping

Birds were captured by mist nets deployed weekly during 1981–1983 (6–10 nets per survey day, average 10–25 mist-net m h^{-1}; Supporting information) and fortnightly in 2019–2021 (12–20 nets per survey day, average 25–50 m h^{-1}). We increased daily sampling effort in 2019–2021 to compensate for a lower sampling frequency compared to 1981–1983. Mist nets were open mostly from dawn to dusk (1981–1983, with some dawn to midday samplings, especially during summer) and dawn to midday (2019–2020) and checked at hourly intervals (Supporting information). Differences between closing times of nets across study time periods were found to only affect the number of birds captured, not the number of species identified (Supporting information). Between 1981 and 1983, the proportion of bird species captured solely after midday was 25% of the total. To avoid bias, these seven rare species were excluded from our analyses (Supporting information).

Trapped birds were collected individually in fabric bags before being identified, ringed and measured following the standard procedures of the EURING criteria (Bairlein 1995). The variables recorded were species, age, sex, type of moult, presence of brood patch, fat and muscle estimates, body mass (± 0.5 g) and tarsus length (± 0.1 mm). All measurements were taken by PJ in 1981–1983 and by JRG and CGE in 2019–2021, including also measurements by PJ on several sampling days to be used in repeatability estimates. We calculated the repeatability between ringers using Pearson's correlation coefficient between measurements (Supporting information) and the intra-class correlation coefficient using parametric bootstrapping and 5000 resamples following the procedures of Nakagawa and Schielzeth (2010) using the R package 'rptR' (Stoffel et al. 2017). We obtained a

significantly high correlation between measures performed by different ringers (r = 0.92–0.99 for all measurement variables; see analysis for tarsus in the Supporting information), and a significantly high measurement repeatability (i.e. intraclass correlation coefficient; n = 5000 resamplings) for most linear measurements of species with sufficient sample size. Nomenclature of all recorded bird species follows the IOC World Bird List (Gill et al. 2021, Supporting information).

Vegetation

Coverage of woody perennials was determined by interception of plants along 30-m linear transects (10 in 1981–1983 and 15 in 2019–2021) randomly distributed throughout the study area. Any plants intersecting the transect, or any vertical prolongation of it, were included. Then, for each individual, the distance between the furthest extent of its canopy directly above the transect line was measured. We estimated the percentage of each species' cover in relation to total transect length and calculated mean values across transects. In 1981–1983, bare ground represented 7.9% of the study area (Supporting information), whereas the rest was covered by woody species, including 16 species of fleshy-fruited shrubs and treelets (72.1%). Dominant species were fleshy-fruited *Pistacia lentiscus* and *Smilax aspera*, followed by leguminous *Ulex parviflorus*. In the 2019–2021 period, the proportion of bare ground increased up to 27.5% (72.5% of the area covered by vegetation), and there was a shift in vegetation communities. Although it is currently dominated by *P. lentiscus* (26.7%), Stone pine *Pinus pinea* is now the second most dominant species, increasing in our study area from less than 1% in the 1980s to 21.4% currently (Supporting information). The main fleshy-fruited species detected in both study periods were *Pistacia lentiscus*, *Rhamnus lycioides*, *Phillyrea angustifolia*, *Olea europaea* var. *sylvestris*, *Ruscus aculeatus*, *Pyrus bourgaeana* and *Myrtus communis*.

Fruit availability

Seasonal and annual fruit production of fleshy-fruited species was quantified by counting all fruits (ripe or unripe with size similar to its ripe stage) present across linear transects randomly distributed throughout the study area. We monitored 10 transects of 15 × 1.25 m in 1981–1983 (area: 187.5 m²) and 15 transects of 30 × 3 m in 2019–2021 (1335 m²). Fruit production censuses were carried out weekly in 1981–1983 and fortnightly in 2019–2021, with 103 and 26 sampling days per period, respectively. We calculated fruit production in several steps. First, we calculated fruit density as the number of final-size fruits in each transect divided by the sampled area (fruits m⁻²). Given the landscape changes resulting in an increase of open ground in 2019–2020 relative to 1981–1983, we expressed fruit availability referred to the woody-covered area. In this way, changes in fruit availability are interpretable in terms of changes in woody cover of fleshy-fruited species, i.e. an inter-decadal decrease in woody cover of fleshy-fruited relative to non fleshy-fruited species would result in lower supply of fleshy fruits. Finally, we calculated the mean fruit production (in fruits ha⁻¹) across all transects for each sampling period. Total fruit production in our study area was 7 592 521 fruits ha⁻¹ in 1981–1983, and 3 997 089 fruits ha⁻¹ in 2019–2021 (almost half of the 1981–1983 production). Interannual fruit production varied among periods. Fruit production and availability were very variable between the two fruiting seasons studied within each period, with much lower fruit availability in 1981–1982 than in 1982–1983 (3 423 693 fruits ha⁻¹ and 4 168 828 fruits ha⁻¹, respectively) and in 2019–2020 compared to 2020–2021 (3 421 576 fruits ha⁻¹ and 575 512 fruits ha⁻¹, respectively). Thus, variation in fruit supply within each of the two periods compared in the snapshot resampling was extensive and illustrative of the interannual variations in fruiting recorded for Mediterranean habitats (Jordano 1984). The major difference in vegetation composition causing the large decay in the fruit supply in the 2019–2021 period was the increased encroachment with stone pines, increased openness of the scrubland sites, and overall decrease in cover of fleshy-fruited species relative to the 1981–1983 vegetation physiognomy (Supporting information).

Data analyses

Bird community composition and turnover of species (beta-diversity)

We initially recorded a total of 113 species (Supporting information). We classified species according to three criteria: 1) migration type; 2) diet; and 3) ecological function. Regarding migration types, species were distinguished into four categories, with the first three belonging to migratory species: Wintering, present in October–March; Summering, present and breeding in May–September; Transient, present for only a brief period of time (e.g. trans-Saharan migrants using the area as a stopover site); and Resident, present all year round. For trophic level classification, we followed the classification of Jordano (1987) and Snow and Snow (1988) and distinguished two broad categories: frugivores sensu lato, including all species which, at least occasionally, feed on fleshy-fruits (i.e. frugivore–insectivore, granivore–frugivore, carnivore–frugivore or omnivore species); and non frugivores sensu stricto, including all other species with no recorded fruit feeding behaviour (i.e. carnivore, insectivore or granivore species; Supporting information). Functional roles were grouped as follows: seed dispersers, species that contribute to seed dispersal, frequently by regurgitation or by defecation of ingested fruits (Snow and Snow 1988); seed predators, species that feed on or damage the fruit seeds; pulp consumers, species that feed on fruit pulp and do not regularly contribute to seed dispersal; and non frugivores for the rest of species that do not feed on plant fleshy-fruits. However, in order to simplify comparisons based on functional categories, we collapsed the last three mentioned into Non seed dispersers (Supporting information).

We calculated species relative abundance (ind. km⁻¹) at the monthly basis by study period. Our initial analysis focused on abundance changes through time period was done for frugivore species (n = 35). As the sample size for some species was limited, analyses of beta-diversity turnover were performed using data of the 20 most abundant frugivorous species of each

study period detected in the bird transects (a total of 27 species). Those represented 94.6% and 86.2% of total abundance of 1981–1983 and 2019–2021, respectively (Supporting information). Species turnover was calculated between study periods for the selected species and according to the categories of migration, trophic level and functional role listed above. In addition, we also calculated species interannual turnover within each period to check whether our results were a consequence of among-year variations. Turnover calculation was based on SER ('species exchange ratio') equations as seen in Hillebrand et al. (2018), which ranges from 0 (no turnover) to 1 (all species are replaced). We used a threshold of five species for including a category in the turnover analyses, which excluded wintering birds. We gave significance to the turnover values by estimating confidence intervals in each case, based on randomisation tests (bootstrap = 5000) using the 'boot' package (Davison and Hinkley 1997, Canty and Ripley 2021).

Migration phenology

The seasonal distribution of species abundance, referred to as monthly mean individuals per km (obtained from transect data), was used to detect peaks (maximum density) and the date of the first and last recordings for each species per year. Due to limited sample size, we restricted these analyses to 11 species, from the 27 most abundant species originally selected (eight resident and three wintering species). We corrected bird abundances by the number of sampled days per period (90 days in 1981–1983 and 27 days in 2019–2021). As we did not sample from April to June in 2020, these months were removed from the comparison. To determine total monthly differences in abundance per migratory type between the two periods, we performed two Mann–Whitney tests using monthly abundances of resident and wintering frugivore species, and species identity as a pairing variable.

Body condition

Using mist-netting, we captured 2257 birds in 1981–1983 and 933 in 2019–2021, corresponding to 55 species with different migratory strategies, diet and functional roles. Mist-netting data were used for analyses of body condition, which was estimated using two different proxies: fat accumulation and residual body mass (expressed as the residuals of body mass regressed on tarsus length, González-Varo et al. 2022). Although fat accumulation is a frequently used proxy for physical condition, residual body mass measures the deficit or excess of grams when controlling for differences in body size, measured as tarsus length (Schulte-Hostedde et al. 2005, Labocha and Hayes 2012).

Fat accumulation was noted with a 0–4 scoring scale in 1981–1983 and a 0–8 scale in 2019–2021 (EURING protocol). Fat categories were used in two analyses; 1) changes in fat content of the frugivore community during three key migratory times; 2) changes in fat scores at the species level across the two timing periods.

Migratory times were classified according to Gordo (2007): Migratory passage, from July to September, when most of our migratory species make a stopover in southern Spain during intercontinental routes; Autumn passage, in October and November, as a stopover step before species' arrival to wintering destinations; and Wintering, from December to March, when just wintering and resident species remain in the study area. In order to make comparisons possible, we standardised fat estimates from both periods by converting scores into two broad qualitative categories: low fat (0–2), and medium–high fat accumulation ($\geq$ 3). We performed a generalised linear model (GLM) with all frugivorous species (migrants and residents, n = 28 species), using fat accumulation categories as response variables, year group and migratory seasons as explanatory variables (including their interaction), and a binomial error distribution. Analyses at the species level were done with data from certain species of interest (n = 13), using a generalized linear model with a Poisson error distribution, using the fat score as response variable and year group as explanatory variable, separated by species.

Residual body mass was calculated based on ordinary least squares regression standardised at the species level; positive values mean that the body mass is higher than expected according to its size ('good' body condition), whereas negative residuals mean the opposite ('bad' body condition). We selected for residual body mass analyses the 6 species for which we had more than 20 complete captures (i.e. captures for which all variables of interest were collected) for each time period: Eurasian blackcap *Sylvia atricapilla*, Sardinian warbler *Curruca melanocephala*, common blackbird *Turdus merula*, European robin *Erithacus rubecula*, European greenfinch *Chloris chloris* and song thrush *Turdus philomelos*. We tested whether residual body mass changed between study periods using a GLM fitted with a Gaussian error. This included migratory versus resident species and their interactions as predictors, and species identity as a random factor. Also, we separately tested the increase/decrease in residual body mass in bird species for which we had at least 10 values in each period. Finally, we assessed monthly variations in body condition in relation to fruit availability using a generalised additive model (GAM), with mean residual body mass of the most abundant frugivore species of our dataset. We used species identity as a random factor to test intercept variation between periods, assuming no change in the relationship between body condition and fruit availability, as there is no biological reason to consider it. Individually, we plotted LOESS regression of six frugivorous birds' weight - tarsus residuals in relation to fruit availability (fruits ha⁻¹).

All analyses were performed in R ver. 4.1.1 (<www.r-project.org>).

Results

Community composition, bird abundance and species turnover across periods

Beta-turnover (species replacement accounting for change in abundance) of the 20 most abundant species of each

period censused with the transects was 0.24 (Table 1, see the Supporting information for a complete list of species), i.e. almost a quarter of species in our study area were exchanged. Losses of species almost doubled the number of gains when we included all the migration categories (wintering, resident, summering and transient, Supporting information). We detected reduced abundances in 2019–2021 relative to 1981–1983 for 12 out of 27 species, especially among wintering birds (Fig. 1) .

We found that the abundance of resident bird species increased from 1981–1983 to 2019–2021 for approximately 60% of species (Fig. 1, Supporting information), whilst the turnover value of 0.33 between study periods illustrated a remarkable species' loss. In turn, we found that the relative abundance of the four main wintering bird species had fallen almost two thirds (66%) between 1981–1983 and 2019–2021 (Table 1, Supporting information). The proportional abundance of frugivores and non-frugivores showed practically no change between study periods (Supporting information), but both groups had gone through a considerable species turnover, with a significant species turnover value for frugivores (0.22). Regarding species' functional groups, birds acting as seed dispersers (SD) have also experienced a decrease in their relative abundance from 75% to 62% between 1981–1983 and 2019–2021, respectively (Fig. 1, Supporting information), with a beta-turnover value of 0.20, and 20 species out of 28 seed dispersers (Fig. 1) showing decreases in abundance in 2019–2021, a significant trend towards consistent decreases across species (binomial test, p = 0.01). Overall, 21 frugivore species out of 32 showed lower abundance in 2019–2021 (Fig. 1) for the comparison of the snapshot resampling, a significantly consistent trend (more decreasing trends among frugivore species than randomly expected; binomial test, p = 0.05). Particularly, some strict frugivorous like *Turdus viscivorus*, *Turdus iliacus* and *Curruca cantillans* practically disappeared from the 2019–2021 censuses, whilst *Curruca melanocephala* is the only seed-disperser species that has greatly increased its abundance, surely due to the change towards a more forested vegetation.

The turnover values between the two periods being contrasted with the snapshot resampling (1981–1983 versus 2019–2021 contrast, Table 1) were above those for the comparisons between different years within the same period (Supporting information). This indicates a magnitude of interdecadal change above the expectations based on interannual variations.

Phenological variation in bird abundances

We identified a shift towards earlier peak abundances in 9 of the 11 frugivorous bird species we analysed (Supporting information). These shifts mean that abundance peaks nowadays consistently occur at least one month earlier than in 1981–1983 (Fig. 2) and significantly deviate towards earlier peaks from a random expectation of seasonal abundance fluctuations (binomial test, p = 0.03); a pattern that was maintained for both the eight resident species (*C. melanocephala, C. undata, C. chloris, C. cooki, P. major, S. rubicola, S. unicolor* and *T. merula*) and one wintering species (*T. philomelos*). Phenological shifts were particularly stark for *C. melanocephala, C. chloris, P. major* and *S. unicolor*, which not only had earlier abundance peaks in 2019–2021 compared with 1981–1983, but also nearly doubled their abundances during these peaks (Fig. 2).

With respect to functional types, 10 out of the 11 mentioned frugivorous species are also legitimate seed dispersers, except for *C. chloris*, which is a seed predator (Supporting information). Therefore, phenological advancements were generalized among all frugivorous species (Fig. 2).

When grouping the phenological data of all recorded species into migratory categories (resident, wintering, summering and transient), we also observed an overall peak advancement in both resident and wintering species' groups (Supporting information). This advancement is seen for both individual species and migratory group's levels. The summering and transient species' groups were not large enough to elucidate consistent changes. For frugivorous species, Mann–Whitney tests revealed that monthly abundances significantly differed between study periods in resident (p ≪ 0.01) and wintering groups (p < 0.05), with a generalized trend for decreased abundances in 2019–2021 (Fig. 1).

Table 1. Species turnover values of different categories (Group) classified according to three criteria (Type). n = number of species included in each group. Turnover represents abundance-based species-exchange ratio (SERa) in 2019–2021 versus 1981–1983, with values ranging from 0 (no change) to 1 (all species replaced). Significant turnover values are marked in bold. '95% percentile CI', confidence interval values based on 5000 bootstrap replicates (95% percentiles). Turnover values not included within the randomised CI range are considered significant. Transient and summering species were excluded from the migratory category because they were not sampled in 2019–2021. * Wintering species were abundant but did not reach the 5 species per study period needed to calculate turnover.

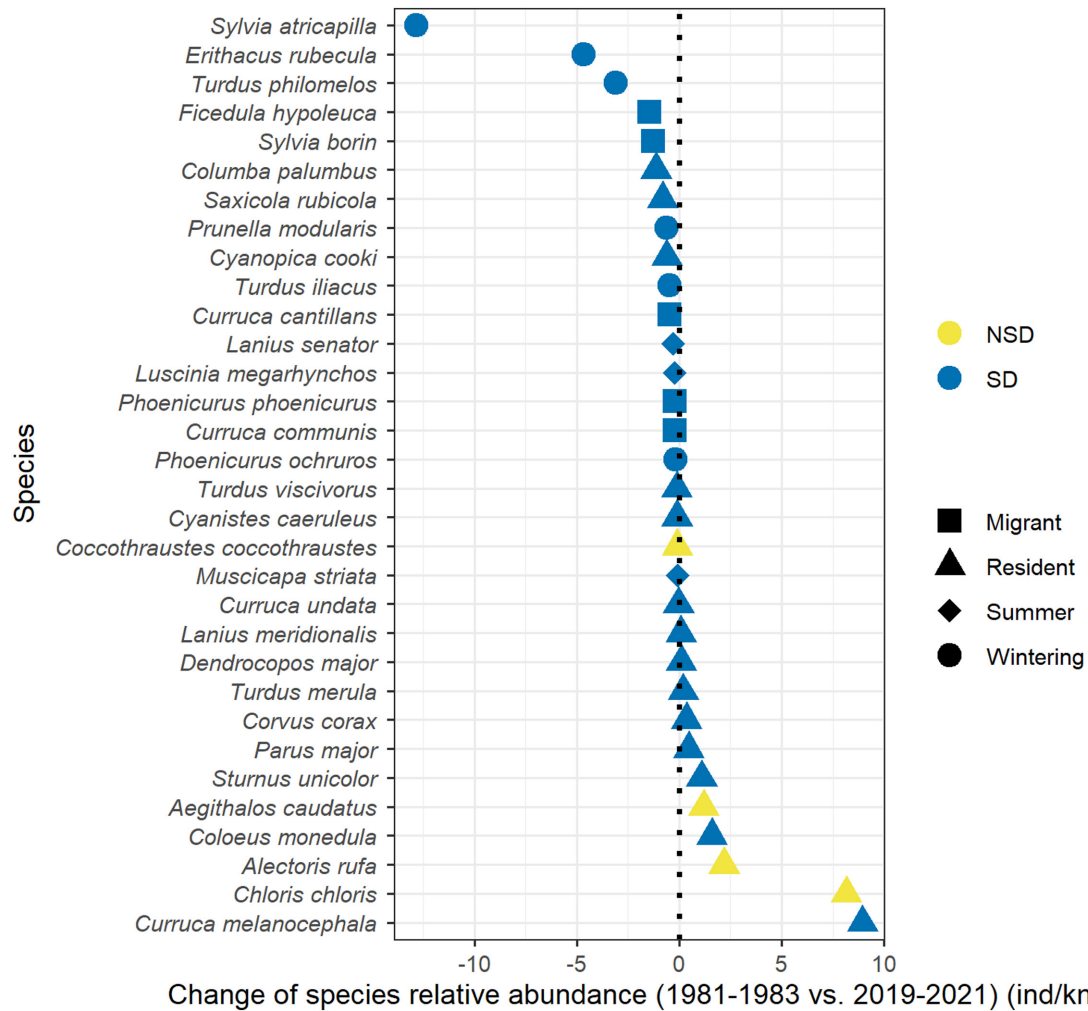| Type	Group	n	Turnover	95% percentile CI
–	All	27	**0.24**	0.55–0.91
Migratory behaviour	Resident	20	**0.33**	0.49–0.93
	Wintering*	4	–	–
Trophic	Frugivores	17	**0.22**	0.50–0.90
	Non-frugivores	10	0.55	0.18–0.99
Functional	Seed dispersers	17	**0.20**	0.47–0.93
	Non-dispersers	10	**0.36**	0.37–0.93

Figure 1. Species abundance change (ind. km⁻¹) between time periods, obtained from the difference in mean abundances in each time period (n = 32). Negative values mean a higher abundance in 1981–1983 (indicating a decrease in the inter-decadal comparison), whilst positive values mean more recorded individuals during 2019–2021 censuses (increase). 21 out of 32 frugivore species showed a decreased abundance, more than expected randomly (binomial test, p = 0.05). Additionally, seed-disperser species also showed more negative shifts than expected (20 of 28 seed-dispersers, p = 0.01). Point shapes correspond to migratory categories, while colours distinguish between seed disperser (SD, n = 28) and non-seed disperser birds (NSD, n = 4).

Temporal changes in body condition

Body fat accumulation of birds trapped in mist nets varied significantly between study periods and within migratory seasons (Table 2A). Birds with a low accumulation of body fat represented more than 65% of captured individuals in each period, whilst birds with medium-high fat accumulation accounted for less than a third of captures in each period (Supporting information). We found two different patterns among year groups: in 1981–1983, the frequency of medium-high fat accumulation in individuals peaked at the migratory passage, whilst in 2019–2021 it peaked at the autumn passage. Individuals with low fat accumulation were detected at similar frequencies across migratory seasons, whilst those with medium-high fat reserves were fewer in 2019–2021, especially during the migratory passage season. We should note that rapid fat accumulation particularly takes place during migration, being greater in migrant individuals than in resident or wintering species. Therefore, observing fewer individuals with medium-high fat accumulation may be either due to an increase in detection of wintering and resident populations in the area, or because migratory birds did not use it as a stopover as much in 1981–1983. Moreover, when analysing changes in fat accumulation at the species level (Fig. 3), we detected reduced fat accumulation in 8 out of 13 species, but no significant increases for any species. Additionally, whilst we detected no significant changes in fat accumulation for summering, transient or wintering species, all resident species accumulated less fat in the 2019–2021 period.

We obtained significant differences in body condition among study periods but not among migratory categories, with the interaction between these factors also being significant (Table 2B). In concordance, we recorded more individuals with a good body condition in 1981–1983 than in 2019–2021,

(A) Resident species' monthly abundances

(B) Wintering species' monthly abundances
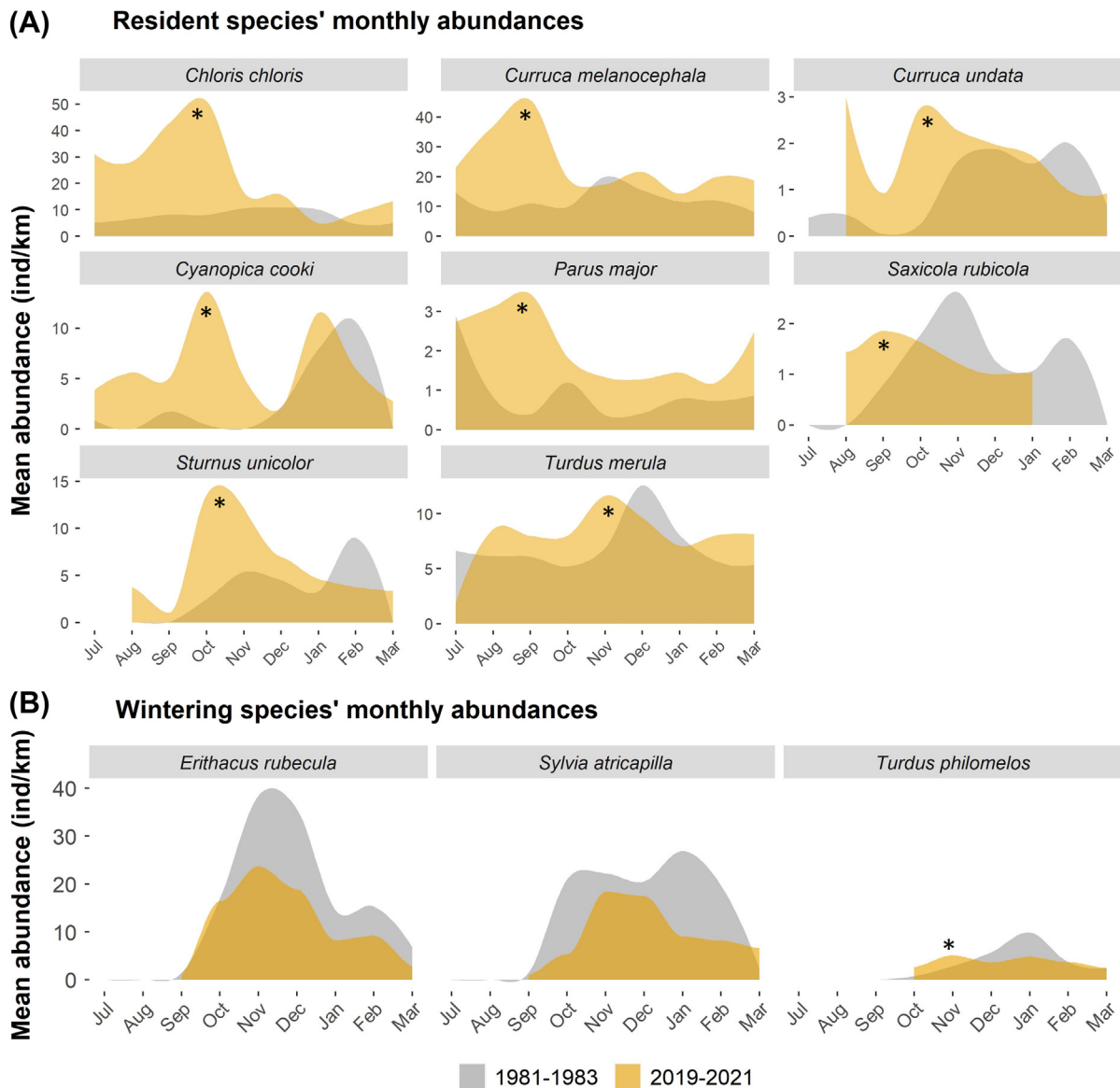
■ 1981–1983 ■ 2019–2021

Figure 2. Monthly densities, expressed as individuals per km, of the different resident (A) and wintering (B) species recorded in each study census. Only frugivorous species were included (n = 11). Species' monthly densities of the 1981–1983 period are plotted in grey, whilst the 2019–2021 records in orange. Black asterisks mark the abundance peaks in 2019–2021.

with a slightly higher median value (Fig. 4A). Furthermore, over a seasonal scale (Fig. 4B), body condition was lower in 7 out of 8 study months in 2019–2021 (August–March, excluding September) when compared to the same months in 1981–1983. This supports a consistent shift towards reduced general body condition throughout the year in Hato Ratón's 2019–2021 avian community (binomial test, p = 0.004). At the species level, we identified that 5 out of 6 species presented a decrease in mean body condition, although the change was especially pronounced for *T. merula*, *S. atricapilla*, *C. melanocephala* and *C. chloris* (Fig. 4C). Only *Erithacus rubecula* showed a body condition that was marginally better in 2019–2020 compared with 1981–1983, meaning that a higher proportion of residuals were above 0 in this particular species.

Both study periods strongly contrasted in fruit production, being approximately twice as high in 1981–1983 than in 2019–2021. By associating birds' body condition with fruit production, we found a generally worse body condition in 2019–2021 across the main frugivorous species (Fig. 5). Unusually, despite finding a positive relationship, residual body mass did not increase linearly with fruit density over the two seasons in each period (Fig. 5). Although we could detect an increase in body condition at fruit production levels above 4 log(fruit ha⁻¹), it decreased at the highest fruit density levels in both time series from 6 to 7.5 log(fruit ha⁻¹). Finally, with regards to individual species regression analysis, we found a neutral response in the five selected species (Supporting information).

Table 2. (A) Generalised linear model (GLM) using a binomial error distribution; qualitative fat categories (low fat and high–medium fat) as a response variable; and year group (1981–1983 or 2019–2021) and migratory season (migratory pass, autumn passage and wintering) as explanatory variables. (B) GLM using a Gaussian error distribution; residual body mass (weight/tarsus length residuals) as response variable; year group and migratory category (resident, wintering, summering and transient) as explanatory variables; and species identity as a random factor. Significant p-values are coloured in bold. The significance codes are: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

(A) Binomial GLM

Response: fat accumulation	Estimate	SE	z-value	Pr (> |z|)
(Intercept)	−1.587	0.097	−16.297	**< 10^{-16}*****
Year group	0.237	0.152	1.556	0.12
Migratory pass	0.915	0.142	6.453	**< 10^{-10}*****
Wintering	−0.183	0.153	−1.193	0.233
Year group: Migratory pass	−1.762	0.380	−4.629	**< 10^{-6}*****
Year group: Wintering	−0.050	0.227	−0.221	0.825

(B) Gaussian GLM

Response: weight ~ tarsus residuals	Estimate	SE	t value	Pr (> |t|)
(Intercept)	0.558	0.183	3.049	**0.002****
Year group	−1.077	0.254	−4.237	**< 10^{-5}*****
Migratory category	−0.350	0.253	−1.384	0.167
Year group: Migratory category	0.750	0.335	2.236	**0.026***

Discussion

In this study, we explored bird community changes between two time periods separated by 40 years (1981–1983 versus 2019–2021) using snapshot resampling (Stuble et al. 2021). We aimed to test whether frugivorous birds showed significant changes over these two time periods in diversity, phenology and body condition. Our results are appropriately controlled by using within-period resampling and repeatability across observers. They indicate that the frugivorous avian community has been markedly altered in terms of diversity, timing and body condition, which could entail long-lasting consequences for seed dispersal services and biodiversity conservation. Moreover, the magnitude of changes in most variables we compared was much larger when comparing between periods (1981–1983 versus 2019–2021) than within each period.

Bird community composition

We have observed a remarkable transformation in Hato Ratón's frugivorous bird community composition and beta-diversity, with a quarter of the main species being replaced from 1981 to 1983. We found fewer frugivorous and seed-disperser bird species. That said, a few resident species (such

as *Chloris chloris* or *Curruca melanocephala*) were more abundant in 2019–2021 than before, likely due to shifts in the area towards a more forested vegetation. Along with losses of frugivorous and seed-dispersers, we also recorded fewer migrant species in 2019–2021, as well as a lower abundance of individuals per species, showing a decrease of 66% among the wintering species. However, we could not test species turnover in this group, and recorded few transient species in 2019–2021. As migrant birds are likely to encounter adverse conditions at several points during their migratory routes (Wilcove and Terborgh 1984), it is difficult to discern the most significant causes of their population decline. Population shifts in European migratory species have been found to be strongly related to climatic conditions in their breeding and wintering grounds (such as our study area) as well as in their provenance areas. For instance, Tellería (2015) studied changes in robin populations' abundance in another area of southern Spain over 15 years. He found that abundance variations were not associated with changes in vegetation structure or fruit production, but rather provided evidence for the changing role of the Mediterranean region as a wintering ground. Additionally, these shifts are likely to be strongly related to climate change (Bellard et al. 2014, Howard et al. 2020). A warmer climate in northern areas could provide enough resources and a more suitable environment for breeding or even wintering, reducing the need for long-distance flights to find southern breeding areas. Therefore, as species may have started breeding at increasingly higher latitudes, their influx may be reduced in our study area. Moreover, as species differ in their capability to track resources in shifting climatic conditions, the more dispersive taxa could be the most capable of returning to traditional breeding areas (Socolar et al. 2016). Our results are consistent with these interpretations, yet broader-scale data from the Mediterranean Basin would be necessary to test the consistency of these trends across different areas.

Vegetation change in our study area likely has an additive effect to climate change, resulting in shifts in the avian community composition. We detected a considerable increase in forest cover, taller vegetation physiognomies, and a reduction in the cover of fleshy-fruited species. This transformed our study area from a low-medium height, shrub-dominated area in 1981–1983, to an area with a larger abundance of pines and a sparser understory at present. Such a transformation of Hato Ratón's vegetation could directly affect the habitat selection of its migratory species, as they are commonly found to prefer wide, open spaces in edge-type areas, in which scrublands with fleshy-fruited species dominate (Zamora et al. 2010). As a result, the spatial distribution of vegetation alongside changes in plant community structure (particularly concerning the abundance decrease of fleshy-fruited plant species) may explain our reduced detection of migrant birds. Furthermore, we cannot discount the profound transformation that Doñana's Natural Area has experienced over the last decades. This is mainly a consequence of anthropogenic changes, such as more intensive agricultural practices, or modification of waterways (Haberl et al. 2009), all of which are
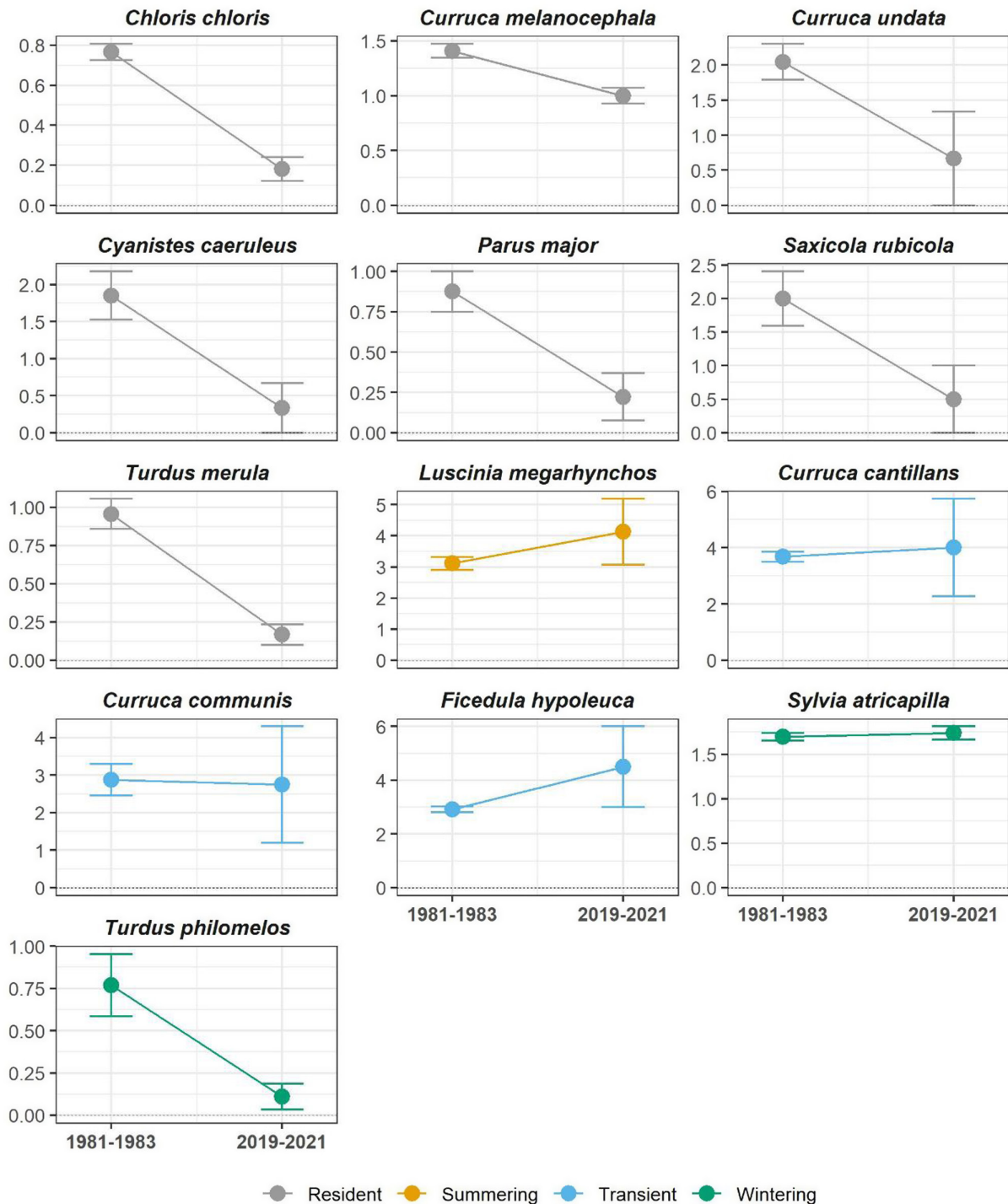
Fat accumulation (species level)

Figure 3. Mean (dot) and standard error (whiskers) values of fat accumulation score for bird species (n = 13) sampled in the two study periods (1981–1983 and 2019–2021). Fat score values were re-scaled and range from 0 to 8.

exacerbated by climatic trends towards higher temperatures and less predictable precipitation (Giorgi and Lionello 2008).

A final explanation for the observed decrease in migrant species could be the simultaneous increase in resident species' populations. Because of area transformation, available resources may not be sufficient to support an avian community as large as in the 1980s. Resident species may therefore prove to be superior competitors, by choosing the best feeding areas before migrant species arrive. For instance, De La Hera et al. (2018) found that *Erithacus rubecula*'s resident
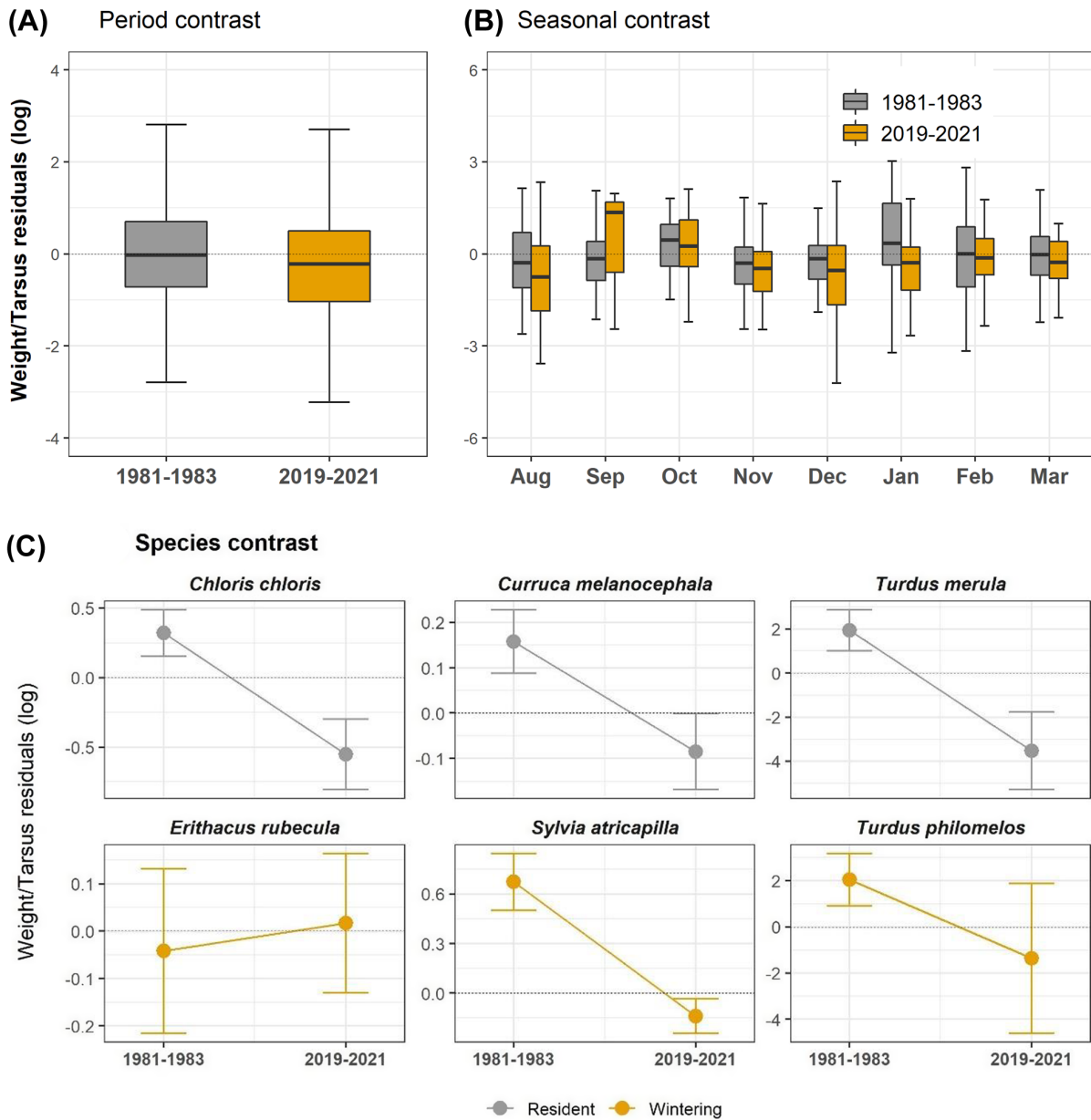
Figure 4. Residual body mass for each species (log values), estimated by the residuals of weight versus tarsus length regressions. (A) changes between study periods, (B) study months and (C) at species level (A and B: n = 27; C: n = 6). Grey dotted lines separate positive ('good' body condition) and negative residuals ('poor' body condition).

populations in southern Spain tend to occupy woodlands, unlike their migrant conspecifics, which usually occupy scrublands. This behaviour is likely to play a role in the development of local adaptations for different habitats within the Mediterranean breeding grounds. Similarly, resident individuals of *Sylvia atricapilla* in southern Spain are larger in body size and tend to be more abundant in forests (Pérez-Tris and Tellería 2002), suggesting a behavioural advantage over their migrant conspecifics. Overall, vegetation shifts in the area towards greater arboreal cover and decline of fleshy-fruited species cover, appear to have favoured a reduced representation of migrants when compared with the resident taxa.

The reduction of legitimate seed-disperser species associated with migrant bird declines could have a major impact on ecosystem function and services (Inger et al. 2015). Since interactions are often lost well before species completely disappear (Valiente-Banuet et al. 2015), a reduction in seed dispersers may already impact ecosystem functioning, with potential ramifications for seed dispersal success and, therefore, direct consequences for the recruitment of fleshy-fruited species and plant community composition. Due to the progressive disappearance of seed dispersers, plant species whose reproduction relies upon them may become less abundant as a result of pervasive seed dispersal limitation.
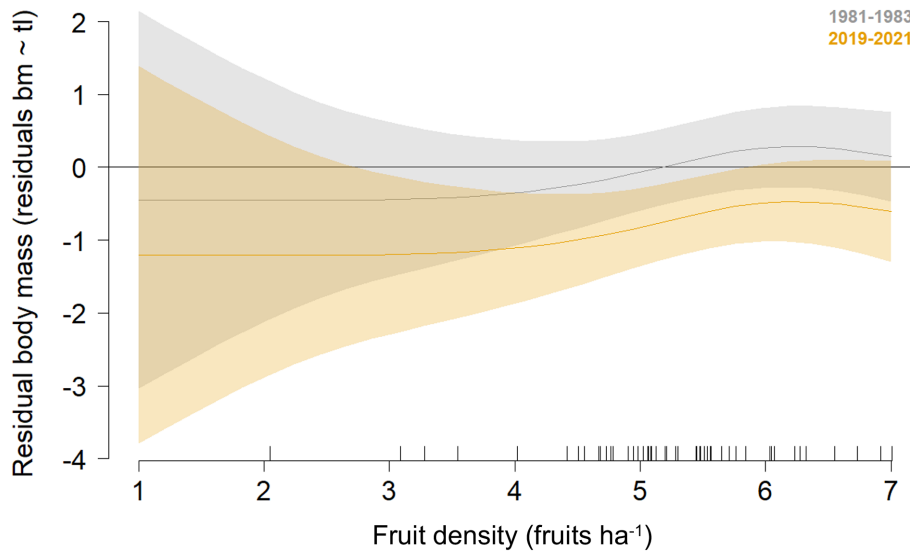
Figure 5. GAM regression of residual body mass (mean residuals weight ~ tarsus) of the different frugivorous species in relation to fruit density (fruits/hectare), all values are logarithmic.

This may eventually favour other species that use abiotic seed dispersal, resulting in a change in plant composition (Gardner et al. 2019). We may have detected this effect in the huge expansion of *Pinus pinea* conifer in our study plots, although this hypothesis warrants further investigation. If this shift is maintained over the coming years, our study area will become increasingly homogeneous, leading to a reorganisation of the avian community and the fleshy-fruited plants that depend upon it.

Bird phenology

At a seasonal scale, we found consistent shifts among seasonal abundance distributions in resident and wintering species. We identified advanced shifts in 9 out of 11 species, with no single species showing a phenological delay when comparing 1981–1983 to 2019–2021. Such results significantly deviate from an expectation of random seasonal fluctuations among species. As these advancements have been detected both in resident and wintering migratory species, our findings may indicate a significant shift towards earlier abundance peaks among frugivorous bird species, though this should be verified at broader geographic and taxonomic scales.

Migratory behaviour has been widely attributed as a resource tracking mechanism of birds with enough phenotypic plasticity to adapt their timing to shifting food-resource peaks (van Schaik et al. 1993, Haest et al. 2020). Whilst plant-feeding species are able to match earlier plant production, birds with an insectivorous diet apparently do not experience phase advancements on the same scale (Butler 2003). Nevertheless, a complex set of factors could ultimately drive avian phenological advancement. For example, adverse climatic conditions in departure areas or migratory routes could affect arrival dates, forcing bird species to increase the number or duration of stopovers during their journey (Gordo

2007). This specific question would require broader spatial and temporal sampling to be adequately addressed.

The wide temporal gap between our sampled decadal periods (1981–1983 versus 2019–2021) means our results cannot be interpreted as long-term trends due to the lack of regular, continuous sampling on an annual basis. In this study, we have instead used this 'snapshot resampling' approach, which is a resampling of historically sampled sites. Ever more frequently used, this method has recently proved reliable as an indicator of global-change impacts and it is more accurate for community-level metrics (e.g. species richness) than for population-level metrics related to a single species (e.g. abundance, Stuble et al. 2021). The most important factor to control for in this method is the inter-annual variability occurring within each of the periods so that spurious variation can be discerned from long-term changes. Our results show lower inter-annual variance within each study period, when compared to the magnitude of the inter-decadal changes among periods. This provides support for the long-term changes we describe. However, we are currently unable to discern whether observed changes in seasonal abundances and distributions are a result of continent-wide shifts due to climate change (Tellería 2015) or instead, are a result of local changes in vegetation, and fruit availability. Although our results are concordant with previous studies that show migrant species are arriving to their wintering grounds earlier as a response to increased temperatures (Butler 2003, Haest et al. 2020, Koleček et al. 2020), our limited temporal sampling precludes us to assert that these advances are consistent trends over time.

Over the decades, increased temperatures may have led to earlier annual fruit production (Gallinat et al. 2015), which is likely to create a pressure for advancement in annual cycles for resident frugivorous species. Earlier reproduction and breeding times seem necessary to best match juvenile

fattening with food availability and support the shifts in abundance peaks that we detected. However, as the ability of species to locally adapt to a changing environment is limited, if the current drivers of biodiversity loss continue, either plant or bird species could reach a limit for their response potential (Foden et al. 2013). This may mean that birds' food resources become limited at crucial moments of their life cycles. If their fattening is compromised, their abundances may decrease rapidly (Blendinger et al. 2015), which would certainly impair the dispersal success of fleshy-fruited plant species. In this scenario, a plant community change will likely occur, as may already be underway in our study plots.

Fat accumulation and body condition index

We identified significant seasonal variation in bird fat accumulation across months and study periods. Birds with low fat accumulation were most common in both sample periods (approx. 75% of recorded individuals). Observations of individuals with medium and high body fat accumulation differed between periods, being less common in the three migratory seasons between 2019 and 2021 relative to birds sampled in 1981–1983. Additionally, in the most recent period, individuals with higher fat reserves became more common in the cooler autumn months (October–November) than in the summer months (July–September) when they had previously peaked. This lower fat accumulation corroborates our findings in body condition index (weight ~ tarsus residuals), showing a quantifiable worsening at decadal, seasonal and species levels. It is concerning that we detected poorer body conditions in the months when migrant species should have already acquired their energetic needs. Feeding on insects is key to gaining sufficient body mass in birds (Bairlein and Gwinner 1994). When insect abundance (and therefore protein availability) is limited in spring or autumn, some migrant species tend to compensate by switching to a more frugivorous diet (Carnicer et al. 2009, Aamidor et al. 2011). Fruit availability generally determines a switch to a more frugivorous diet. However, it also depends on the nutritional content and size of fruit available (Jordano 1988, Blendinger et al. 2015). If the availability of fruits is drastically reduced, functions like migratory activity, breeding or moult (Bairlein and Gwinner 1994) may be severely compromised, affecting migratory and reproductive success.

Similar to the observed decline in migratory species' body condition, we also detected inferior general body condition in resident bird species. This is especially apparent in the case of resident *T. merula*, whose widely decreased body condition in 2019–2020 supports the idea that fruit availability is the main cause of our results. Even though fruit production in 1981–1983 was exceptionally high, particularly in the 1982–1983 season (4 168 828 fruits ha^{-1}), the decline of fleshy-fruited species present in our area (from 72% to 51% of vegetation cover), increased cover of pines and reduction of woody cover, is likely the main cause of this shift. We must consider that, in such a seasonal habitat as our study area, a temporal mismatch between bird species and fruit supply may occur in the near future, becoming exacerbated if global change drivers continue their expansion.

Concluding remarks

In our Hato Ratón study site, the local bird assemblage has experienced major changes in recent decades that affect almost every aspect of their life cycles, including population dynamics, migratory and feeding behaviour, and body condition. Although birds are showing plastic responses to environmental changes, this is unlikely to be sufficient, and the signs of decline are increasingly evident. As bird species are globally widespread and diverse, identifying the most prominent causes for their changes in abundance is a complex task. Here we show evidence of the decline of seed-disperser birds in a 40 year period, which may trigger negative feedback mechanism in which seed dispersal is disrupted. This could lead to impaired seed dissemination and limited recruitment of fleshy-fruited plants; less food availability for the avian community; and an acceleration of frugivore decline. There is still time for appropriate vegetation management actions to be implemented, since the ecological services of seed dispersers can be effectively restored when thresholds of disturbance have not yet been reached (e.g. fleshy-fruited shrubland restoration after fires, Zamora et al. 2010). Such necessary actions are technically feasible and require favouring the restoration of the Mediterranean's lowland scrubland vegetation and species composition whose dominant species are fleshy-fruited and frugivore-dependent.

Author contributions

Maria Campo-Celada: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Pedro Jordano**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation

(equal); Methodology (lead); Resources (equal); Software (equal); Supervision (lead); Writing – review and editing (lead). **Ana Benítez-López**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Software (equal); Supervision (equal); Writing – review and editing (equal). **Carlos Gutiérrez Expósito**: Data curation (equal); Investigation (equal); Methodology (lead); Writing – review and editing (equal). **Julio Rabadán-González**: Data curation (lead); Investigation (equal); Methodology (lead); Validation (equal); Writing – review and editing (equal). **Irene Mendoza**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (lead); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p2ngf1vrt> (Campo-Celada et al. 2021).

Supporting information

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

References

Aamidor, S. E. et al. 2011. During stopover, migrating blackcaps adjust behavior and intake of food depending on the content of protein in their diets. – Integr. Comp. Biol. 51: 385–393.

Bairlein, F. 1995. Manual of field methods: European–African songbird migration network. – European Science Foundation.

Bairlein, F. and Gwinner, E. 1994. Nutritional mechanisms and temporal control of migratory energy accumulation in birds. – Annu. Rev. Nutr. 14: 187–215.

Bellard, C. et al. 2014. Vulnerability of biodiversity hotspots to global change. – Global Ecol. Biogeogr. 23: 1376–1386.

Blendinger, P. G. et al. 2015. Nutrients in fruits as determinants of resource tracking by birds. – Ibis 157: 480–495.

Blendinger, P. G. et al. 2016. Fruit selection by Andean forest birds: influence of fruit functional traits and their temporal variation. – Biotropica 48: 677–686.

Burns, K. C. 2002. Seed dispersal facilitation and geographic consistency in bird-fruit abundance patterns. – Global Ecol. Biogeogr. 11: 253–259.

Butler, C. J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. – Ibis 145: 484–495.

Campo-Celada, M. et al. 2021. Data from: Assessing short and long-term variations in diversity, timing and body condition of frugivorous birds. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.p2ngf1vrt>.

Canty, A. and Ripley, B. 2021. boot: bootstrap R (S-plus) functions. – <https://cran.r-project.org/web/packages/boot/index.html>.

Carnicer, J. et al. 2009. The temporal dynamics of resource use by frugivorous birds: a network approach. – Ecology 90: 1958–1970.

Cuadrado, M. 1992. Year to year recurrence and site-fidelity of blackcaps *Sylvia atricapilla* and robins *Erithacus rubecula* in a mediterranean wintering area. – Ringing Migr. 13: 36–42.

Davison, A. C. and Hinkley, D. V. 1997. Bootstrap methods and their applications. – Cambridge Univ. Press.

De La Hera, I. et al. 2018. Habitat segregation by breeding origin in the declining populations of European robins wintering in southern Iberia. – Ibis 160: 355–364.

Duijns, S. et al. 2017. Body condition explains migratory performance of a long-distance migrant. – Proc. R. Soc. B 284: 20171374.

Foden, W. B. et al. 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. – PLoS One 8: e65427.

Gallinat, A. S. et al. 2015. Autumn, the neglected season in climate change research. – Trends Ecol. Evol. 30: 169–176.

Gardner, C. J. et al. 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. – Nat. Commun. 10: 4590.

Gill, F. et al. 2021. IOC world bird list (v11.1). – doi: 10.14344/IOC.ML.11.1.

Giorgi, F. and Lionello, P. 2008. Climate change projections for the Mediterranean region. – Global Planet. Change 63: 90–104.

González-Varo, J. P. et al. 2022. Fruit abundance and trait matching determine diet type and body condition across frugivorous bird populations. – Oikos 2022: e08106.

Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. – Clim. Res. 35: 37–58.

Haberl, H. et al. 2009. Towards an integrated model of socioeconomic biodiversity drivers, pressures and impacts. A feasibility study based on three European long-term socio-ecological research platforms. – Ecol. Econ. 68: 1797–1812.

Haest, B. et al. 2020. Weather at the winter and stopover areas determines spring migration onset, progress and advancements in Afro-Palearctic migrant birds. – Proc. Natl Acad. Sci. USA 117: 17056–17062.

Hansen, A. J. et al. 2001. Global change in forests: responses of species, communities and biomes: interactions between climate change and land use are projected to cause large shifts in biodiversity. – Bioscience 51: 765–779.

Hillebrand, H. et al. 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. – J. Appl. Ecol. 55: 169–184.

Howard, C. et al. 2020. Disentangling the relative roles of climate and land cover change in driving the long-term population trends of European migratory birds. – Divers. Distrib. 26: 1442–1455.

Inger, R. et al. 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. – Ecol. Lett. 18: 28–36.

IPBES 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service. – IPBES secretariat, Bonn, Germany. <https://doi.org/10.5281/zenodo.3831673>.

Jetz, W. et al. 2007. Projected impacts of climate and land-use change on the global diversity of birds. – PLoS Biol. 5: e157.

Jordano, P. 1984. Relaciones entre plantas y aves frugívoras en el matorral mediterráneo del sur de España. – PhD thesis, Univ. of Seville, Spain.

Jordano, P. 1985. El ciclo anual de los Paseriformes frugívoros en el matorral mediterráneo del sur de España: importancia de su invernada y variaciones interanuales. – Ardeola 31: 69–94.

Jordano, P. 1987. Frugivory, external morphology and digestive system in mediterranean sylviid warblers *Sylvia* spp. – Ibis 129: 175–189.

Jordano, P. 1988. Diet, fruit choice and variation in body condition of frugivorous warblers in Mediterranean scrubland. – Ardea 76: 193–209.

Jordano, P. 2014. Fruits and frugivory. – In: Gallagher, R. S. (ed.), Seeds: the ecology of regeneration in plant communities. CABI, pp. 18–61.

Kharouba, H. M. and Wolkovich, E. M. 2020. Disconnects between ecological theory and data in phenological mismatch research. – Nat. Clim. Change 10: 406–415.

Koleček, J. et al. 2020. Shifts in migration phenology under climate change: temperature vs abundance effects in birds. – Clim. Change 159: 177–194.

Labocha, M. K. and Hayes, J. P. 2012. Morphometric indices of body condition in birds: a review. – J. Ornithol. 153: 1–22.

Nakagawa, S. and Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. – Biol. Rev. 85: 935–956.

Newbold, T. et al. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. – Proc. R. Soc. B 280: 20122131.

Nowak, L. et al. 2019. Projecting consequences of global warming for the functional diversity of fleshy-fruited plants and frugivorous birds along a tropical elevational gradient. – Divers. Distrib. 25: 1362–1374.

Pachauri, R. K. et al. 2014. Climate Change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. – IPCC.

Parrish, J. D. 1997. Patterns of frugivory and energetic condition in nearctic landbirds during autumn migration. – Condor 99: 681–697.

Pérez-Tris, J. and Tellería, J. L. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. – J. Anim. Ecol. 71: 211–224.

Quintero, E. et al. 2020. Fruit resource provisioning for avian frugivores: the overlooked side of effectiveness in seed dispersal mutualisms. – J. Ecol. 108: 1358–1372.

Saino, N. et al. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. – Proc. R. Soc. B 278: 835–842.

Schulte-Hostedde, A. I. et al. 2005. Restitution of mass–size residuals: validating body condition indices. – Ecology 86: 155–163.

Snow, B. and Snow, D. 1988. Birds and berries. – A&C Black.

Socolar, J. B. et al. 2016. How should beta-diversity inform biodiversity conservation? – Trends Ecol. Evol. 31: 67–80.

Stoffel, M. A. et al. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. – Methods Ecol. Evol. 8: 1639–1644.

Stuble, K. L. et al. 2021. The promise and the perils of resurveying to understand global change impacts. – Ecol. Monogr. 91: e01435.

Studds, C. E. et al. 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. – Nat. Commun. 8: 14895.

Tellería, J. L. 2015. The decline of a peripheral population of the European robin Erithacus rubecula. – J. Avian Biol. 46: 159–166.

Valiente-Banuet, A. et al. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. – Funct. Ecol. 29: 299–307.

van Schaik, C. P. et al. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. – Annu. Rev. Ecol. Syst. 24: 353–377.

Visser, M. E. et al. 1998. Warmer springs lead to mistimed reproduction in great tits *Parus major*. – Proc. R. Soc. B 265: 1867–1870.

Wilcove, D. S. and Terborgh, J. W. 1984. Patterns of population decline in birds. – Am. Birds 38: 10–13.

Winger, B. M. et al. 2019. A long winter for the Red Queen: rethinking the evolution of seasonal migration. – Biol. Rev. 94: 737–752.

Zamora, R. et al. 2010. Positive adjacency effects mediated by seed disperser birds in pine plantations. – Ecol. Appl. 20: 1053–1060.

Zurell, D. et al. 2018. Long-distance migratory birds threatened by multiple independent risks from global change. – Nat. Clim. Change 8: 992–996.