

No evidence for an effect of vegetation productivity on the structure and diversity of a reed-bed associated passerine assemblage during autumn migration

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Abstract. The structure of a species assemblage at given sites constitutes a key ecological parameter to understand the dynamics of bird assemblages. The aim of this paper is to (1) quantify how variable is a passerine assemblage associated with an inter-tidal reedbed area at a main stopover site in the Atlantic flyway in northern Iberia and to explore potential factors explaining the variation, with emphasis on the vegetation productivity, and (2) to test whether inter-annual fluctuations reflect possible demographic trends. Migratory birds, especially those species which show high flexibility to stop over in some places or others using an opportunistic strategy, should be expected to land in larger numbers and stay for longer periods at given stopover sites in years with higher vegetation productivity, thus with a higher amount of insect prey, since this would permit achieving higher fuel deposition rates. We used ringing data collected at Txingudi marshlands during the autumn migration of 2007–2016. The assemblage had a relatively simple structure, because few species dominated in number over the rest. Reed Warblers *Acrocephalus scirpaceus* dominated the assemblage in nine out of ten study years, supporting the importance of the site for the species. As compared with the other two most abundant passerines (the Sedge and Willow Warblers, *A. schoenobaenus* and *Phylloscopus trochilus*, respectively), the ratio between these three warblers varied from year to year, with the Willow Warblers having much higher annual fluctuations than the other two species. This is likely linked to an opportunistic exploitation of the reed bed by this species, but we did not find significant any effect of vegetation productivity (quantified by Normalized Difference Vegetation Index, NDVI) on the structure and diversity of the bird assemblage. Annual fluctuations in species' contribution to the assemblage did not vary linearly, except for the Bluethroat *Luscinia svecica*. Only for Bluethroats the proportion of captures and the mean number of captures declined from year to year. The structure and diversity of the assemblage did not seem to be affected by local conditions hence factors working at larger spatial scales or at the origin region of the migrants captured at Txingudi apparently may be more relevant at explaining the structural traits of the assemblage.

Key words: *Acrocephalus*, Atlantic flyway, Bluethroat, demographic trends, stopover, Willow Warblers

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INTRODUCTION

The movement of migrant species through the annual cycle brings deep changes in the structure and diversity of bird assemblages (*sensu* Stroud et al. 2015). Apart from seasonally, such assemblages can also vary from year to year and due to so many additional causes (González-Gajardo et al. 2009, Pons & Clavero 2010, Aarif et al. 2014). Thus, annual fluctuations in a proportion of certain species in a stop-over bird assemblage may result from year-to-year differences in the exploitation

of the stop-over site (Arizaga et al. 2016) or reflect population tendencies that are linked to some influential factors operating at the breeding grounds or along the migratory flyway (Newton 2004). In other words, the factors driving the structural traits of a bird assemblage at a particular site can operate from local to large spatial scales.

Many studies dealing with avian assemblages focus on describing their structure during a particular, normally isolated occasions (Herrera 1980, Carrascal 1984, Galarza 1987, Paracuellos 1997),

but less frequently rely on long-term analyses where potential causes are addressed (Sebastian-Gonzalez et al. 2010). Such long-term analyses contribute to understanding which factors drive the main changes at the assemblage and community levels. As a proxy of food supply, vegetation productivity is considered to be one of the main drivers of animal abundance at a given spatial scale (Stienen et al. 2000, Saino et al. 2004, Klaassen et al. 2010, Trierweiler et al. 2013). A good index used for that is the Normalized Difference Vegetation Index (NDVI), which shows positive values (up to +1) in areas with dense vegetation and negative values (up to -1, though normally ranges from 0 — bare soil — to 1) where there is little or no vegetation. For a given vegetation patch, the greener the plants, the higher the NDVI is, and accordingly the higher the amount of insect prey should theoretically be available (Zwarts et al. 2009). The advantage of using this index is that is remotely obtained (via Landsat satellites) and we can obtain historical data, so it is ideal for long-term studies. In this context, it can be stated that the presence and more particularly the abundances of certain species in an assemblage might increase under scenarios of high food supply (Rogalla & Arizaga 2018), that would be possible in years of high vegetation productivity. Migratory birds, especially those species which show high flexibility to stop over in some places or others (even in some habitats or others) using an opportunistic strategy, should be expected to land in larger numbers and stay for longer periods at given stopover sites in years with higher vegetation productivity, since this would permit achieving higher fuel deposition rates (Weber et al. 1999).

Wetlands are among the most threatened habitats in the world and, in parallel, many species that depend on such ecosystems suffer from moderate to strong population declines, including many migratory species (Zwarts et al. 2009). In this scenario, the analysis of migratory bird assemblages associated to wetlands is of ecological, management and conservation interest (Poulin et al. 2000, Green et al. 2002, Zwarts et al. 2009). The estuaries along the coast of the Bay of Biscay are the primary natural wetland areas on the Atlantic facade of northern Iberia. As compared to a relatively poor breeding assemblage supporting small population sizes from a peninsular standpoint (González & Pérez-Aranda 2011), the estuaries and coastal marshes from northern Iberia have a remarkable avian conservation value since they are used by high numbers of migrating and

wintering birds (e.g., Navedo et al. 2007, Mendiburu et al. 2009, González & Pérez-Aranda 2011, Arizaga et al. 2014a, b).

The aim of this paper is to (1) quantify variation in the assemblage of passerines associated with an inter-tidal reedbed that is known to be one of the main stopover sites for marsh-associated birds in their autumn migration through the Atlantic flyway as well as explore a potential role of vegetation productivity in explaining the variation and, (2) test whether annual fluctuations in species proportions reflect possible demographic trends. A particular prediction would be that years with higher vegetation productivity, so in theory with more aphids (*Hyalopterus* spp.) in the reed bed, should be correlated with a higher proportion of aphid-specialists (for instance Sedge Warblers *Acrocephalus schoenobaenus*) and/or opportunistic species that can take advantage local peaks of food availability (Rogalla & Arizaga 2018).

MATERIALS AND METHODS

Study area and data collection

The Txingudi marshes are located at the southeastern edge of the Bay of Biscay and they are the first wetland that migrant birds coming from northern Europe via the Atlantic flyway find when they meet Iberia (Etzaniz et al. 1998, Arizaga et al. 2011b). More particularly, our research was carried out at the Jaizubia stream (one of the main wetlands of Txingudi; 43°21'00.00''N, 1°48'44.52''W). The sampling area consists of an inter-tidal zone comprising a mosaic of mudflats, low halophytic vegetation and reed beds (*Phragmites* spp.). These reed beds are used by a high number of passerines that stopover in Txingudi during the autumn migration period, en route to their wintering areas either in southern Iberia or Africa (Arizaga et al. 2011b). These migrants from abroad overlap with resident species/populations or with migrants such as Reed Warblers *Acrocephalus scirpaceus* that also breed within the region (Pagaldai & Arizaga 2015).

During a period of 10 years (2007–2016), we kept a constant-effort ringing site operating on a daily basis from 1 August to 30 September. This sampling period was designed to capture the peak of passage of many migratory passerines including the *Acrocephalus* species complex, Willow Warblers *Phylloscopus trochilus* or Bluethroats

Luscinia svecica, which were the main focus of this monitoring scheme (Mendiburu et al. 2009). This sampling period captured most or even virtually all the migration period of these species besides some *Acrocephalus* warblers (in particular *A. schoenobaenus*), where very early passing birds, especially adults, can occur within the area by mid- or the end of July and may have been not captured. Our study, however, included all the captured avian assemblage since we also wanted to quantify the importance of local resident birds as compared with migrants.

Each day, the sampling was carried out during a period of 4 h starting at dawn. Overall, we used 204 linear m of 2.5 m high, 16 mm mesh mist net placed always in the same site across the reed bed. From 2007 to 2012, we used a tape-lure with the song of a male of Aquatic Warbler *Acrocephalus paludicola* in order to attract this species to the nets (Julliard et al. 2006), whilst the tape lure was not used from 2013 onwards. It must be acknowledged, however, that the tape lure may also attract other species as well. Once captured, each bird was ringed and a number of additional individual traits were also measured (e.g., Arizaga et al. 2011a, Andueza et al. 2013), though they were not used in this paper.

Statistical analyses

Before the analyses the dataset was filtered to remove recaptures of individual birds caught twice or more per year (campaign), so each individual was considered only once in a year. Recaptures from individuals ringed abroad were considered as captures in the first capture event and, thereafter, as recaptures. With this information, we calculated the proportion of captures per species and year. Overall, we obtained 14507 unique (individual) captures. Some of them were recaptured in subsequent years after being first captured, so we worked with a data set of 14917 captures, with each individual bird being considered only once in a year (campaign).

First, we explored the proportion of captures of those species which were found to be predominant. A chi-square test was used to analyse whether the ratio between the five most abundant species in the assemblage varied between years.

Using this same filtered data set (each individual bird considered only once per year, and including all passerines), we conducted a Hierarchical Analysis of Clusters in order to see the relationship among different years according to their similarity based on Morisita-Horn index, which is

very responsive to dominant taxa (Magurran & McGill 2011). This index was calculated as $[2 \times \sum(x_i y_i)] / [(\sum x_i^2 / X^2) + (\sum y_i^2 / Y^2)] \times XY$, where x_i is the number of times a given species i is found in sample X , y_i is the number of times a given species i is found in sample Y , and X and Y are the number of species at samples X and Y , respectively. The decision to select this index was based on our aim to quantify the role of inter-annual variations in the relative abundance of the most common species on bird assemblage structure. Clusters were built using the UPGMA method and the PAST software (Hammer et al. 2001).

To determine to what extent the structure and diversity of the assemblage varied annually we calculated two ecological indices of diversity and dominance (H and D , respectively) using the software PAST (Hammer et al. 2001). The H index is calculated as $-\sum(p_i \times \ln(p_i))$, where p_i was the proportion of captures of each species. The D index is calculated as $\sum(p_i)^2$. Again, in this case we considered each individual bird only once per year, and included all species. Using a bootstrapping approach, a 95% confidence interval associated to the yearly mean values was obtained and, therefore, it can be stated that overlapping confidence intervals reveal no (statistical) differences among years.

We also computed Linear Models (LM) to explore whether the proportion of captures of a certain species and the diversity and dominance indices varied between years, as well as in relation to the NDVI, which is a proxy of the reed bed productivity (e.g., Bresciani et al. 2009). Tape lure was considered as a factor in all the models, while year and the residual NDVI values over date (see below for further details) were included as covariates. Year and the residual NDVI values were not correlated ($r = 0.33$, $p = 0.346$). Preliminary analyses also including an effect of rain and/or temperatures from June to September revealed that none of such climatic covariates influenced our object variable, so we finally decided to omit them from our models. NDVI values were calculated using data provided by Landsat 7 or 8 (depending on year) red (R) and infra-red (IR) band layers for a square (pixel) situated in the middle of our sampling reed bed area (data obtained from earthexplorer.usgs.gov). The size of the pixel given by Landsat was 30×30 m, so it fully fixed within the reed bed zone existing of our study area, with no vegetation from the surroundings being included. Thereafter, with the "raster" function in QGIS (QGIS Development Team 2009) we calculated

the NDVI values as: $(IR-R)/(IR+R)$. NDVI values were calculated for R and IR data obtained only in August. Data from September were not used since there were five years for which there were no data from this month owing to the presence of clouds (have in mind that NDVI is calculated from just a single Landsat passage per month and the presence of clouds can result in the lack of data). In August, the presence of clouds in 2010 forced us to take the data from this year from September. Overall, the NDVI values calculated for this article were obtained from 3 August to 3 September (mean: 13 August; for details see Appendix 1). Given this variation, and considering that the peak of passage of most of the studied species was in August (for details see Mendiburu et al. 2009), that there were five years without NDVI values for September and that the reed bed is greener in August as compared to September, we considered that working only with NDVI values from August was acceptable. However, when we made a simple regression of NDVI values over date, we obtained a significant, negative effect of date on NDVI (linear regression: adjusted $r = -0.705$, $p = 0.014$). Therefore, we decided to use the residual values of this regression as a date-controlled NDVI.

Complementarily, we also run LM on the standardized number of captures (captures/100 linear m of mist nets) to test whether this variable varied linearly (i.e., we aimed to detect linear trends) along the study period. LM were run using the software R (R Core Team 2014).

RESULTS

The most frequently captured bird species was the Reed Warbler (4,990 unique captures), followed by the Sedge and Willow Warblers (2,902 and 2,796 unique captures, respectively). Overall, these three species summed up to a 70.5% of all the captures. The overall number of species ringed was 55.

The assemblage of passerines was dominated by three species which represented, respectively, a 34%, 20% and 16% of all the captures (Fig. 1). Deviations from this total mean, however, were important and, therefore, strong annual variations appeared. A paradigmatic case of such variations was the Willow Warbler, species that showed a coefficient of variation of almost 100%, and the Common Starling *Sturnus vulgaris*, with a value close to 150% (Fig. 1).

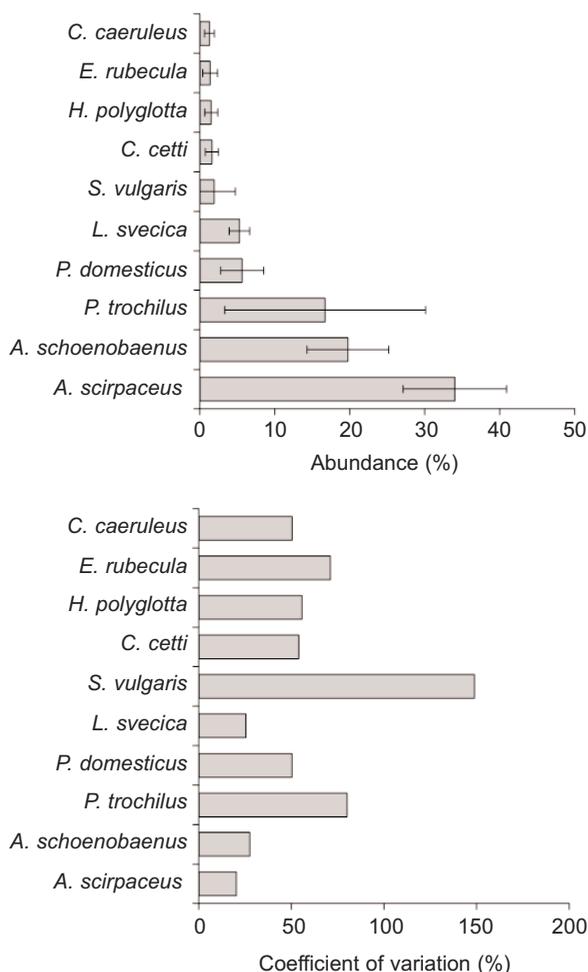


Fig. 1. Relative abundance (\pm SD), and variation coefficients associated to mean values of the ten most abundant species captured with mist nets at a reed bed area in Jaizubia, northern Iberia, during the months of August–September, period 2007–2016. Within each year, each individual bird has been considered only once for the analysis.

Reed Warblers were observed to dominate the assemblage in nine out of ten campaigns (Table 1). Overall, the ratio between these five most commonly captured species was not constant ($\chi^2 = 2082.90$, $df = 36$, Monte Carlo $p < 0.001$), indicating significant inter-annual variation. On average, the difference in the proportion (\pm SD) of Reed Warblers in relation to the Sedge and Willow Warblers was $14.2\% \pm 7.4\%$ and $17.2\% \pm 19.6\%$, respectively. Given the observed SD values in these two cases, it can be stated that the ratio between the Reed and Sedge Warblers tended to be more constant compared to the ratio between the Reed and Willow Warblers.

Regression analysis did not detect a significant linear effect of year on the proportion of captures

Table 1. Relative abundance (%) of the reed-bed associated passerines captured in Jaizubia with mist nets, and accounting for 5% or more of the total abundance at least in a year from 2007 to 2016.

Species	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
<i>A. scirpaceus</i>	32.2	40.0	39.5	30.8	26.0	36.7	39.6	42.5	32.1	20.9
<i>A. schoenobaenus</i>	20.9	18.7	18.3	30.2	17.8	14.0	25.8	20.3	20.7	10.8
<i>P. trochilus</i>	12.9	6.3	19.0	15.6	21.5	13.6	4.7	4.3	18.7	50.6
<i>P. domesticus</i>	8.8	3.8	3.8	4.7	5.3	11.9	7.2	4.6	4.2	2.3
<i>L. svecica</i>	6.6	7.3	4.8	5.6	5.9	5.5	5.7	4.9	4.3	2.4
Other species (combined)	18.6	23.9	14.5	13.0	23.5	18.3	17.1	23.4	20.0	13.0
Sample size	1974	1119	2413	1528	1232	1070	1129	1175	1254	2020

for the five most abundant species (Table 2), except for the Bluethroat, which was found to decrease (Table 2). The tape lure and the NDVI did not have any significant effect on the proportion of captures of any of the four studied species (Table 2).

The Hierarchical Analyses of Clusters revealed two main clusters that may be characterized by: (1) 2016, when the assemblage was dominated by Willow Warblers (which comprised about 50% of all the captures in that year); and (2) the rest of years (Fig. 2; Cophenetic correlation: 0.924, boot. probability for these two clusters: 100%). If we

look at these other years in detail, still we might separate three groups: (1) 2011, where the three main species had similar contributions (around a 20%) to the assemblage; (2) 2008–2013–2014, which were years with poor representation (ca. 5%) of Willow Warblers, high proportion of Reed Warblers (almost 40%); (3) and the rest of years, which were characterized by a slightly higher proportion of Willow Warblers (12–18%), 30–38% of Reed Warblers (Table 1).

Table 2. Beta-parameter estimates (\pm SE) of linear models of the proportion of captures of the five most abundant birds captured with mist nets at the reed bed of Jaizubia, from 2007 to 2016. Effects: year (linear effect), tape lure (year using and not using tape lure with a male aquatic Warbler’s song; reference: year without lure), NDVI, Normalized Difference Vegetation Index. We also show the adjusted R^2 and the significance values of each model.

Linear Models	B	SE (B)	p
Reed Warbler ($R^2 = 0.15$, $p = 0.637$)			
Year	-2.09	1.56	0.229
Lure	-9.92	9.41	0.332
NDVI	+1.48	27.27	0.959
Sedge Warbler ($R^2 = 0.17$, $p = 0.660$)			
Year	-1.54	1.25	0.262
Lure	-6.56	7.50	0.416
NDVI	+7.51	21.74	0.742
Willow Warbler ($R^2 = 0.03$, $p = 0.488$)			
Year	+4.40	2.86	0.175
Lure	+18.49	17.25	0.325
NDVI	+16.28	49.97	0.756
House Sparrow ($R^2 = 0.21$, $p = 0.712$)			
Year	+0.13	0.66	0.856
Lure	+3.12	3.99	0.464
NDVI	+8.81	11.55	0.475
Bluethroat ($R^2 = 0.61$, $p = 0.035$)			
Year	-0.43	0.18	0.051
Lure	-0.88	1.07	0.444
NDVI	-4.57	3.10	0.191

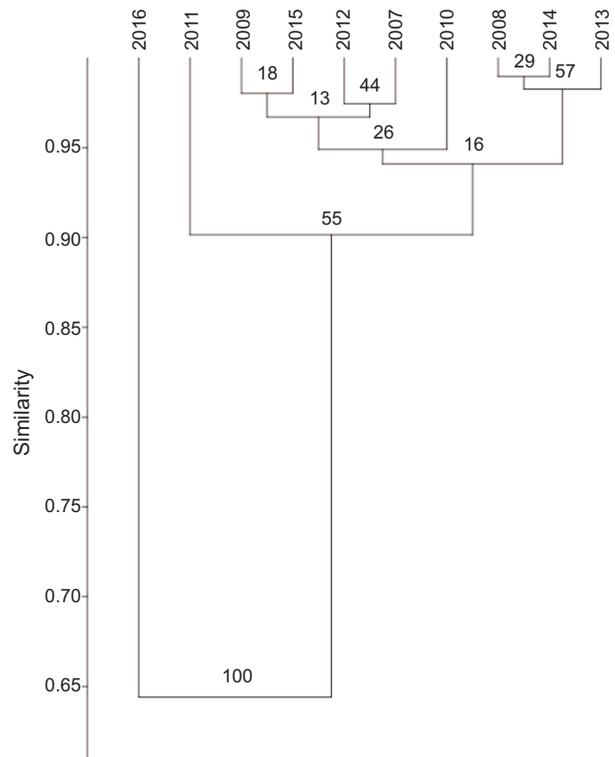


Fig. 2. Diagram derived from a Hierarchical Analysis of Clusters used to see the relationship among years based on the Morisita index of captures of passerines at Jaizubia during the months of August–September from 2007 to 2016. Bootstrap (1,000 replicates) probability values for clusters are also shown.

Ecological indices of diversity and dominance were observed to vary from year to year (Fig. 3). Maximum values in diversity (so minimum in dominance) were found in 2006–2007 together with 2010, 2011, 2013 and 2014. By contrast, 2016 showed the lowest values of diversity. None of these two indices had a linear trend across the years nor varied in relation to the use of tape lure or NDVI (all p values >0.05). Note that, particularly 2016, was the year with an exceptionally high proportion of captures of Willow Warblers (Table 1).

Models of demographic trends revealed that twospecies — the Bluethroat and, nearly significantly, the Reed Warbler — had negative population trends, and one — the Willow Warbler — had a positive trend, once the effect of the tape lure was controlled (Table 3).

DISCUSSION

This is the first study aiming to quantify the temporal variation of an assemblage mostly

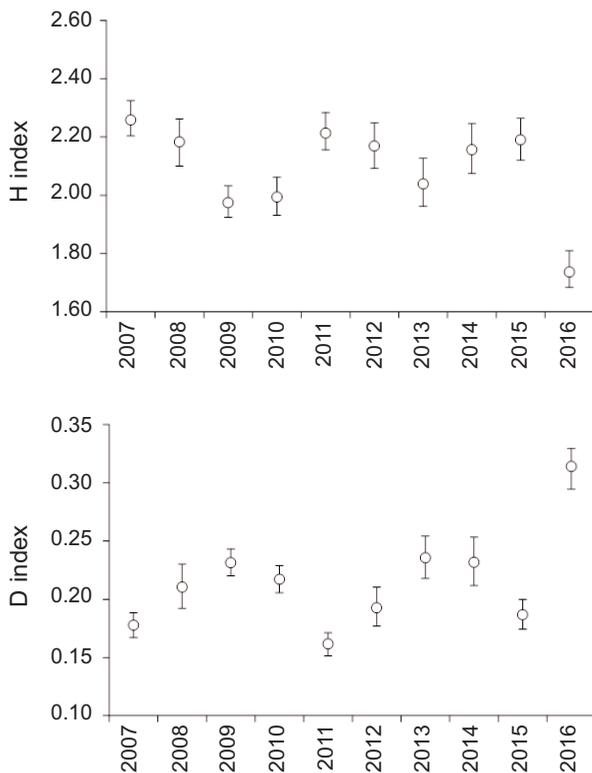


Fig. 3. Mean (\pm 95% confidence interval) diversity and dominance index values (H and D, respectively) of the reed-bed associated assemblage of passerines captured with mist nets during the autumn migration period from 2007 to 2016.

Table 3. Beta-parameter estimates (\pm SE) of linear models of the standardized number of captures (captures/100 linear m of mist nets) of the five most abundant birds captured with mist nets at the reed bed of Jaizubia, from 2007 to 2016. Effects: year (linear effect), tape lure (year using and not using tape lure with a male Aquatic Warbler's song; reference: year without lure).

Linear Models	B	SE (B)	p
Reed Warbler ($R^2 = 0.01$, $p = 0.061$)			
Year	-0.32	0.18	0.075
Lure	-0.74	1.07	0.491
Sedge Warbler ($R^2 < 0.01$, $p = 0.298$)			
Year	-0.15	0.15	0.374
Lure	-0.08	0.90	0.932
Willow Warbler ($R^2 = 0.04$, $p < 0.001$)			
Year	+0.90	0.21	< 0.001
Lure	+2.81	1.23	0.022
House Sparrow ($R^2 = 0.01$, $p = 0.017$)			
Year	-0.02	0.03	0.596
Lure	+0.20	0.19	0.301
Bluethroat ($R^2 = 0.02$, $p = 0.001$)			
Year	-0.10	0.03	0.002
Lure	-0.28	0.18	0.135

composed by reed- or marsh-associated birds (mainly passerines) in the Basque region and in the Cantabrian region in Spain as well. Our assemblage was characterized by having a relatively poor structure, since few species are found to dominate in number over the rest. This result, however, is in line with what we should expect from a sampling area with a high proportion of monospecific reedbeds, which are known to host passerine assemblages dominated by a few species and accounting for fairly low richness of passerines (Paracuellos 1996, Poulin et al. 2000, Torralvo 2007).

Reed Warblers were found to dominate the assemblage in nine out of ten study years, supporting the importance of the site for the species. As compared with the other two most abundant passerines (the Sedge and Willow Warblers), Reed Warblers are the only species breeding in the reed bed of Txingudi (Pagaldai & Arizaga 2015). Separating local and non-local Reed Warblers in August–September is nearly impossible at an individual level, owing to a high morphological overlap between these two types of birds (Pagaldai & Arizaga 2015). Analyses on recaptures of local breeding birds (known to breed at Jaizubia), however, reveal that they tend to leave Txingudi along August, and hence the proportion of non-local to local Reed Warblers increases from August to September.

The ratio between these three warblers varied from year to year, with the Willow Warblers having much higher annual fluctuations than the other two species. Even though Willow Warblers primarily occupy forested habitats, they also exploit other habitat types, including reedbeds (e.g., Lara & Fajardo 2018), especially in cases of abundant food supply (Cramp 1992) (in this case superabundance of reed aphids; Grandío 1998). A previous analysis on Willow Warblers in Txingudi demonstrated that fuel deposition rate and fuel load tended to be higher in those years when the species was more abundant, suggesting an opportunistic stopover exploitation (Rogalla & Arizaga 2018). In this context, 2016 was a very exceptional year, with Willow Warblers accounting for ca. 50% of all the captures. Note also that the tape lure was not used in 2016. Probably much of the yearly variation in the assemblage structure was due to the presence of species that exploit the reed bed opportunistically, likely coinciding with peaks of food supply (reed aphids). Unfortunately, the abundance of aphids was not measured in all these sampling years and, therefore, we cannot determine direct link between bird numbers and aphids. It is true, however, that aphids tend to concentrate in zones with a high reed productivity (i.e. where the reed beds are greener, J. Arizaga pers. obs.), and the NDVI values correlate with this productivity (e.g., Tóth 2018). The NDVI of August, which could be used as a surrogate of food supply for the aphids, and therefore an indirect proxy of their abundance, however, showed no relationship with the proportion of captures of any of the three four studied species. Causes underlying this lack of a significant relationship remain unknown to us, and future research is called to play a role to disentangle to what extent vegetation productivity at a local scale explains bird assemblage structural patterns. In part, it cannot be excluded that the temporal resolution was too low (one record per month and, sometimes, cloudiness made such measurements impossible). The use of NDVI values is reported to be very useful in backward analyses where we want to study the effect of vegetation productivity over phenological patterns obtained from long-term data series (Zwarts et al. 2009). However, it is likely that the high accuracy of this method demonstrated at large scales might worsen at smaller scales. In this scenario, it might be priority to test whether records of productivity measured directly from the vegetation are well represented by NDVI values.

Annual fluctuations in species' contribution did not vary linearly (i.e., did not show linear trends), except in the Bluethroat. The proportion of captures of Bluethroats in the zone was observed to decrease at a mean annual rate of -0.32% during a period of 10 years (2007–2016). Thus, whilst during the first five years the species had an annual mean proportion of > 5% over the rest of species, this proportion was situated in a mean value under 5% during the last five years. In parallel, the mean number of captures of this species also decreased, so in this case the decreasing importance of Bluethroats within the assemblage was caused by a parallel decreasing population trend. Txingudi collects Bluethroats from the *Luscinia svecica namnetum* and the *L. s. cyanecula* subspecies (Arizaga et al. 2011a), mainly coming from France (mostly *namnetum*) and Germany and the Benelux (*cyanecula*) (Arizaga & Tamayo 2013). The European population is considered to be stable or even increasing in certain regions (BirdLife International 2015), so there would be no reason to link the findings obtained at Txingudi with population trends detected at a European scale. Further research is needed to explain such results, including both a detailed analysis on the habitat use and the species' ecology at Txingudi (to detect possible threats at a local level), and the comparison with other stopover sites situated on the Atlantic flyway.

By contrast, Reed Warblers had nearly significantly negative population trends in our zone but in this case this did not have a reflection in the proportion of captures. Causes promoting temporal variation in a bird assemblage can be of very different origin and operate at different spatial scales. At a large scale level, demographic parameter fluctuation (e.g. in survival or productivity) between origin regions and from one year to the next may result in annual variations in a bird assemblage dominated by migratory birds at a particular zone. At the same time, local conditions might result in variation in e.g. food availability of given prey types that could also result in bird assemblage annual variations. Thus, rainy years could result in higher vegetation productivity, and this may lead to higher food supply (Zwarts et al. 2009). Temperature is also expected to have a role (e.g., due to its potential influence on both vegetation growth and insect abundance), but more difficult to predict. Thus, it can be stated that higher temperatures combined with abundant rain should increase vegetation productivity, but hot and dry years might result in decreasing

freshwater contribution to the marsh and an increase of the salinity due to tide influence, which finally might promote lower vegetation productivity (Burdick et al. 2001), and less food for birds. Interestingly, we found no evidence supporting an effect of the vegetation productivity in August (measured on the reed bed) on bird proportions. Thus, the structure and diversity of the assemblage did not seem to be affected by local conditions and factors working at larger spatial scales or at the origin region of the migrants captured at Txingudi seem to be more relevant at explaining the structural traits of the assemblage of reed- and marsh-associated birds of this site (and likely other similar sites across the flyway) during migration period.

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STRESZCZENIE

[Struktura i zróżnicowanie zespołu ptaków wróblowych związanych z trzcinowiskami podczas jesiennej migracji nie ma związku z produktywnością roślinności]

Struktura zespołu ptaków występujących na danych terenie stanowi kluczowy parametr ekologiczny dla zrozumienia dynamiki tych zespołów. Przyjmuje się, że ptaki wędrowne, zwłaszcza te gatunki, które wykazują dużą plastyczność w wyborze miejsc przystankowych podczas migracji, zatrzymują się liczniej oraz pozostają przez dłuższy czas w danym miejscu przystankowym w latach o wyższej produktywności roślinności. Wyższa produktywność powinna bowiem przekładać się na większą ilość owadów, a to z kolei pozwala na zgromadzenie większych zapasów energetycznych koniecznych do dalszej wędrówki. Celem pracy było określenie, jak zmienny jest zespół ptaków wykorzystujący podczas jesiennej wędrówki przybrzeżne trzcinowiska w północnej części Półwyspu Iberyjskiego, będące głównym miejscem przystankowym podczas ich migracji, oraz zbadanie potencjalnych czynników, w tym produktywności roślinności, wyjaśniających tę zmienność. Analizowano także czy obserwowane między sezonami wahania liczebności poszczególnych gatunków odzwierciedlają ich trendy demograficzne.

Dane zostały zebrane w latach 2007–2016, podczas obrączkowania ptaków na stałych powierzchniach odłowu w okresie wędrówki jesiennej (1 sierpnia–30 września) na mokradłach Txingudi (zachodni kraniec Pirenejów). Okres odłowów był dobrany tak, aby obejmował szczyt przelotu wróblowych, szczególnie gatunki z rodzaju *Acrocephalus*, oraz piecuszki i podróżniczki. Odłowy prowadzono codziennie przez 4 godziny, rozpoczynając o wschodzie słońca, za pomocą 204 sieci ornitologicznych umieszczonych w tych samych miejscach. Dodatkowo, w latach 2007–2012 wykorzystywano głos samców wodniczki, aby przywabić w okolice sieci wędrujące ptaki tego gatunku, choć jest prawdopodobne, że wabione były także inne gatunki. W analizach uwzględniono tylko pierwsze schwytywanie osobnika w danym roku. Aby opisać strukturę i bogactwo zespołu ptaków policzono współczynniki zróżnicowania zespołu oraz dominacji. Jako wskaźnika produktywności trzcinowisk będących miejscem przystankowym ptaków użyto znormalizowanego różnicowego wskaźnika wegetacji — NDVI określanego dla sierpnia danego roku (Apendyks 1).

Łącznie podczas 10 lat badań schwytano 14 507 osobników reprezentujących 55 gatunków. W związku z tym, że część z nich schwytana była także w kolejnych sezonach, baza danych użyta do analiz zawierała informacje o 14 917 odłowach

konkretnych osobników. Badany zespół ptaków wróblowych miał stosunkowo prostą strukturę, ponieważ był on zdominowany przez kilka gatunków (Fig. 1). Trzy gatunki — trzcinniczek, rokitniczka i piecuszka stanowiły łącznie ponad 70% wszystkich odłowionych ptaków. Trzcinniczek dominował w zespole w dziewięciu z dziesięciu sezonów (Tab. 1), potwierdzając znaczenie badanego miejsca przystankowego w wędrówce tego gatunku. Procentowy udział każdego z trzech najliczniejszych gatunków w zespole wahał się między sezonami, przy czym największe fluktuacje odnotowano dla piecuszka, co jest prawdopodobnie związane z oportunistyczną eksploatacją trzciniowisk przez ten gatunek. Nie stwierdzono istotnego wpływu produktywności roślinności, określanego przez wskaźnik NDVI, na strukturę i różnorodność zespołu ptaków, ani na poszczególne gatunki analizowane osobno (Tab. 2, 3). Zaobserwowano wyraźną zmienność

sezonową zarówno we współczynniku dominacji, jak i różnorodności zespołu (Fig. 3). Analizując poszczególne sezony stwierdzono, że najbardziej od pozostałych odbiegał rok 2016, kiedy zespół wróblowych był zdominowany przez piecuszka (Fig. 2). Zarówno udział, jak i standaryzowana liczba schwytań (liczba schwytań/100 m sieci ornitologicznych) każdego z pięciu najliczniejszych gatunków w zespole nie wykazywały liniowych trendów w okresie objętym badaniami za wyjątkiem podrózniczka, u którego nastąpił spadek obu parametrów (Tab. 2, 3), oraz piecuszka, u którego standaryzowana liczba schwytań wzrastała z roku na rok (Tab. 3).

Uzyskane wyniki wskazują, że struktura i bogactwo zespołu nie są zależne od lokalnych warunków na trzciniowiskach będących miejscem przystankowym, a raczej od czynników operujących w większej skali przestrzennej.

Appendix 1. NDVI values obtained for the months of August (and, exceptionally, September) for the reed bed area sampled in Txingudi from 2007 to 2016.

Year	NDVI value	Date
2007	0.39344	03 August
2008	0.13636	05 August
2009	0.36634	15 August
2010	0.03158	03 September
2011	0.01010	30 August
2012	0.33333	07 August
2013	0.37476	11 August
2014	0.31623	05 August
2015	0.28447	23 August
2016	0.38303	03 August
2017	0.32445	06 August