Sex differences in migration timing influence the network structure of avian assemblages at a stopover site

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Abstract

1. Shifts in migration phenology aimed at minimizing possible mismatches between the timing of breeding and seasonal peaks in the availability of food resources are a well-documented phenomenon in birds. As the extent of phenological adjustments are likely to differ between species, populations, sexes and age classes, these shifts may exert a strong influence on the potential interferences among co-migrants during their journey to breeding grounds. This can be particularly true for species showing asynchronous migration driven by sex-related mechanisms (i.e., protandry), for which not only the decision on 'when', but also 'with whom' to move might represent a way to minimize the costs associated with migrations.
2. Here, we used an extensive dataset from 16 years of standardized bird monitoring at the spring stopover area on the island of Ponza (Italy), to study how long-term changes in the phenology of species with protandric migration patterns affect the rewiring of potential interferences in avian assemblages.
3. For each year, we reconstructed the temporal co-occurrence networks of females and males of 17 sexually dimorphic species known to exhibit phenological shifts in their migratory behaviour and measured network-specific properties related to connectivity and cohesion. We also provided a measure of 'co-migration fidelity', defined as the degree to which females and males tend to follow a consistent order of association over time.
4. Co-occurrence networks in males showed higher cohesion and lower connectivity than their female's counterparts and a more clustered pattern in terms of co-migration fidelity, with species wintering in sub-Saharan Africa having a more

pronounced tendency to aggregate in semi-independent groups of species characterized by common timing of migration with different foraging strategies.

5. The observed differences in the rewiring of associations over time showed an increasing clustering of species having common responses to changing migration phenology in males, but not in females. This finding suggests a sex-decoupled effect of changing migration phenology on the onset of potential interferences in migratory birds, possibly influencing the global migration economy of landbirds in the Palearctic-African migration system.

Keywords: protandric migrations; stopover areas; co-occurrence networks; migration phenology; co-migration patterns

Introduction

Migration represents a key life-history event for a huge variety of species, involving the seasonal movement of individuals in response to temporal and geographic variations of resource availability (Gauthreaux Jr., 1982). Alongside endogenous (e.g., circannual rhythms) and exogenous (e.g., photoperiodic cues) mechanisms (Gwinner, 1996; Maggini et al., 2010), the onset of favourable environmental conditions and food availability *en route* are key elements driving the timing of migration in birds (Hasselquist et al., 2017; Thorup et al., 2017; Ruthrauff et al., 2019).

Global change poses a major threat to animal migration as it drives restructuring of important phenological events worldwide (Walther et al., 2002; Cresswell & McCleery, 2003; Visser et al., 2004). As climate change does not act equally across the globe, the timing at which major phenological changes occur might not always be the same across biota. For instance, arrival dates at breeding grounds of the Central-European populations of Pied flycatchers (*Ficedula hypoleuca*) showed no significant synchronization with advances in food-peak dates due to warming temperature, leading to a drastic decline (ca. 90%) in the abundance of those populations arriving after the peak (Both et al., 2006). Overall, differences in climatic conditions along migratory routes, as well as at wintering, stopover and breeding areas (Tryjanowski et al., 2002; Ahola et al., 2004; Gordo et al., 2005) increase the chance of phenological mismatches, (de)synchronizing the potential interactions between birds and the species with which they interact, including their food sources, predators and competitors.

Within this context, migratory connectivity, defined as the ‘geographic linking of individuals and populations between one life cycle stage and another’ (Webster et al.,

2002) represents a key factor having far-reaching consequences at multiple ecological scales, from individual fitness to community dynamics and ecosystem functioning. To date, most studies relied on a purely spatial perspective aimed at determining the extent to which different areas of a species' annual range are linked by the movement paths of individuals (Webster et al., 2002; Finch et al., 2017). The quantification of migratory connectivity can give insights on how changing climatic conditions *en route* might influence the ability of areas used by species to sustain migratory flows (e.g., migratory hot spots, *sensu* Bellisario, 2018). However, an explicit consideration of the temporal dimension (*sensu* Bauer, 2016) is fundamental to understand 'how', 'when' and 'for how long' species change their migratory patterns and what are the consequences at multiple ecological levels.

Species are known to change their migration phenology by advancing their departures from wintering areas in response to endogenous and/or exogenous mechanisms associated with changing climate conditions (Bairlein & Winkel, 2001; Lehikoinen et al., 2004; Maggini et al., 2020). However, such responses differ between species, and factors as population, sex, age, ecological requirements might affect the ability of species to change migration phenology (Hötker, 2002; Saino et al., 2004; Rubolini et al., 2007; Both, 2010; Hedlund et al., 2014; Emmenegger et al., 2016). A typical example is protandry, with males advancing their departures with respect to females, thus leading to asynchronous (differential) migratory dynamics within species (Rainio et al., 2007). Moreover, phenotypic plasticity and microevolutionary changes can influence the long-term responses of species to track changes along migratory routes, leading in this case to differences in the consistency of migration pattern (i.e., how repeatable migration phenology and synchrony are over time, Bauer, 2016).

Migrations involve the simultaneous movement of multiple species at once, connecting widely separated and diverse communities potentially having a strong impact on the dynamic and stability of ecosystems. Migratory routes of different species often converge both in space and time (i.e., co-migration, *sensu* Cohen & Satterfield, 2020), creating the conditions for the emergence of direct and indirect ecological interactions, including competition, predation, facilitation and even social interactions (Cohen & Satterfield, 2020). For instance, studies have shown how the dynamic and prevalence of parasites transmission, as well as transient dynamics in lake ecosystems, can be somehow related to migration timing (Brodersen et al., 2008; Peacock et al., 2020). Similarly, the onset of intra- and interspecific competition may be affected by synchronous and asynchronous migrations, by excluding inferior competitors from high-quality foraging areas (Eichhorn et al., 2009, Beauchamp, 2012) or promoting coexistence when the joint use of a resource increases its quality and productivity (Holdo et al., 2007). Migration timing can also influence the outcomes of social interactions, as observed in songbirds migrating along the coasts of Baltic Sea, which use acoustic information as cues to assess the suitability of potential stopover habitats during landfall (Németh & Moore, 2007; Mukhin et al., 2008). However, despite the ecological importance of emerging interactions between co-occurring migrants, we still lack a proper understanding on how long-term phenological changes acting on sexes affect the restructuring of avian assemblages *en route*.

Investigating the causes and the effects of changing migration phenology from a community point of view entails inherent difficulties associated with the need to constantly track and monitor animals across oceans and continents (Cohen & Satterfield, 2020). A further source of uncertainty derives from the need to

appropriately model multi-species temporal movements to identify recurrent patterns in the aggregation of species and forecast the consequences of global change on migrations. Within this context, co-occurrence analysis and co-occurrence networks are valuable tools to elucidate mechanisms driving species assemblages. Recently, García-Navas et al. (2021) used null model approaches on 20 years of abundance data to investigate co-occurrence patterns in bird communities inhabiting habitats at different degree of productivity, showing the role of social information and microhabitat preferences over interspecific competition. Furthermore, Montaño-Centellas (2020) used spatial data to build and explore co-occurrence networks of avian mixed-species flocks across elevation gradients, identifying changes in interactions as the main driver of species turnover of Andean flocking birds. Co-occurrence networks can thus provide a useful framework to capture complex properties of animal movement with simple graphical metrics (Pasquaretta et al., 2021), while keeping in mind that the actual ecological meaning of links must be critically evaluated (see Blanchet et al., 2020 and references therein).

Here, we used time series data spanning 16 years of bird ringing activity at the Mediterranean spring stopover area of Ponza (Italy), to study how long-term changes in the migration phenology of African-European migratory landbirds (Maggini et al., 2020) correlate with the rewiring of potential associations in species showing asynchronous migrations driven by protandry. We used daily abundances to reconstruct the temporal co-occurrence networks of females and males, and measured network-specific properties associated with connectivity and cohesion to test the hypothesis that sex-dependent differences in the timing of migration would lead the onset of different patterns of associations in response to endogenous mechanisms driving migration.

Materials and methods

Sampling site and bird ringing activities

The study was conducted on Ponza (Fig. 1), a small island in the Tyrrhenian Sea with an extension of ca. 9.87 km^2, located about 50 km off the Western coast of Italy (40°55' N, 12°58' E), where we have been monitoring spring migration through capture and ringing since 2002 (http://www.inanellamentoponza.it). Ponza is located along one of the main Mediterranean migratory routes and attracts a large number of African-European migratory landbirds during spring migration (Maggini et al., 2020). The bird capture season started in March and ended in May almost every year (exact start and end dates can be found in the supplementary TableS1 in Maggini et al., 2020). Mist nets were opened every day except for days with heavy rain or strong winds (>15 knots) and the number of days with reduced effort was less than 1% of the total. Mist-nets were checked hourly from dawn until one hour after dusk, and birds were captured throughout the day with an average of 227 m of mist-nets over the time-period. We kept the net brand and model (Lavorazione Reti Bonardi, Monte Isola, BS, Italy, http://www.vbonardi.it/; 2.4 m height, 16 mm mesh size), as well as the vegetation height constant throughout the entire study period. After being captured, birds were ringed and measured using standard EURING procedures (Bairlein, 1995). For the purposes of this study, we selected a sub-sample of the 17 most abundant species characterized by sexual dimorphism (Table 1), using ringing data over a period of 16 years (2005 to 2020), during which the procedures were fully standardized.

Network inference

For each year of survey (n = 16), we reconstructed the temporal co-occurrence networks for both females and males by means of the ranked correlation on absolute abundances. Correlational methods are becoming increasingly popular for inferring co-occurrence networks from time series data, as they do not require any *a priori* estimation of underlying parameters, being however able to capture signals of potential interferences among species within communities (Sander et al., 2017). We thus calculated all pairwise Spearman rank correlations using the daily abundance data for each species with each other species in the previous time step (i.e., the lag-1 correlation, Sander et al., 2017). We used the packages 'Hmisc' (Harrel & Dupont, 2021) and 'qvalue' (Storey et al., 2020) of R (R Core Team, 2020), adjusting the significance of correlations using the Bonferroni-Holm procedure. Here, we focused only on positive co-occurrences, and links were considered significant for correlation coefficients $r > 0.3$ and $p < 0.05$ (Steinhauser et al., 2008). We used unweighted links, where potential co-occurrences were considered irrespective of the strength of the correlation.

Network co-occurrence metrics

For each year and sex, we measured descriptive metrics (number of co-occurring species and realized co-occurrences), as well as metrics related to network connectivity (connectance and link asymmetry) and cohesion (modularity). The number of co-occurring species, s, measures the number of species in each network having significant

temporal co-occurrences, while realized co-occurrences, L, describe the actual number of associations measured in the network. Connectance, C, measures the proportion in the number of realized co-occurrences from the pool of all possible ones between species of a network, providing a measure of how well associations are distributed between species (i.e., high values of C indicate an overall tendency of species to co-occur simultaneously with each other). To account for possible differences in the size of inferred networks (i.e., different number of nodes/species) that might inflate the comparison between connectance values, C was expressed as a proportion of the maximum possible connectance for each network, $C = L/[s(s-1)/2]$. We used the skewness to quantify the level of asymmetry in the frequency distribution of the number of realized co-occurrences within a network (i.e., the degree frequency distributions *sensu* Tylianakis et al., 2010). The more skewed the distribution, the greater will be the degree to which species tend to form sub-clusters of species occurring with frequency higher than expected. Finally, we used an eigenvector-based maximizing algorithm (i.e., the Louvain algorithm, Blondel et al., 2008) to measure modularity (Q), which quantifies the strength of division of a network into modules (or clusters) of densely connected nodes (Newman & Girvan, 2004). The higher the modularity, the greater the tendency of networks to cluster into subgroups of species characterized by common migration timing (i.e., high temporal co-occurrence). See Fig. 2 for a complete description of the metrics and the rationale behind their use.

The yearly measured network parameters were filtered by means of a simple moving average (SMA), with the aim of reducing background noise in the original time series and emphasizing the signal that might contain trends. Specifically, we used SMA with an automated selection procedure based on the Akaike information criterion to find the

optimal order of the moving average (Svetunkov & Petropoulos, 2017). Fitted values were then used to search for significant differences between sexes and for the existence of significant trends in the time series of measured parameters. We measured the network metrics with the package 'igraph' (Csardi & Nepusz, 2005) of R, while we used the functions 'sma' and 'sen.slope' in the packages 'smooth' (Svetunkov, 2021) and 'trend' (Pohlert, 2020), respectively, to smooth the time series and measure the Mann-Kendall statistics.

Species' co-migration fidelity

We defined the 'species co-migration fidelity' as the frequency with which two species tend to co-occur in the same module over the years. Formally, we measured this tendency by computing the level of similarity between the classifications of females and males given by modularity through the normalized mutual information (*nmi*, Danon et al., 2005). Modularity allows obtaining a classification of species based on their association to a given module in each year. For each sex we created a matrix with rows corresponding to species and columns to years, with entries indicating the module to which species belonged. The normalized mutual information was then quantified by considering the row vectors of matrices (i.e., species), measuring the pairwise congruence based on module affiliation. If two species have always been part of the same module over the years (i.e., perfect congruence, high fidelity), then $nmi = 1$; conversely, if two species never co-occurred within the same module over the years (i.e., independent, no fidelity), then $nmi = 0$. The result is therefore a symmetric

similarity matrix expressing the pairwise mutual information among species in females and males.

We used the multivariate homogeneity of groups dispersions (a multivariate analogue of Levene's test for homogeneity of variances) to test for the effect of wintering sites and foraging niches on the variability of co-migration fidelity. We therefore divided the species in three main groups (Table 1) corresponding to those wintering either north of the Sahara Desert (North African), in the sub-Saharan belt extended between the Sahara Desert and the Sudan savannah (Sahel), or in the Afrotropical ecozone (Tropical). Following Pigot et al. (2020), species were also characterized by considering their main foraging niches, which describe different combinations of diet (carnivorous feeding on invertebrates, invertivores *sensu* Pigot et al., 2020 and generalists), foraging manoeuvre (glean and sally) and substrate (surface, aerial and ground). Dispersion in co-migration fidelity was calculated as the average similarity of individual observations to their group centroid in the multivariate space, with smaller dispersion indicating high co-migration fidelity among species. Data were bias-adjusted by applying a square root correction to account for the small and unequal number of samples among groups. Between-groups differences were evaluated by means of a permutational multivariate analysis of variance (PERMANOVA) under the null hypothesis of no difference in dispersion between groups. The normalized mutual information and homogeneity of multivariate dispersions were measured by using the function ‘compare’ and ‘betadisper’ in the ‘igraph’ and ‘vegan’ (Oksanen et al., 2020) packages of R, respectively.

Results

General overview

A total of ca. 90,000 individuals where ringed during the study period for the 17 species selected in our work, with males accounting for greater numbers (ca. 51,000) than females (ca. 38,000). The number of caught individuals showed a right-skewed distribution in both sexes, with few species (e.g., the whitethroat *Sylvia communis*, the whinchat *Saxicola rubetra* and the European pied flycatcher *Ficedula hypoleuca*) showing relatively high numbers and most of the species (e.g., western black-eared wheatear *Oenanthe hispanica*, the European turtle dove *Streptopelia turtur*, and the woodchat shrike *Lanius senator*) less abundant. More details on the distribution patterns of species over the years can be found in Fig. S1 of Supporting Information.

Co-occurrence network structures

Co-occurrence networks showed significant differences between females and males for almost all measured parameters (Fig. 3a), with the only exception for the number of realized co-occurrences (t = - 0.995, df = 15.606, p < 0.335). Females showed a significantly (although not overly pronounced) lower number of co-occurring species (t = -9.291, df = 29.96, p < 0.001) and higher connectance (t = 11.875, df = 26.196, p < 0.001), while both link asymmetry (t = -17.685, df = 28.754, p < 0.001) and modularity (t = -6.877, df = 18.991, p < 0.001) were lower with respect to males (Fig. 3a).

The trend analysis highlighted substantial differences between the structural parameters of different networks (Fig. 3b). Females showed an almost stable number of co-occurring species, realized co-occurrences and connectance, while both modularity

and link asymmetry significantly decreased (Fig. 3b). Males showed a significant trend for all parameters, with the only exception of the number of realized co-occurrences (Fig. 3b). While the number of potential co-occurring species significantly increased over the years, the number of realized co-occurrences was almost stable (Fig. 3b). Interestingly, connectance showed a significant decrease corresponding to an increase of both modularity and link asymmetry (Fig. 3b).

Species' co-migration fidelity

Co-occurrence networks differed in the distribution of normalized mutual information among species (Fig. 4). Females were characterized by medium to wide ranges of the index and a poorly defined clustering structure, with three species acting as outliers (i.e., the less abundant *Oenanthe hispanica*, *Upupa epops* and *Lanius senator*, Fig. S1 in Supporting Information). Conversely, the range of the index was very restricted in males, with species belonging to (at least) four main clusters and no outliers (Fig. 4). Interestingly, species that were characterized by wide ranges of the index in females' networks (e.g., *Merops apiaster*, *Hirundo rustica*) had an extremely narrow dispersion in their male counterparts (Fig. 4).

The multivariate homogeneity of groups dispersions test did not show differences in co-migration fidelity between sexes when considering the wintering sites. However, the extent to which species in females and males tended to co-occur in the same modules over the years was dependent on their supposed wintering sites ($F_{♀}$ = 4.739, $p_{♀}$ = 0.0269; $F_{♂}$ = 5.878, $p_{♂}$ = 0.014). Both for females and males, species wintering in North Africa showed high dispersion (greater in females) with respect to those

wintering in the sub-Saharan belt and the Afrotropical ecozone (post-hoc Tukey's test $p = 0.033$), with these latter showing no significant differences and low dispersion (post-hoc Tukey's test $p > 0.5$). Overall, foraging niches were not associated with co-migration fidelity, neither in females, nor in males ($F_{♀} = 1.193$, $p_{♀} = 0.383$; $F_{♂} = 1.887$, $p_{♂} = 0.179$).

Discussion

Using an extensive dataset covering 16 years of standardized bird ringing activity, we found that sex-dependent differences in the phenology, synchrony and consistency of migration timing (*sensu* Bauer et al., 2016) have the potential to rewire the pattern of species co-occurrence within the Palearctic-African migration system, with possible long-term consequences for community dynamics and species coexistence (Suttle et al., 2007). In our sample of species, males always showed lower connectivity, higher modularity and higher co-migration fidelity than females, with almost all structural parameters following significant temporal trends. These findings indicate an ever-increasing likelihood of males to cluster into semi-independent groups of highly associated species characterized by common timing of migration, and of females to undergo the opposite pattern.

At the population level, migration phenology represents a key mechanism to cope with temporal changes in the availability of key-resources to maximize fitness at breeding grounds (Radchuk et al., 2019), whereas at community level it may be viewed as a ‘timetable’ determining ‘when’ and ‘for how long’ species interfere with each other (*sensu* Rudolf, 2019). Our findings suggest that differences in the migration timing of

females and males affect the outcome of potential interferences in a very different way. The overall tendency of females to be strongly connected and less cohesive indicates a more homogenous distribution of associations among species, unlike males which instead show higher cohesion than connectivity and, thus, a more heterogenous distribution of associations. Such differences might be related to differences in the migratory behaviour among species such as, for instance, the degree of protandry.

Sex differences in the timing of migration are widespread across animal taxa (Morbey & Ydenberg, 2001). In particular, protandry, the early arrival of males at stopover and/or breeding sites (Coppack & Pulido, 2009; Maggini & Bairlein, 2012) is a common feature in the spring migration of Palearctic-African migratory birds (Rubolini et al., 2004). Although there is no general consensus on the proximate causes regulating protandrous migration in birds (Kokko et al., 2006; Coppack & Pulido, 2009; Samplonius & Both, 2017), selection for early male arrival might have important consequences at the population level (Kokko, 2006). However, migration involves hundreds of species moving very often in overlapping time windows, so that the cumulative effect of protandry might have far reaching consequences for the outcomes of interspecific interferences in multi-species assemblages (Saino et al., 2010).

Our results suggest that protandry might act as a mechanism promoting a clustered distribution in the migration timing of species, by allowing the temporal aggregation/segregation between males. For instance, protandrous species such as the barn swallow (*Hirundo rustica*), the wheatear (*Oenanthe oenanthe*) and the collared flycatcher (*Ficedula albicollis*) all group together in a common cluster characterized by low variability in the values of normalized mutual information (Fig. 4). Others, such as the Eurasian golden oriole (*Oriolus oriolus*), the whitethroat (*Sylvia communis*) and the

whinchat (*Saxicola rubetra*) belong to a completely different and well-separated cluster. These findings indicate the onset of synchronous migration patterns between species belonging to the same cluster, and the temporal segregation between species in different clusters, ultimately suggesting how the degree of protandry can be linked to some extent to co-migration fidelity in males. Further investigations are required to study the role of different mechanisms underlying the degree of protandry, such as the intensity of sexual dimorphism in determining the observed pattern of co-occurrence.

The network inference method used in this work considers all the pairwise correlations between the ranked abundances across the whole duration of the ringing activity. Therefore, a significant co-occurrence is given by the degree to which the timings of migration of two species are significantly correlated, regardless of the time window in which they occur. As a consequence, species can be significantly associated because their abundances covary across the whole ringing period, or because their peaks are limited within specific time-windows. Moreover, abundances may not necessarily follow a unimodal distribution, as species might exhibit more than one peak as, for instance, in the case of a bimodal distribution with peaks centred at the beginning and the end of the spring passage. The high temporal connectivity, low asymmetry and modularity suggest a clear tendency of females to have an overall interspecific synchrony in the migration timing. The opposite is true for males, whose pattern of migration translates into a differential synchronization between species. Furthermore, we found such patterns to be consistent over time and within sexes, with females and males significantly decreasing and increasing, respectively, both the link asymmetry and modularity. These findings suggest an ever-increasing tendency for females to synchronize their migration timing and for males to undergo a temporal segregation

among species having different responses to endogenous factors driving migration, possibly suggesting the role of selective pressures operating on a single sex only (Kokko, 1999).

One possible explanation for the different effects between sexes is that while most studies on protandry agree on a fitness advantage for early male arrivals, independently of the mechanisms driving it, the same studies suggest that for females the costs of late arrival might be lower than those associated with arriving too early to the breeding area (Kokko 2006; Saino et al. 2010; Samplonius & Both, 2017). Therefore, ecological factors related, for example, to food availability or competition for nesting sites might have a stronger channelling effect than environmental conditions, which appear to be the main determinant of the costs of premature arrival for males.

Early studies have shown that changes in the spring migration phenology of birds crossing the Mediterranean Sea can be related to specific ecological factors associated with travel distance and competition for nesting sites, as well as to the degree of sexual dimorphism in species (Rubolini et al., 2005). For instance, species wintering closer to the breeding areas, such as those wintering in North Africa, seem to be less affected by variation in the migration schedule due to their ability to better track changing conditions in the breeding grounds (Both & Visser, 2001). Latitudinal differences in wintering sites might thus affect the phenology of spring migration by advancing the peak date of passage of species wintering further north compared to sub-Saharan ones (Maggini et al., 2020). Moreover, recent findings have shown a substantial increase (up to one day *per* year) of the migration window for species wintering south of the Sahara Desert (from ca. 25 to ca. 40 days, Maggini et al., 2020), possibly related to more favourable conditions at wintering areas allowing for faster refuelling rates and, thus,

earlier departure and/or longer residence time. Our findings suggest that, in the long term, such patterns might result in higher co-migration fidelity for species wintering in the sub-Saharan belt and in the Afrotropical ecozone, resulting in an overall consistency in the species' changes in phenology, synchrony and consistency of migration timing.

How migratory birds manage to track and adapt to changing environmental conditions during their journey to breeding areas still remains an open question, often related to the extent to which shifts in migration phenology are driven by microevolutionary changes or phenotypic plasticity (Jonzén et al., 2006; Spottiswoode et al., 2006; Gienapp et al., 2007). Notwithstanding, phenotypic plasticity recently received increasing support as a mechanism able to provide faster adaptive responses, especially for species travelling shorter distance and undergoing faster rates of phenotypic change as immediate response to changing environmental conditions (Usui et al., 2016). However, how the cumulative (plastic) responses of species affect the composition of ecological communities remains unclear (but see Turcotte & Levine, 2016). Although our study provides only indirect evidence, the results suggest that the supposed lower ability of species wintering further away from the breeding sites to track changes along the migratory route might increase the fragmentation of species' migration timing. Indeed, the low dispersion and the significant high co-migration fidelity found in trans-Saharan migrants indicate a clear tendency to arrive at the stopover site in well-defined groups of species characterized by common changes in migration phenology. Conversely, species wintering further north (i.e., North Africa) did not show the same co-migration fidelity, being also characterized by high dispersion of the index. However, we caution that these results may depend on the low number of species belonging to the North African group, which might inflate the outcomes of our analysis. Notwithstanding, our

findings would suggest that different migratory behaviours not only allow for better tracking of changing conditions along the route but has also the potential to homogenise the rewiring of possible association through times. Put otherwise, the cumulative effect of phenotypic plasticity might have opposite directional outcomes at the whole community level, by fragmenting (or homogenizing) the synchrony and consistency of phenological changes in species with low (or high) plastic responses.

Consequences for coexistence

Although co-occurrence patterns cannot be used to infer real interspecific interactions, they can reveal the emergence of potential interferences among species, especially when these are forced to share small areas in limited time frames, such as in migratory bottlenecks. This is the case of stopover areas, where birds stop to rest, refuel and seek shelter during their migration activity, and where the decision on where, when and how long to rest is driven by physiological adaptations associated with migratory behaviour and habitat quality (Fusani et al., 2009; Lafleur et al., 2016; Ferretti et al., 2021). For instance, the amount of forest cover and productivity relates to the two-step mechanism determining the spatiotemporal use of stopover areas, by serving as cues to identify high-quality habitat prior to landing and by sustaining refuelling rates of migrants (Buler & Moore, 2011; Lafleur et al., 2016). Overall, stopover areas are important to replenish energetic reserves, where the availability of suitable habitats can influence the subsequent flight range (Bayly et al., 2013; Gómez et al., 2017). However, stopover sites can have different functions not exclusively related to foraging, as their ecological context (e.g., proximity to ecological barriers, spatial isolation) and intrinsic

characteristics (e.g., diversity and abundance of resources) may determine the use made by migrants (Mehlman et al., 2005; Maggini et al., 2020; Ferretti et al., 2021).

A recent study on passerine migrants in the stopover area of Ponza has shown that most species rest for no longer than one day and, in most cases, they are not able to successfully refuel (Maggini et al., 2020). These results corroborate the hypothesis that refuelling might not be the main reason to land in this area and that, probably, birds need a simple rest before continuing the last part of their journey (Ferretti et al., 2019; Ferretti et al., 2020). Therefore, coexistence at stopover areas might not be driven exclusively by mechanisms avoiding competition for resources, but also to some sort of social interactions to avoid, for instance, the risk of predation or to gain information on novel habitats and resources (Németh & Moore, 2007; Mukhin et al., 2008; Cooper et al., 2014).

In our study, the majority of 17 selected species (ca. 60-70%) has a strictly carnivorous diet (invertivores *sensu* Pigot et al., 2020), feeding mainly on insects, being however characterized by variable foraging niches (Pigot et al., 2020). Several studies have shown that trophically similar species switch to using different foraging substrates, as well as different attack manoeuvres to avoid competition and allowing coexistence (Kent & Sherry, 2020; Pigot et al., 2020). This is the case of species living in highly competitive environments as, for instance, large colonies of seabirds, where slight differences in foraging niches represent an evolutionary adaptation to reduce niche overlap (Petalas et al., 2021). Our findings show no association between co-migration fidelity and foraging strategies, neither in females, nor in males, possibly suggesting the onset of sex-independent foraging mechanisms promoting coexistence at stopover area.

However, if refuelling is not the main reason for migrants to land in the area (Maggini et al., 2020), the onset of some sort of social (facilitative) interactions would explain the observed intersexual differences in species' co-migration fidelity. Social interactions in migratory birds have been observed in songbirds migrating south through Europe, which use interspecific calls as cues to stopover habitat quality during landfall (Mukhin et al., 2008). Also, other studies have shown the use of conspecific social information during diurnal migration by American crows (*Corvus brachyrhynchos*), which take advantage of information from other diurnally migrating bird species to locate patchily distributed carrion (Ward & Raim, 2011). More recently, Gayk et al., (2020) showed how wood warblers songbirds migrating in mixed-species flocks produce short vocalizations called 'flight calls' to reduce disorientation during migration or to increase the chance of finding high quality stopover sites, a pattern even more pronounced in phylogenetically close species breeding at the same latitude with overlapping migration timing.

Although indirectly, our findings suggest that in species with protandric migration the onset of social facilitative interactions, as cues for stopover selection or to avoid predation and disorientation, might differ between sexes. The observed tendency of males to migrate in well-defined subgroups of (almost always the same) species with synchronized migration times can be explained by the need to optimize the costs associated with predation risks *en route* and optimal resting at stopover area, to improve their competitive ability for territories at breeding areas. This would explain why, for instance, the same pattern has not been observed in females, for which the costs for territory acquisition are only marginal if compared with the risks associated with predation. Therefore, late departures and higher overall synchronization among females

would favour a lower risk of predation during their journey to breeding areas (i.e., predation-dilution effect Jones, 2003; Harts et al., 2016).

Conclusions

As animal migrations involve the simultaneous movement of individuals and species in space and time, the emergence of potential interactions is far from been rare and capable of influencing the costs and benefits of migration. Long-term phenological changes have the potential to determine the timetable dictating ‘when’, ‘how long’ and ‘with whom’ species interfere with other members of the community. Furthermore, the consistency and synchronization of such changes between individuals, species, or even sexes might influence the global economy of migration. For instance, asynchronous migrations can be observed in those species characterized by high rates of protandry, where males usually precede females during migration at the breeding and/or stopover sites. Although our results are based on a sub-sample (i.e., sexually dimorphic species) of the whole set of species passing through Ponza, they clearly indicate that advances in departures by males has led to (and could lead in the near future to) a consistent migration fidelity of those species characterized by common responses to endogenous mechanisms driving migration. Further studies, extending the taxonomic and spatiotemporal coverage of the analysis, by including for instance the whole set of ringed species, as well as information at wintering, stopover and breeding areas, will be necessary to better understand the consistency of observed patterns. Notwithstanding, our study represents an important step toward the need of considering temporally explicit data to gain new insights on the consequence of species- and sex-specific long-

term changes in migration phenology on the restructuring of avian assemblages *en route*.

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Conflict of Interest

The authors have no conflict of interest to declare.

Authors' contributions

BB conceived the paper together with CC; BB analysed the data and led the writing of the manuscript; MC prepared and analysed the data. IM and LF contributed to data collection and to writing of the manuscript. All authors have no perceived conflict of interest and contributed critically to the writing of the manuscript and gave final approval for publication.

Data Availability Statement

The data used to perform the analyses in this paper can be found at https://phaidra.vetmeduni.ac.at/view/o:114. The R script used to extract the daily

abundances of the 17 species selected in this study from the original dataset is available upon appropriate request to the corresponding author.

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List of Tables

Table 1 – List of the 17 bird species analysed in this study, with summary statistics subdivided for females and males referred to the period 2005-2020. Acronyms for different foraging niches: I-Sa, Invertivore sally air; Gen, Generalist; I-A, Invertivore aerial; I-Sg, Invertivore sally ground; G-G, Generalist ground; I-Ga, Invertivore glean arboreal; I-G, Invertivore ground.

		Total number of individuals		Mean (± SD) number of individuals		Range [min-max]			
Genus	species	Females	Males	Females	Males	Females	Males	Wintering areas	Foraging niche
Ficedula	*albicollis*	804	877	50.25 (± 48.664)	54.812 (± 46.313)	[2-153]	[3-131]	Afrotropical ecozone	I-Sa
Ficedula	*hypoleuca*	4,858	6,032	303.625 (± 129.534)	377 (± 163.376)	[112-601]	[141-791]	Afrotropical ecozone	Gen
Hirundo	*rustica*	3,395	2,076	212.187(± 60.648)	129.75 (± 48.537)	[104-337]	[62-239]	Afrotropical ecozone	I-A
Lanius	*senator*	293	342	18.312 (± 7.226)	21.375 (± 8.155)	[7-31]	[10-42]	sub-Saharan belt	I-Sg
Merops	*apiaster*	338	359	21.125 (± 10.613)	22.437 (± 15.543)	[9-48]	[2-66]	Afrotropical ecozone	I-Sa
Oenanthe	*hispanica*	159	315	9.937 (± 14.308)	19.687 (± 25.394)	[1-58]	[1-86]	sub-Saharan belt	I-Sg
Oenanthe	*oenanthe*	968	1,168	60.5 (± 27.371)	73 (± 43.411)	[20-109]	[19-150]	sub-Saharan belt	I-Sg

Oriolus	*oriolus*	751	626	46.937 (± 27.155)	39.125 (± 36.131)	[3-107]	[1-148]	Afrotropical ecozone	Gen
Phoenicurus	*ochruros*	677	2,137	42.312 (± 41.272)	133.5625 (± 205.261)	[2-166]	[1-698]	North Africa	I-Sg
Phoenicurus	*phoenicurus*	3,431	4,647	214.437 (± 154.813)	290.437 (± 207.451)	[63-596]	[28-702]	sub-Saharan belt	I-Sg
Saxicola	*rubetra*	5,367	6,255	335.437 (± 192.966)	390.9375 (± 341.965)	[4-734]	[3-1137]	Afrotropical ecozone	I-Sg
Saxicola	*torquatus*	315	624	19.687 (± 25.801)	39 (± 57.507)	[2-79]	[1-241]	North Africa	I-Sg
Streptopelia	*turtur*	251	1,639	15.687 (± 20.544)	102.437 (± 189.231)	[2-66]	[13-686]	sub-Saharan belt	G-G
Sylvia	*atricapilla*	1,692	2,483	105.75 (± 83.113)	155.187 (± 145.732)	[18-256]	[6-418]	North Africa	Gen
Sylvia	*cantillans*	4,792	9,535	299.5 (± 318.388)	595.937 (± 422.811)	[7-1328]	[20-1435]	sub-Saharan belt	I-Ga
Sylvia	*communis*	10,159	11,523	634.937 (± 486.846)	720.187 (± 670.526)	[6-1634]	[7-1955]	sub-Saharan belt	I-Ga
Upupa	*epops*	309	589	19.312 (± 25.351)	36.812 (± 34.037)	[4-112]	[6-134]	sub-Saharan belt	I-G

List of Figures

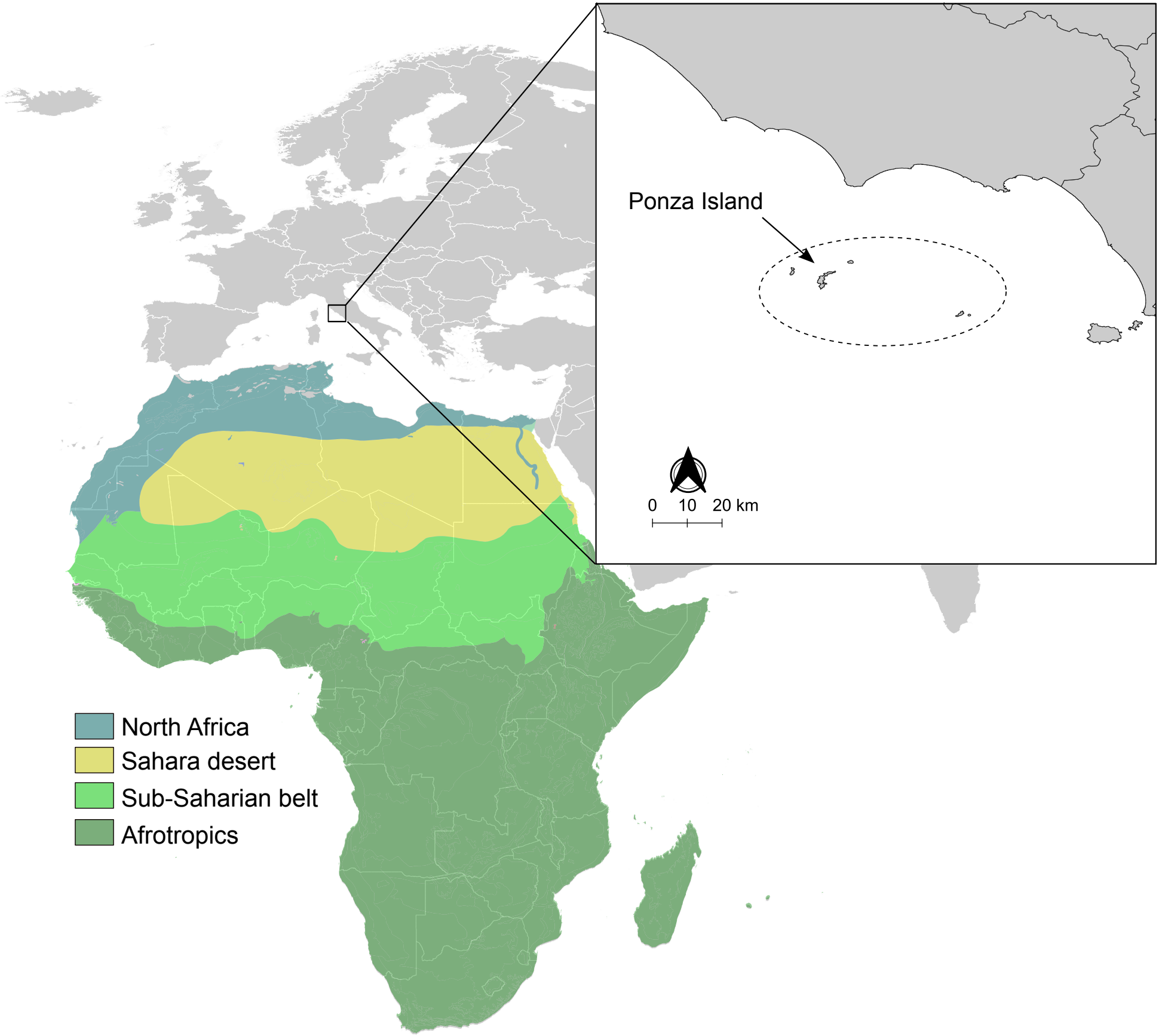
Figure 1 – Geographical framework of the study area within the Palearctic-African migration system. The dotted circle in the box shows the "Pontine" islands system with the exact location of Ponza Island. Colours in the map show a synthetic view of the main African ecoregions corresponding to the supposed wintering areas of species used in this study.

Figure 2 – Illustrative scheme of tested hypothesis. Definitions, biological interpretations and predictions of network metrics are reported in the upper table. We hypothesized that differences in the synchrony and consistency of migration timing should allow for different patterns of aggregation between sexes, with temporal co-occurrence networks in males being less connected (low connectance and high asymmetry) and more cohesive (high modularity) than in females. Advances in the migration timing of males (i.e., protandry) should increase the probability of specific groups of species to co-occur more frequently, fragmenting the networks in modules of tightly associated species (coloured silhouette in the figure). Bird silhouettes were downloaded from http://phylopic.org/, which provides online repositories without restrictions on use.

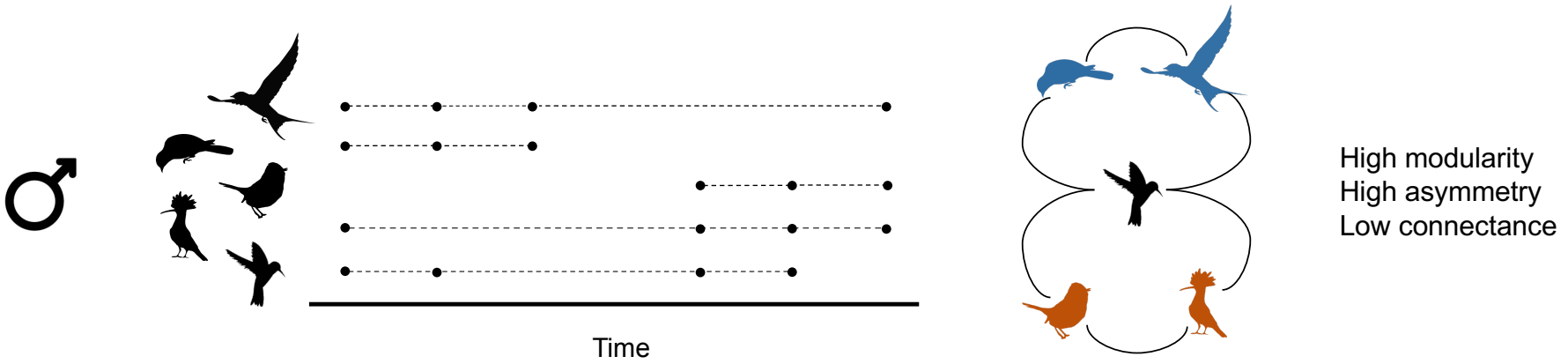
Figure 3 – Boxplots showing the distribution (a) and observed trends (b) of network metrics in females (in red) and males (in blue). Dashed black lines in each plot in (b) indicate the original time series, while solid and dotted lines show the measured trends

and uncertainty in trend slopes, respectively. Asterisks indicate the significance of trends (Mann-Kendall statistic: $^{*}p < 0.05$; $^{***}p < 0.001$).

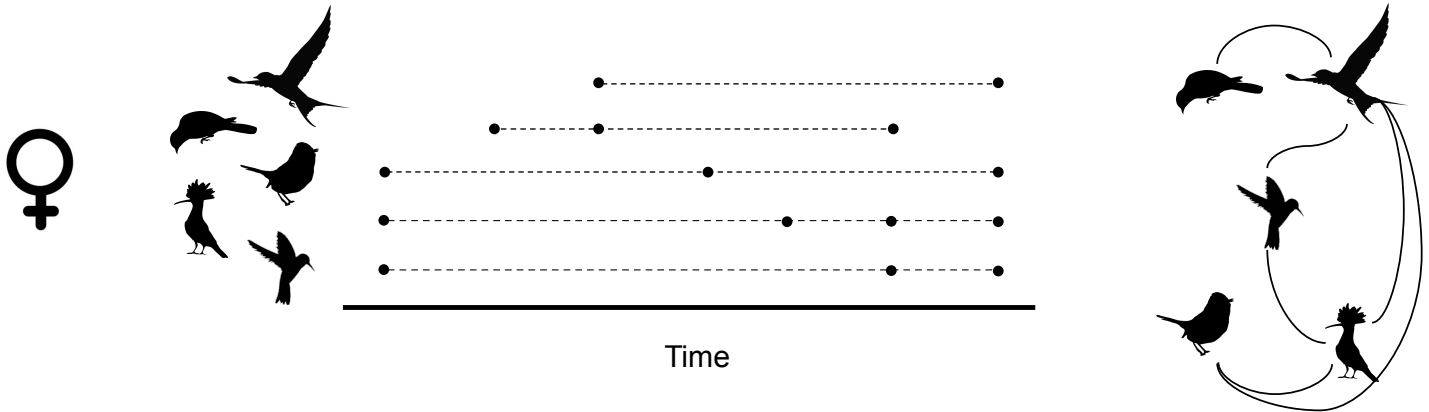
Figure 4 – Density heatmaps with hierarchical clustering showing the distribution of the species pairwise normalized mutual information in different networks (*aka* species' co-migration fidelity). Numbers on the right side of the plots show the quantiles and mean of distributions. Densities are computed by means of a gaussian kernel estimator with a bandwidth of 0.9 times the minimum of the standard deviation and the interquartile range divided by 1.34 times the sample size to the negative one-fifth power (Silverman's 'rule of thumb', Silverman 1986).


Ponza Island
0 10 20 km
North Africa
Sahara desert
Sub-Saharian belt
Afrotropics

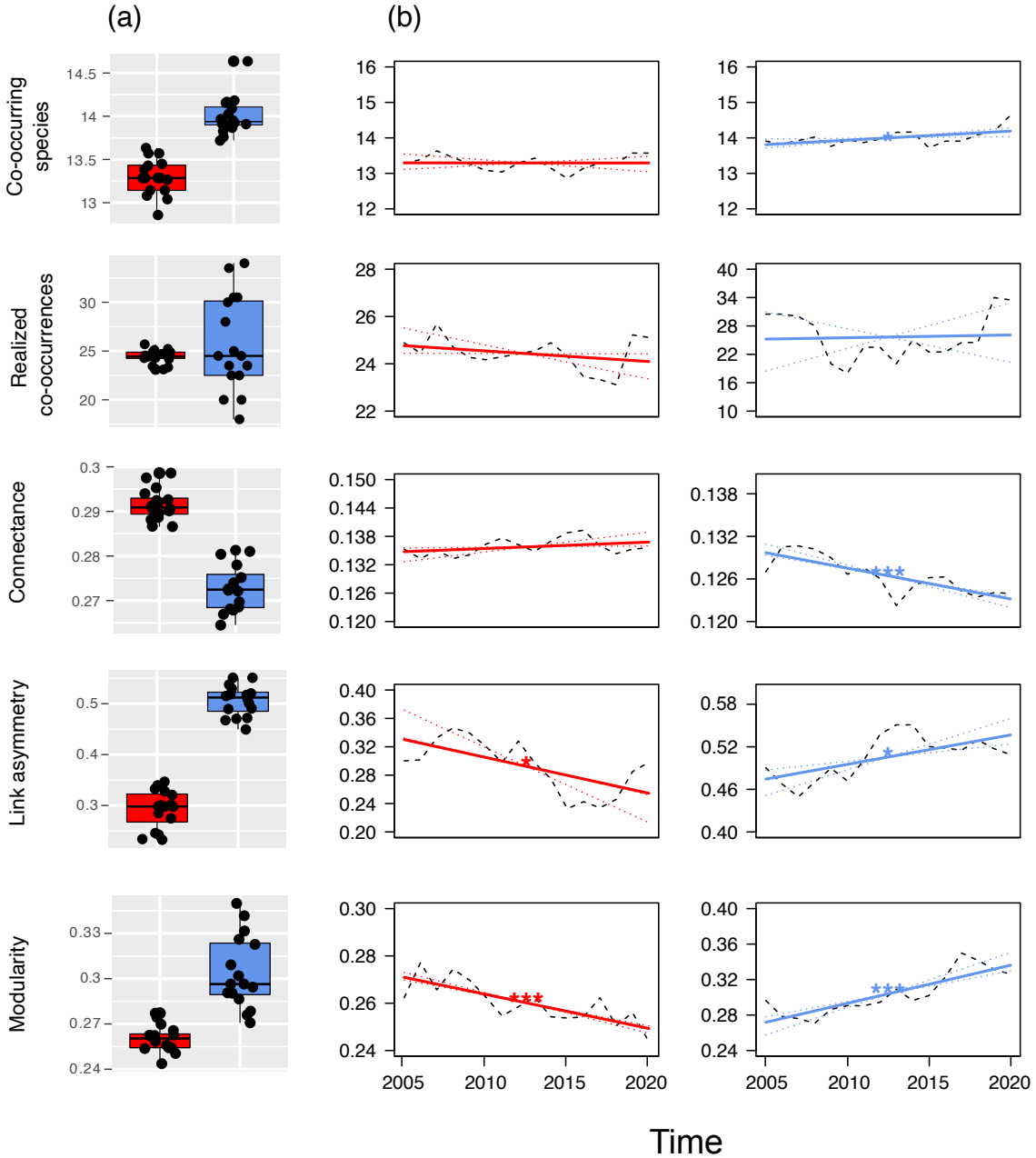
METRICS	DEFINITION	BIOLOGICAL INTERPRETATION	PREDICTION
Connectance	Proportion of observed associations out of all potential ones in the network.	Summarizes how many of all possible pairwise associations occur in the observed networks.	Connectance in males' networks should be lower than females due to a high proportion of species creating sub-groups of species tightly associated (i.e., modules).
Link asymmetry	Asymmetry in the degree distribution of associations within the network.	Summarizes how uneven the number of associations is among species.	Asymmetry is expected to be higher in males' network, reflecting an uneven rewiring of associations due to common timing in the migration pattern of some species.
Modularity	Measures the strength of network division into modules having dense connections between the nodes within the same modules but sparse connections between nodes in different modules.	Summarizes the degree to which species in the networks tend to create homogenous groups of tightly associated species.	Modularity is expected to be higher in males' network, with species being more evenly associated due to common patterns in the migration timing of some species.

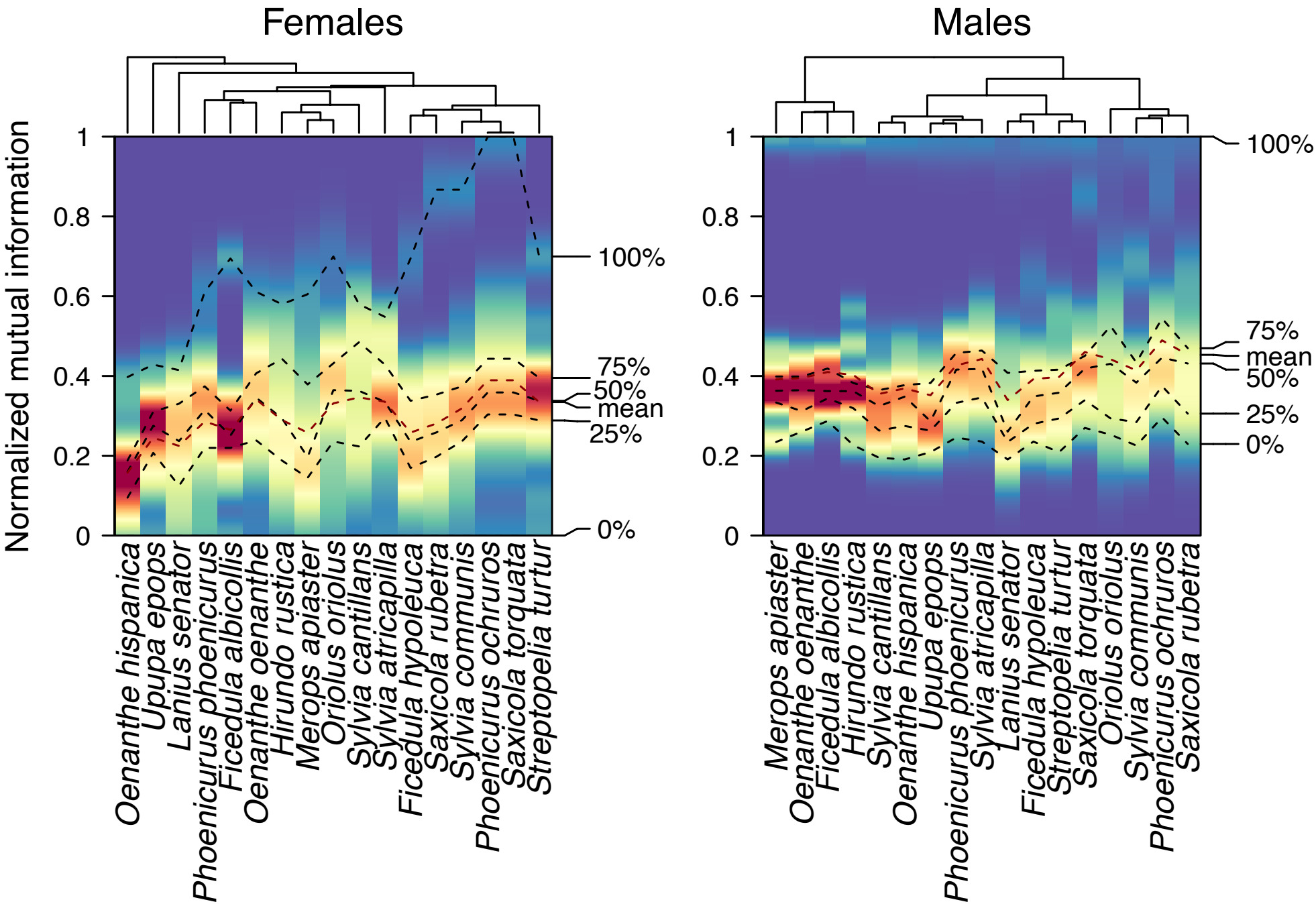


High modularity
High asymmetry
Low connectance



Low modularity
Low asymmetry
High connectance


(a)
(b)
Co-occurring species
Realized co-occurrences
Connectance
Link asymmetry
Modularity
Time


Females
Males
Normalized mutual information
1
0.8
0.6
0.4
0.2
0
100%
75%
50%
mean
25%
0%
Oenanthe hispanica
Upupa epops
Lanius senator
Phoenicurus phoenicurus
Ficedula albicollis
Oenanthe oenanthe
Hirundo rustica
Merops apiaster
Oriolus oriolus
Sylvia cantillans
Sylvia atricapilla
Ficedula hypoleuca
Saxicola rubetra
Sylvia communis
Phoenicurus ochruros
Saxicola torquata
Streptopelia turtur
Merops apiaster
Oenanthe oenanthe
Ficedula albicollis
Hirundo rustica
Sylvia cantillans
Oenanthe hispanica
Upupa epops
Phoenicurus phoenicurus
Sylvia atricapilla
Lanius senator
Ficedula hypoleuca
Streptopelia turtur
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Sylvia communis
Phoenicurus ochruros
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