

Limited potential for bird migration to disperse plants to cooler latitudes

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Climate change is forcing the redistribution of life on Earth at an unprecedented velocity^{1,2}. Migratory birds are thought to help plants to track climate change via long-distance seed dispersal^{3,4}. However, seeds may be consistently dispersed towards cooler or warmer latitudes depending on whether a plant species fruiting period coincides with the northward or southward migrations. Here we assess the potential of plant communities to keep pace with climate change via long-distance seed dispersal by migratory birds. To do so, we combine phenological and migration information with data on 949 seed-dispersal interactions between 46 bird and 81 plant species from 13 woodland communities across Europe. While most plant species (86%) in these communities are dispersed by birds migrating south, only 35% are dispersed by birds migrating north, a subset phylogenetically clustered in lineages with fruiting periods that overlap with the spring migration. Moreover, only a few Palearctic migrant species provide most of this critical dispersal service northwards. The potential of migratory birds to assist a small non-random sample of plants to track climate change latitudinally is expected to strongly influence the formation of novel plant communities, thereby affecting their ecosystem functions and community assembly at higher trophic levels.

Anthropogenic climate change is forcing the redistribution of life on Earth at an unprecedented rate^{1,2}. The distribution of organisms is constrained by the climatic conditions they can tolerate, namely their climatic envelope⁵. Driven by global warming, climatic envelopes are shifting towards higher (cooler) latitudes^{6,7}. The mean global velocity at which organisms need to shift their distributional range to retain the same temperatures has been estimated at 4.2 km per decade, although estimates exceed 100 km per decade in some regions^{2,8}. A crucial question is whether species and locally adapted genotypes will be able to move sufficiently fast to track a rapidly changing climate, which depends upon their dispersal

capacities^{5,7,9,10}. Tackling this issue is key for understanding and predicting the impacts of climate change on biological communities and the ecosystem functions they mediate, including those affecting human welfare and even climate itself via vegetation shifts^{1,11}.

Plants are the cornerstone of terrestrial ecosystems, yet there is a major knowledge gap regarding their dispersal abilities and latitudinal range shifts under current rates of global warming^{5-7,9-11}. Dispersal beyond range edges is necessary for plant species to colonize novel areas that become suitable due to climate change^{6,12}, whereas dispersal within species ranges allows the immigration of genotypes from warm-adapted populations to cooler areas that are getting warmer¹³. However, plants are sessile and the dispersal of their seeds (the process that allows new individuals to recruit far away) generally occurs within 1 km of source plants¹⁴⁻¹⁷. While local dispersal is crucial for plant recruitment, it is clearly insufficient to track current climate change, particularly in plants with generation times of several years to decades^{12,18}. Therefore, long-distance seed dispersal is required, but we need a better mechanistic understanding of these less frequent, yet highly relevant, seed-dispersal events¹⁹. Recently, migratory animals have been identified as possible suppliers of these dispersal events^{3,4} because they can transport viable seeds over tens or even hundreds of kilometers in short time periods^{3,20,21}. The most striking evidence comes from the Canary Islands (Atlantic Ocean), where about 1.2% of birds caught in migration by Eleonora's falcons (*Falco eleonora*) were found to carry seeds in their guts from the mainland, over 170 km away²⁰. Further evidence comes from island colonization by fleshy-fruited plants^{22,23}, mechanistic models parameterized with empirical data of migratory movements and gut retention times of ingested seeds²⁴, and large-scale patterns of plant genetic structure along migratory routes²⁵ (Supplementary Discussion 1). While such events seem rare, they are numerically compensated by billions of birds migrating every year worldwide through seasonal and directional displacements that are highly predictable in space and time²⁶.

In the northern hemisphere, birds typically migrate towards the equator in autumn (post-nuptial migration) and towards the North Pole in spring (pre-nuptial migration)²⁶. Thus, plants could be consistently dispersed towards warmer or cooler latitudes depending on whether their fruiting period overlaps with southward or northward bird migrations, respectively (Extended Data Fig. 1). Surprisingly, the relationship between migration directionality, plant phenology and dispersal potential towards cooler latitudes has been overlooked to date, despite this being crucial to predict the ability of plants to track climate change^{5,6,11}. In this study, we provide the first assessment of the potential of European plant communities to keep pace with climate change via long-distance seed dispersal towards cooler latitudes. We combined data on fruiting phenology and bird migration with information of pairwise interactions between frugivorous birds and fleshy-fruited plants from 13 woodland communities distributed across Europe (Fig. 1a). We focused on fleshy-fruited plants because many of their seed dispersers are migratory birds that far outnumber (both numerically and functionally) resident frugivores in European forests and woodlands^{27,28}. Moreover, fleshy-fruited plants are an important component of woody floras, accounting for a mean of 35% of species in temperate forests and 44% in Mediterranean woodlands²⁹.

We used data on seed-dispersal networks, that is, local communities of interacting bird and plant species whose links describe the presence and intensity of pairwise interactions³⁰, in this case, the quantity of seeds of each plant species dispersed by each bird species (Fig. 1b). Importantly for the purpose of this study, all networks were sampled all year-round, covering the entire fruiting phenology of all plant species and the entire migration periods of all migratory birds (Extended Data Table 1). The 13 study networks were distributed across the Mediterranean ($n = 6$) and temperate ($n = 7$) biomes of Europe (Fig. 1a), and included a total of 949 interactions (range = 24–204 per network) between 46 bird species (range = 8–21) and

81 plant species (range = 8–29) (Extended Data Tables 1, 2). Most plant species were woody (89%), the remainder being herbs (Extended Data Table 2).

In each network, we partitioned each bird-plant interaction according to the migratory state of the bird: migrating southward, migrating northward and non-migrating (Fig. 1b). To do so, we collated and combined information on the fruiting phenology of the plants and the phenology of bird migrations (Extended Data Fig. 1) (see Methods). Then, for each plant species i , we calculated the fraction of its total interaction weight (F_i) corresponding to interactions with each of the migratory states of the birds (Fig. 1b and Extended Data Fig. 2). These calculations considered whether bird populations were full migrants or partial migrants, where a fraction of the population migrates and the rest stays as residents²⁶ (see Methods for details).

Our analysis tested whether the proportion of plant species interacting with migrating birds (prevalence), the frequency of such interactions, and the number of bird species dispersing each plant species were significantly associated with the migration direction (northward or southward; see details in Methods). We used generalized linear mixed models to account for the non-normal error distributions and repeated measures per network and plant species. We also tested for differences between Mediterranean and temperate biomes in plants' dispersal potential towards cooler latitudes because these biomes differ in fruiting seasonality: Mediterranean woodlands are characterized by longer fruiting seasons²⁹, which increase the probability of phenological overlap with the northward spring migration. We found that the majority (86%) of plant species across European communities are dispersed by birds migrating south, whereas only about one third (35%) are dispersed by north-migrating birds (direction: $P < 0.001$; Fig. 2a and Extended Data Table 3). This trend was consistent across biomes, but less pronounced in Mediterranean (80% and 42%) than in temperate communities (89% and 29%) (interaction 'biome \times direction': $P = 0.008$; Fig. 2a and

Extended Data Table 3). Note that the sums of these percentages are greater than 100% because interactions with south- and north-migrating birds are not mutually exclusive (Fig. 1b), and many plant species are dispersed during both migrations (Extended Data Fig. 2 and Supplementary Methods). The interaction frequency between plants and migrating birds was also much higher during the southward (36%) than during the northward (11%) migration (direction: $P < 0.001$) (Fig. 2b and Extended Data Table 3). This trend was also consistent across biomes, but more pronounced in Mediterranean (40% and 9%) than in temperate communities (32% and 13%) (interaction 'direction \times biome': $P = 0.011$) (Fig. 2b). Finally, plants were dispersed by more bird species migrating south than north (estimated mean = 2.9 and 2.3 species per plant, respectively; direction: $P = 0.017$), a small but consistent difference across biomes (Fig. 2c and Extended Data Table 3). Importantly, these results were not an artefact of analysing networks sampled with different methods (Supplementary Discussion 2). Our findings are congruent with general patterns in fruiting seasonality and bird migrations, as the fruiting peak in temperate and Mediterranean plant communities occurs between late summer and early winter²⁹, when migratory birds move southwards²⁶.

We further tested whether closely related plant species tend to have similar seed-dispersal interactions with birds migrating south or north. The rationale is that the fruiting period of plants shows a phylogenetic signal³¹ and can thus be related to the phenological overlap with seasonal migrations (Fig. 1b). We calculated the mean interaction frequency with birds migrating in either direction at the plant species level, both across all networks ($n = 81$ species) and separately across Mediterranean ($n = 53$ species) and temperate ($n = 45$ species) networks (Fig. 2d). We found no phylogenetic signal for interaction frequency with southward migrants (all Pagel's $\lambda \ll 0.01$, $P = 1.0$). Conversely, we detected a strong phylogenetic signal for interaction frequency with northward migrants, both when considering all networks ($\lambda = 0.944$, $P = 1.2 \times 10^{-6}$) and when considering plants from Mediterranean ($\lambda =$

0.895, $P = 0.025$) or temperate ($\lambda = 0.999$, $P = 0.001$) networks separately. We also detected significant phylogenetic signal for phenological variables describing the fruiting period of the study plants, namely the start and end dates, and the period length (Extended Data Fig. 3). Accordingly, most lineages moving northwards are characterised by long fruiting periods (e.g., *Juniperus* spp.; labels 3–5 in Fig. 2d) or late fruiting periods that extend until the spring of the next calendar year (e.g., *Hedera* spp.; labels 29–30 in Fig. 2d). By contrast, plant lineages not dispersed by northward migrants are characterised by short fruiting periods between summer and early winter (e.g., *Arum* spp. and *Prunus* spp.; labels 6–7 and 65–71 in Fig. 2d, respectively). Our results indicate that the potential of plants to track climate change is clustered in certain lineages, which suggests that the novel communities that may emerge in northern latitudes in the long term will incorporate non-random subsets of the evolutionary tree of southern floras. This phylogenetic filtering might have unanticipated consequences for ecosystem functions³² and community composition at higher trophic levels^{33,34}.

European migratory birds can be classified into two distinct groups according to their migratory strategy: Palearctic migrants winter in southern Europe and northern Africa, whereas Afro-Palearctic migrants winter in sub-Saharan Africa²⁶. In addition, both groups differ in their population trends; in contrast to Palearctic migrants, Afro-Palearctic migrants are experiencing major population declines across Europe for reasons that remain poorly understood^{35,36}. More bird species per community dispersed seeds during the southward than during the northward migration (mean = 9.5 and 5.9, respectively), a difference that was consistent across biomes (Extended Data Fig. 4). Yet, most of these species were Palearctic migrants (Fig. 3a), particularly during the northward migration (mean = 87%; direction: $P = 0.005$) and in temperate communities (mean = 89%; biome: $P = 0.003$) (see Extended Data Table 4). Furthermore, we found that both migrant types differed in their functional relevance as seed dispersers, measured in terms of their interaction frequency (the proportion of the total

interaction weight per network with all birds in migration; see Methods for details). Palearctic migrants accounted for almost all interaction frequency (Fig. 3b), particularly during the northward migration (mean = 98%; direction: $P < 0.001$; see Extended Data Table 4). Palearctic migrants were also significantly more relevant in temperate (mean = 98%) than in Mediterranean communities (mean = 87%; biome: $P < 0.001$), where Afro-Palearctic birds played a more important role, particularly when migrating south (interaction ‘direction \times biome’: $P = 0.008$). These results reveal that almost all seed-dispersal services towards cooler latitudes in Mediterranean (98%) and temperate (99%) communities across Europe are provided by a handful (~ 5) of Palearctic migrant species per locality. This stronger role of Palearctic migrants can be explained by their occurrence in Europe during the winter (when invertebrates are scant and fruits abound) and their earlier spring migration northwards³⁷.

Finally, we assessed the identity and importance of different bird species contributing to seed dispersal during their northward migration. For this, we obtained bird species strength, which measures the sum of plant dependencies (relative interaction frequencies) on each bird species and, therefore, quantifies a bird species’ relevance for community-wide seed dispersal towards cooler latitudes (see Methods). To do so, we used sub-networks of the original networks that only included interactions during northward migration (blue links in Fig. 1c). Then, we obtained the cumulative species strength per biome as the sum of species strengths across Mediterranean and temperate sub-networks (Fig. 3c). Results showed that a few Palearctic migrants are disproportionately important during their northward migration. Across Mediterranean communities, the blackcap (*Sylvia atricapilla*) was by far the most important species followed by the European robin (*Erithacus rubecula*) and the song thrush (*Turdus philomelos*) (Fig. 3c); these three species accounted for 73% of cumulative strength (blackcap: 49%, robin: 15%; song thrush: 9%). Across temperate communities, the blackbird (*T. merula*) was prominently the most relevant species followed by the mistle thrush (*T.*

viscivorus) and the fieldfare (*T. pilaris*) (Fig. 3c); these thrushes accounted for 69% of cumulative strength (blackbird: 44%, mistle thrush: 15%; fieldfare: 10%). Thus, bird species did not have similar relevance in both biomes (Extended Data Fig. 5). Remarkably, the key bird species for plant dispersal towards cooler latitudes are, in general, common and abundant birds, highlighting their importance for the functioning and dynamics of ecological communities³⁸. However, their functional role in providing long-distance seed dispersal towards cooler latitudes could be at risk because bird migrations are already being disrupted by climate change^{39,40}. Moreover, some of these species are severely hunted, both legally and illegally, particularly in the Mediterranean region. In fact, *S. atricapilla* and *T. philomelos* are in the top five of the most illegally hunted birds (estimated over 1 million individuals of each species killed per year⁴¹).

Available evidence shows that seed-dispersal distances by resident animals are typically insufficient for plants to track current climate change; however, it suggests that migratory birds can supply the long-distance dispersal services required (Supplementary Discussion 1). Given that our approach is based on mainstream migratory movements, our results provide a general template on the potential for directional, long-distance seed dispersal. A further step to accurately estimate dispersal distances and directionality requires detailed movement data of migratory birds, which are necessary for the development of mechanistic seed-dispersal models²⁴. Such data are expected to come during this decade, as we are witnessing a revolution in next-generation GPS tags that will allow tracking of small frugivorous birds with unprecedented spatiotemporal resolution⁴².

The Earth is warming rapidly and is expected to continue to do so in the near future^{2,8}. Our study reveals that only about a third of fleshy-fruited plant species across European biomes will benefit from the directed long-distance dispersal by migratory birds towards northern latitudes to track favourable conditions. These few ‘winners’ are phylogenetically

clustered in plant lineages characterized by either long or late fruiting periods, and are mostly dispersed by a few common bird species whose relevance is biome-specific. Our findings are expected to be broadly generalizable to other regions in the northern hemisphere (North America and Asia), where the fruiting period of most fleshy-fruited plants occurs in autumn^{43,44}, when most birds move southwards, and where bird migration is a much more obvious phenomenon than in the southern hemisphere²⁶. The extent to which our findings are generalizable to other plant-bird systems, such as aquatic plants dispersed internally or externally by waterbirds^{21,45,46}, deserves further research. Understanding large-scale dispersal is necessary to develop conservation practices aimed at halting and mitigating biodiversity loss driven by climate change¹. Our study suggests that migratory birds are only helping a phylogenetically clustered minority of plant species to disperse towards cooler latitudes, while they are dispersing most species towards increasingly drier and hotter regions. This divergent dispersal is expected to strongly influence the formation of novel communities in the future. Finally, our results provide a baseline to assess whether climate-driven phenological shifts will exacerbate or improve this situation.

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Fig. 1 | Location of the 13 European seed-dispersal networks studied and network with bird-plant interactions in relation to bird migration. **a**, Study sites in Portugal, Spain, United Kingdom, Germany, Italy and Poland. Symbols denote the biome of the locations (Mediterranean or temperate). **b**, Hypothetical seed-dispersal network illustrating how the weight of each pairwise interaction ij can be partitioned in relation to the migratory state of the bird using the phenological overlaps between the seed-dispersal period of plant species and periods of no migration, northward migration and southward migration of bird species (Extended Data Fig. 1). F_i are interaction frequency values out of the total interaction weight of each plant species i which was with birds migrating south, north or with non-migrating birds.

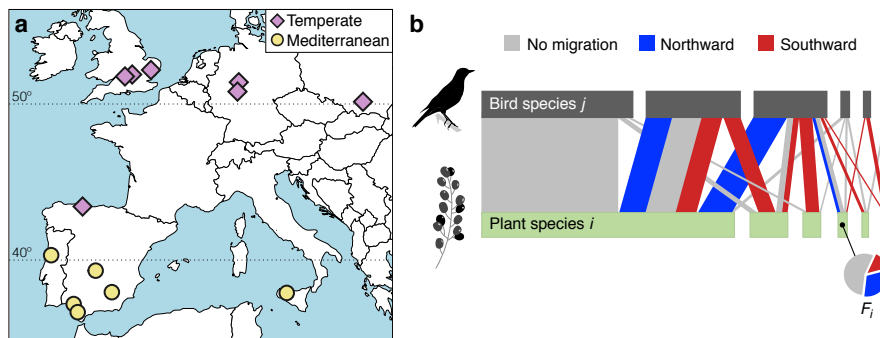


Fig. 2 | Seed-dispersal interactions of plants with migratory birds in relation to migration direction (southward or northward) and biome (Mediterranean or temperate). Large dots and bars denote means \pm 95% confidence intervals estimated by generalized linear mixed models predicting (a) the proportion of plant species interacting with birds during migration ($n = 434$ observations from 13 networks across plant species and directions) (b) the frequency of interactions with migrating birds when these occurred (zeros excluded; $n = 260$ observations), out of the total seed-dispersal interactions, and (c) the number of bird species dispersing each plant species ($n = 260$ observations). Circles denote mean values for each seed-dispersal network, whereas tiny dots denote plant-level data. **d**, Dated phylogeny of the fleshy-fruited plants in the studied networks, with root at 325 million years (shown in Extended Data Fig. 3). Numbers at the tips indicate species' codes (see species names in Extended Data Fig. 3). Coloured circles at the right of the tips indicate species-level means in interaction frequency (F_i) with birds migrating south or north calculated across all networks (All) and, separately, for Mediterranean (Med) and temperate (Tem) networks (max. frequency means in All, Med and Tem, respectively: southward = 0.80, 0.80 and 0.76; northward = 0.30, 0.23 and 0.34).

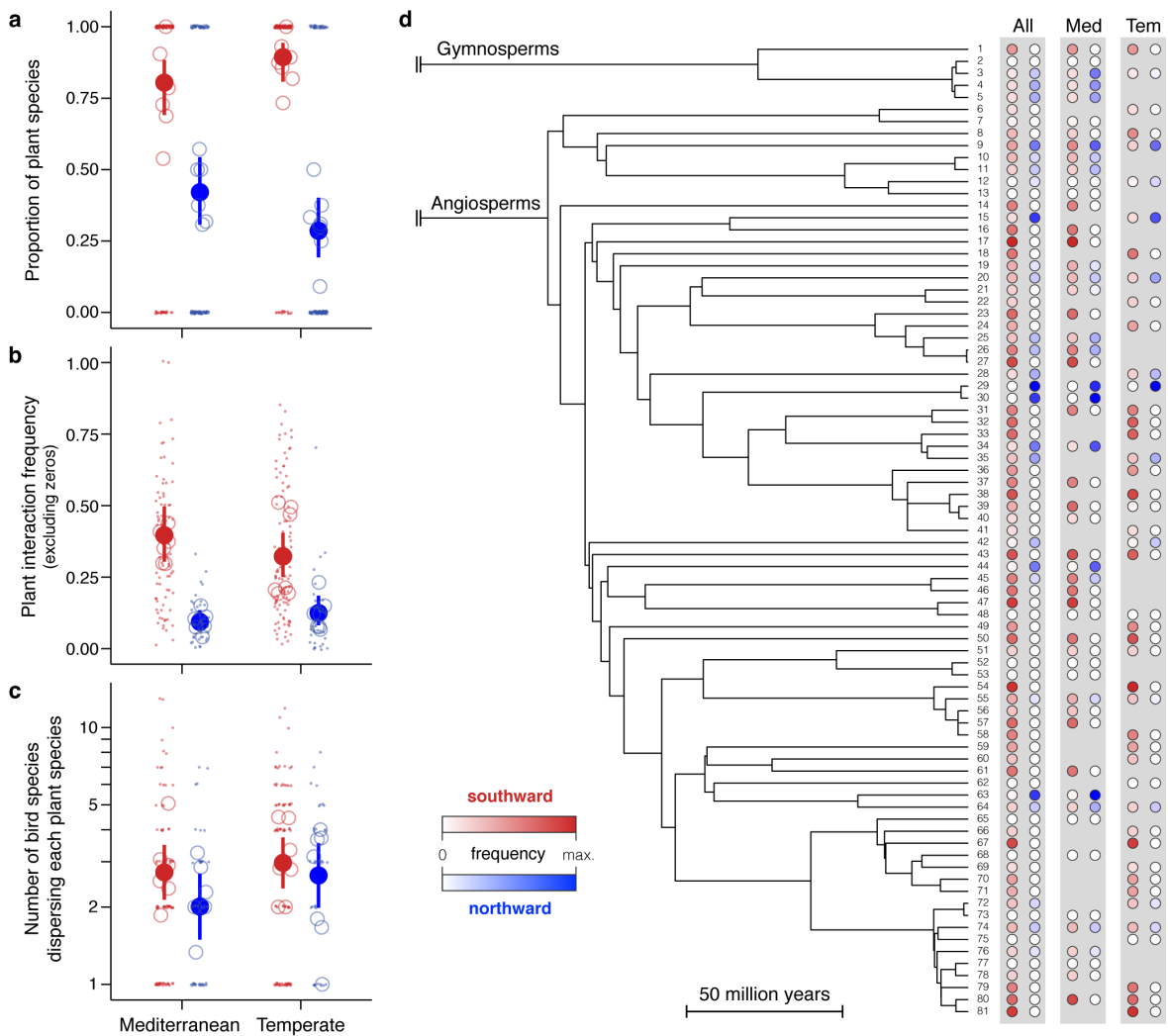
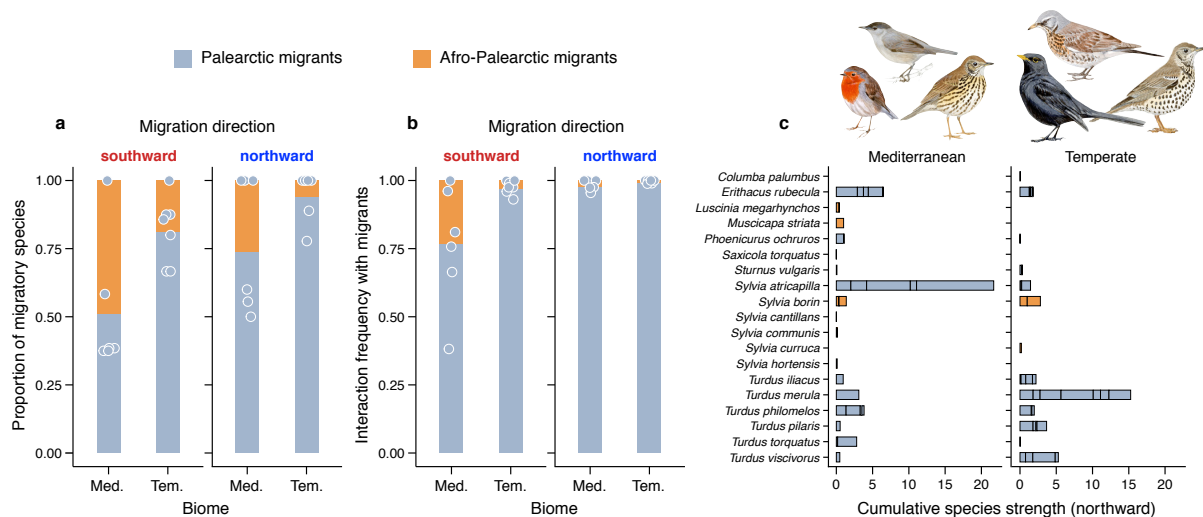


Fig. 3 | Relevance of Palearctic and Afro-Palearctic migratory birds dispersing seeds during their southward and northward migration in Mediterranean and temperate communities. **a**, Mean proportion of Palearctic and Afro-Palearctic species (pre-Saharan and sub-Saharan wintering ranges, respectively) dispersing seeds while migrating, in relation to migration direction (southwards or northwards) and biome (Mediterranean or temperate). **b**, Mean relative contributions of Palearctic and Afro-Palearctic migrants to network-level interaction frequency with migratory birds during their southward and northward migrations in Mediterranean and temperate communities. Circles in **(a)** and **(b)** denote network-level observations for Palearctic migrants. **c**, Relevance of bird species for seed dispersal towards cooler latitudes across Mediterranean and temperate fleshy-fruited plant communities, measured as the cumulative strength of bird species in sub-networks of interactions between plants and birds migrating north (blue links in Fig. 1b). Species strength quantifies a bird species' relevance across the whole plant community and high cumulative values are found in bird species with high strength values in multiple sub-networks within each biome. Bird drawings represent the three most relevant species in each biome (from left to right, *Erithacus rubecula*, *Sylvia atricapilla*, *Turdus philomelos*, *T. merula*, *T. pilaris* and *T. viscivorus*). [Illustration credit: Juan M. Varela]



Methods

Study seed-dispersal networks

We refer to interacting communities of frugivorous birds that disperse the seeds of fruiting plants as networks, which are interaction matrices where each row i represents a plant species and each column j represents a bird species. Elements in the matrices (w_{ij}) denote whether pairwise plant-bird interactions were observed ($w_{ij} > 0$) or not ($w_{ij} = 0$) and, if so, their value account for interaction weight.

Our study includes 13 seed-dispersal networks evenly distributed between the Mediterranean ($n = 6$) and the temperate biomes ($n = 7$) of Europe^{47,48} (Extended Data Table 1). All these networks are quantitative (interactions are weighted) and were sampled in natural forests and woodlands, most of them in lowland habitats (< 600 m a.s.l.) where agricultural fields surround the remnant vegetation. The single exception is the ‘Nava Correhuelas’ network, located on a well-preserved Mediterranean mountain at 1600 m a.s.l.. Eight of the 13 networks include new data obtained by the authors and five were compiled from previous studies^{27,49-51}. Seven of the eight new networks were sampled within the EU project MOBILELINKS, through field sampling of bird-dispersed seeds and subsequent disperser identification by means of DNA-barcoding analysis⁵² (see next section). The other six networks were obtained either through focal plant observations of birds feeding on fruits or through dietary analysis of birds captured in mist nets (Extended Data Table 1). In networks obtained through focal observations, we focused exclusively on pairwise interactions where the bird behaves as a legitimate seed disperser (swallowing the fruit and defecating or regurgitating viable seeds), discarding pulp-pecking and seed-predation interactions⁵³.

Importantly, the study networks were sampled all year-round (for 1–6 years; mean = 2 years), a prerequisite to cover the entire fruiting periods of all local fleshy-fruited species, as well as the pre-nuptial and post-nuptial migration periods of all migratory birds; the single

exception was the network from Sorensen²⁷ which was sampled during nine months (August to early May), covering most of the year and both migrations (Extended Data Table 1). We thus avoided using other European networks⁵⁴⁻⁵⁶ that were sampled during short temporal periods (5–6 months). The study networks included a total of 949 interactions between frugivorous birds and fleshy-fruited plants (median = 52 per network, range = 24–204). Some interactions occurred in more than one network, resulting in 563 unique pairwise interactions between 46 bird species (median = 14 per network, range = 8–21) and 81 plant species (median = 15 per network, range = 8–29). The number of bird species, plant species or interactions did not differ significantly between Mediterranean and temperate networks ($P \geq 0.20$ in one-way ANOVAs $\log_{10}[n] \sim \text{biome}$). Bird and plant species included 16 and 28 families, respectively (Extended Data Table 2). The plants included trees and shrubs (79% of species), herbs (11%) and woody vines (10%), thus, most plant species (89%) were woody.

Because we were interested in the seed-dispersal function, we expressed the interaction weights (w_{ij}) of all networks as the number of seeds of each plant species i (or the seed-rain density as seeds per m^2) dispersed by each bird species j . These weights were directly obtained in networks that sampled bird-dispersed seeds, either in seed traps for subsequent DNA-barcoding analysis or in droppings from birds captured in mist nets (see next section). Yet, in networks based on feeding observations, interaction weights were originally expressed as number of bird visits to focal plants⁵³. We then converted number of visits into number of seeds through the following two steps. First, we converted visits into fruits consumed using the parameters of a linear mixed model ($R^2_{\text{GLMM}(m)} = 0.924$) fitted to data from two European networks^{56,57} for which the number of both visits and fruits consumed were recorded for each pairwise interaction (Supplementary Methods). In a second step, we converted fruits consumed into seeds dispersed by multiplying the former by the average number of seeds per fruit of each plant species, which was obtained from the literature^{50,58-60} and from data

generated by the authors. Where the product did not result in an integer, values were rounded to the nearest integer.

All networks were combined into a single data table for subsequent incorporation of data on seed-dispersal phenology and bird-migration periods (see below), with columns for network identity, network biome, network country and bioclimatic zone, plant and bird species, and interaction weight. Hereafter, we refer to ‘seed-dispersal period’ rather than to ‘fruiting period’ because part of our phenological data was based on the presence of seeds dropped by birds in seed traps or during mist netting (see details below).

Methods for the new network data

Authorship of the eight new (unpublished) networks is shown in the ‘Author contributions’ section.

MOBILELINKS networks

Community-wide seed dispersal by frugivorous birds was sampled within the EU project ‘MOBILELINKS’ (H2020-MSCA-IF-2014-656572) in seven European landscapes (plots of 1–4 km²) located in Spain, United Kingdom, Germany, Italy and Poland (Extended Data Table 1). Six of these plots were sampled for one year (2016–2017) and one site for two complete years (2013–2015). In all plots, seed traps were placed beneath tree and shrub canopies (natural perches), and under electricity pylons (anthropogenic perches) used by birds, to quantify the magnitude of bird-mediated seed rain in the landscape (see ref.⁶¹). Seed traps were 0.22 m² plastic trays covered with wire mesh to prevent post-dispersal seed removal. Between 40 and 77 seed traps (mean = 46.3) were monitored in each study plot. Sampling surveys, in which the number of bird-dispersed seeds per trap was recorded, were conducted fortnightly; seeds were visually identified by comparison with a reference collection (see details below). The route used to survey the seed traps was also used as a 1-m wide single fixed belt transect

(range 2630–9110 m length, mean 4410 m) to search for bird-dispersed seeds and quantify seed rain in canopy-free open interspaces, where bird-mediated seed rain is less likely⁶¹. Individual seeds or droppings with seeds were sampled for DNA-barcoding (see below) analysis into 1.5- or 2.0-ml sterile tubes that were labelled and stored in a freezer at –20°C until DNA extraction. Because DNA-barcoding identification generally fails (PCR failure) in 5–10% of samples^{28,52,61}, some bird-dispersed seeds visually detected outside the transects were also sampled for DNA-barcoding analysis aiming at increasing sample sizes, particularly for locally rare plant species. Conversely, only a subsample of the seeds was generally sampled when seed traps received many seeds of certain plant species; e.g. 40–50% of the hyper-abundant *Pistacia lentiscus* seeds in Garrapilos during its fruiting peak; see ref.²⁸.

We used DNA-barcoding analysis (mitochondrial COI: cytochrome *c* oxidase subunit I) to identify the bird species responsible for the seed-dispersal events, as DNA of animal origin can be extracted from the surface of defecated or regurgitated seeds^{28,52,61}. Detailed laboratory protocols for DNA extraction, PCR, sequencing and species identification can be found in the Supplementary Methods. Resulting sequences were identified at the species level based on best sequence matches in the ‘BARCODE OF LIFE DATA’ identification system (BOLD⁶²: www.boldsystems.org), typically at a 98–100% similarity (Supplementary Fig. 1). We successfully identified the disperser species of 2991 samples (i.e. 2991 sequences; 123–1753 per network) including 3014 interaction events between a bird-plant species pair, and containing 4812 seeds (144–2193 per network); overall 3234 samples containing 5181 seeds were analyzed, with an identification success of 92.5% (PCR failure occurred in 7.5% of samples). All barcoding sequences obtained in the present study are publicly available in the data file ‘MOBILELINKS_DNA_barcoding_data.csv’ deposited at the DRYAD repository (<https://doi.org/10.5061/dryad.15dv41nx3>).

After DNA extraction for bird DNA barcoding, we visually identified seed species according to their morphology. To do so, we compared the seeds against a personal reference collection (owned by JPGV) and pictures from a guide of seeds of European fleshy-fruited species that includes plants from the Mediterranean and temperate biomes⁵⁸. The exception were 11 samples whose initial identification was not possible and for which we conducted DNA-barcoding analysis using chloroplast MaturaseK gene (*matK*)⁶³ (see detailed lab protocols in the Supplementary Methods). Seed species from these 11 samples were identified through the following three steps: (1) we obtained a short list of species from the best sequence matches in BLAST⁶⁴; (2) we used such short list to identify candidate fleshy-fruited plant species that were present around the study sites; and (3) we used the final reduced list of candidate plant species to identify seed species visually according to seed morphology, as explained above. Thus, this DNA-barcoding analysis served us to short list and guide visual identification (see details in the Supplementary Methods). All seed samples are stored by JPGV at the laboratory of Botany in the University of Cádiz (Spain), and plant sequences are publicly available in the data file ‘MOBILELINKS_DNA_barcoding_data.csv’ deposited at the DRYAD repository (<https://doi.org/10.5061/dryad.15dv41nx3>).

We used DNA-barcoding identifications to calculate the relative contribution (f_{ijk}) of each bird species j to the seed-rain density of plant species i beneath perch type k as $f_{ijk} = n_{\text{DNA-}ijk} / n_{\text{DNA-}ik}$, where n_{DNA} is the number of DNA-barcoded seeds. We then estimated the seed rain of each plant species dispersed by each bird species beneath different perch types as $sr_{ijk} = sr_{ik} \times f_{ijk}$, where sr_{ik} is average seed rain (seeds per m²) of plant species i measured in seed traps located beneath perch type k (see similar procedures in refs.^{28,65}). Finally, we calculated the site-level (network-level) seed-rain density of each plant species dispersed by each bird species (sr_{ij}) as the weighted mean of sr_{ijk} values across perch types, using the

number of seed traps per perch type as weighting factor. The result (sr_{ij}) was the interaction weights (w_{ij}) of pairwise interactions in these networks, expressed as ‘seeds per m²’.

Vale Soeiro network

Community-wide seed dispersal by frugivorous birds was sampled in a plot of natural woodland of ~0.5 km² located in central Portugal. A total of 168 m of mist nets of different lengths (nine mist nets of 15 m, two of 12 m and one of 9 m) were operated fortnightly during 5 h after dawn for six years (2012–2018). Nets were visited every 30 min and captured birds were individually placed in ringing bags for up to 30 min until they ejected droppings. Out of a total of 4462 bird captures, 1330 produced droppings with seeds ($n = 3398$ seeds).

Defecated or regurgitated seeds were later extracted and identified by comparison with a reference collection. A quantitative seed-dispersal network was built where w_{ij} represented the total number of seeds of each plant species i dispersed by each bird species j .

Seed-dispersal phenology

Seed-dispersal phenology is the period in which plants bear ripe fruits and disperse their seeds. We obtained bioclimate-level data on seed-dispersal phenology of the plant species in the study networks; the bioclimatic zone of the study networks is shown in Extended Data Table 1. We targeted on bioclimate-level phenology because the dispersal period of a given plant species may differ between bioclimatic zones⁶⁶. We used distinct data sources: published studies^{27,50,55,59,67-77}, where information was extracted from figures, tables and text; and our own data associated to the new eight networks we obtained through fortnightly sampling surveys. Published studies included data on entire fleshy-fruited plant communities (e.g. ⁶⁷), in some cases associated to the published networks we compiled (e.g. ^{50,59,72}), as well as data on specific taxa (e.g. ^{68,70}). In some cases, we also used personal observations for the phenology of certain plant species at specific bioclimatic zones. From each data source, we

obtained the ‘start’ and the ‘end’ of the seed-dispersal period ($D_{\text{start}}-D_{\text{end}}$) of each plant species. We used a monthly scale (0–12) where exact values represent the transition between months (e.g. 0 = end of December – beginning of January; 1 = end of January – beginning of February; etc.) and half values represent the midpoint within months (e.g. 1.5 = mid-February). For instance, a fruiting period from mid-June to late September was expressed as $D_{\text{start}} = 5.5$ and $D_{\text{end}} = 9$. We added 12 to D_{end} whenever it belonged to the next calendar year; hence, a dispersal period from mid-November to late March was expressed as $D_{\text{start}} = 10.5$ and $D_{\text{end}} = 15$ (3 + 12) (see Extended Data Fig. 1). Most phenological data were obtained at a 0.5-month accuracy (~2 weeks), although in a few data sources the information was found at a 0.25-month accuracy. We obtained data for 143 of the 150 unique ‘plant species–bioclimate’ combinations (95%) from 288 original data entries as, in many cases, we obtained data from multiple sources or years for the same plant species at a particular bioclimate (see Extended Data Fig. 6). When the same data source included information from different fruiting seasons (e.g. ^{72,76}), we averaged D_{start} and D_{end} values of each plant species across seasons. Then, we obtained unique D_{start} and D_{end} values for each ‘plant species–bioclimate’ combination by averaging across data sources. With this procedure, we aimed at conservatively obtaining the most representative and generalizable seed-dispersal period of each plant species within each bioclimate. We also obtained the minimum D_{start} and the maximum D_{end} recorded, that is, the longest fruiting period per ‘plant species–bioclimate’ combination in order to perform a complementary analysis using a less conservative approach (Supplementary Discussion 2). For the seven remaining ‘plant species–bioclimate’ combinations lacking specific information, we used data from the closest bioclimate. For example, we used phenological data of *Rhamnus lycioides* from thermo-Mediterranean bioclimate for one meso-Mediterranean network. Phenological data were finally incorporated into the network data (see section ‘*Directional migration in seed-dispersal interactions*’ below).

Migrant types and phenology of bird migrations

We used published information^{59,78-85} and our own data (periodic bird censuses and mist netting captures) to classify the bird species in each study network as ‘resident’ (non-migrant), ‘Palearctic migrant’ (birds that breed in Europe and winter in southern Europe and pre-Saharan Africa) and ‘Afro-Palearctic migrant’ (birds that breed in Europe and winter in sub-Saharan Africa)²⁶. Palearctic migrants are often partial migrants, that is, only a fraction of their populations migrates while the other fraction behaves as resident²⁶. For this reason, we characterized the proportion of migrants (P_{migrants}) in the bird populations of the study networks by means of a semi-quantitative variable: 0, non-migrant population; 0.1, only a minor fraction migrates; 0.25, a larger fraction migrates but non-migrants prevail; 0.5, roughly half of the population migrates; 0.75, migrants prevail; 0.9, only a minor fraction does not migrate; 1: the whole population migrates (for this variable, we also used published information^{79,80,82,83,86-92} and our own data). Hence, Palearctic migrants showed P_{migrants} values ranging from 0.1 to 1. We also classified fully migrant populations ($P_{\text{migrants}} = 1$) as ‘wintering’, ‘summer-breeding’ or ‘transient’ depending, respectively, on whether birds occur locally during the winter, the breeding season, or during short periods while migrating (stopover site)²⁶.

We obtained country-level phenological data for the pre-nuptial (northward) and post-nuptial (southward) migrations of the bird species in the study networks (see countries in Extended Data Table 1). In this case, we targeted on country-level phenology to capture geographical variation in the timing of migrations, as this information was mainly obtained from bird migration atlases of the study networks’ countries: Iberia (Spain and Portugal)^{79,80}, Italy^{82,83}, the UK⁸⁶, Germany⁸⁷ and Poland⁸⁸. We also obtained data from specific references from Poland⁸⁹⁻⁹² and websites from recognized ornithological organizations in the case of Spain (www.seo.org/listado-aves-2)⁸¹ and the UK (www.birdtrack.net)⁹³. We gathered

phenological data for the 119 unique ‘bird species–country’ combinations. From each data source, we obtained the ‘start’ and the ‘end’ of both the northward (N : prenuptial) and southward (S : postnuptial) migration periods ($N_{\text{start}}-N_{\text{end}}$ and $S_{\text{start}}-S_{\text{end}}$, respectively) from figures, tables and text. All phenological data were obtained at a 0.5-month accuracy (~ 2 weeks). As with seed-dispersal phenology, we used a monthly scale in which exact values represent the transition between months and half values represent the midpoint within months (see ‘Seed-dispersal phenology’). Only in 3 cases (2.5% of the 119 ‘bird species–country’ combinations) for which we did not obtain some of the four migration dates at the country level ($N_{\text{start}}-N_{\text{end}}$ and $S_{\text{start}}-S_{\text{end}}$), we used migration phenology available for the Western Palearctic region⁸⁵ or at a continental coarse scale (www.eurobirdportal.org). Phenological data were finally incorporated into the network data (see section ‘*Directional migration in seed-dispersal interactions*’ below).

Directional migration in seed-dispersal interactions

Phenological overlap during migrations

For each plant-bird interaction in each network, we calculated the phenological overlap between the seed-dispersal period of the plant and the northward and southward migration periods of the bird ($O_{\text{north-}ij}$ and $O_{\text{south-}ij}$, respectively; O units are months). We calculated these overlaps as the difference between the minimum ‘end’ and the maximum ‘start’ of both periods; $O_{\text{north-}ij} = \min(D_{\text{end-}i}, N_{\text{end-}j}) - \max(D_{\text{start-}i}, N_{\text{start-}j})$, and $O_{\text{south-}ij} = \min(D_{\text{end-}i}, S_{\text{end-}j}) - \max(D_{\text{start-}i}, S_{\text{start-}j})$. Prior to these calculations, we added 12 to the dates of the northward migration (spring) of bird species j whenever the seed-dispersal period of plant species i extended to the next calendar year (if $D_{\text{end-}i} > 12$). This solved, for instance, the fact that a period of northward migration $N_{\text{start-}j} - N_{\text{end-}j} = 2-4$ does not overlap mathematically with a seed dispersal period $D_{\text{start-}i} - D_{\text{end-}i} = 10-16$, despite there being a true phenological overlap ($N_{\text{start-}j} - N_{\text{end-}j} = 2-4 = 14-16$). Negative and ‘NA’ values obtained were converted into zeros (no

overlap) as they represented, respectively, the lack of either phenological overlap or migration (resident birds). We provide a graphical representation for the overlap calculations of this section in Fig. 1b and Supplementary Fig. 3.

Total phenological overlap

Apart from the phenological overlap during migrations, we also calculated the total phenological overlap ($O_{\text{total-}ij}$) as the whole period during which a bird species coincides locally with the seed-dispersal period of each plant species in the study networks. When bird populations were fully or partially resident ($P_{\text{migrants}} < 1$), the bird species occurs locally all year round and, thus, $O_{\text{total-}ij}$ was equal to the length of the seed-dispersal period ($O_{\text{total-}ij} = D_{\text{end-}i} - D_{\text{start-}i}$). When bird populations were transient (only occur locally during migration), $O_{\text{total-}ij}$ was equal to the sum of phenological overlap during northward and southward migrations ($O_{\text{total-}ij} = O_{\text{north-}ij} + O_{\text{south-}ij}$). In the case of wintering migrants, their occurrence in the local communities spans from their arrival at the beginning of the southward migration (S_{start}) to the end of their departure at the end of the northward migration (N_{end}); thus, for wintering migrants: $O_{\text{total-}ij} = \min(D_{\text{end-}i}, N_{\text{end-}j}) - \max(D_{\text{start-}i}, S_{\text{start-}j})$. In the case of summer migrants, their presence in local communities spans from their arrival at beginning of the northward migration (N_{start}) to their complete departure at the end of the southward migration (S_{end}); thus, for summer migrants: $O_{\text{total-}ij} = \min(D_{\text{end-}i}, S_{\text{end-}j}) - \max(D_{\text{start-}i}, N_{\text{start-}j})$. Whenever $D_{\text{end-}i}$ extended to the next calendar year ($D_{\text{end-}i} > 12$), we added 12 to the migration dates in order to calculate the actual $O_{\text{total-}ij}$ (Supplementary Fig. 3).

Frequency of seed-dispersal interactions during migrations

We then used the phenological overlaps during migration ($O_{\text{north-}ij}$ and $O_{\text{south-}ij}$) and the total phenological overlap ($O_{\text{total-}ij}$) to calculate, for each plant-bird interaction ij , the frequency of seed-dispersal interactions in which the bird is migrating northward as $F_{\text{north-}ij} = P_{\text{migrants-}j} \times O_{\text{north-}ij} / O_{\text{total-}ij}$, and southward as $F_{\text{south-}ij} = P_{\text{migrants-}j} \times O_{\text{south-}ij} / O_{\text{total-}ij}$. The calculation was the

fraction of the total phenological overlap accounted for by each migration period and weighted by the proportion of migrants in the bird population ($P_{\text{migrants-}j}$). For instance, if $O_{\text{north-}ij} = 3$ and $O_{\text{total-}ij} = 6$, then $F_{\text{north-}ij} = 0.5$ if the whole bird population migrates ($P_{\text{migrants-}j} = 1$; $F_{\text{north-}ij} = 1 \times 3/6$), but $F_{\text{north-}ij} = 0.05$ if only a minor fraction of the bird population migrates ($P_{\text{migrants-}j} = 0.1$; $F_{\text{north-}ij} = 0.10 \times 3/6$). For fully resident populations, $O_{\text{north-}ij}$, $O_{\text{south-}ij}$ and $P_{\text{migrants-}j}$ equal 0, and thus $F_{\text{north-}ij}$ and $F_{\text{south-}ij}$ too. We calculated the frequency of seed-dispersal interactions in which the bird is non-migrating as $F_{\text{non-}ij} = 1 - (F_{\text{north-}ij} + F_{\text{south-}ij})$. Through this approach, we made the assumption that interaction frequency is uniformly distributed throughout $O_{\text{total-}ij}$. We consider it to be a conservative assumption because the magnitude of seed dispersal by frugivorous birds throughout the fruiting season can be roughly constant (our assumption), unimodal symmetric, unimodal skewed, or even multimodal, depending on the plant species (e.g. refs.^{27,50,71}) and the local context (e.g. ref.⁷⁴).

Finally, for each plant species i in each study network, we calculated the frequency of seed-dispersal interactions during which the bird is migrating south ($F_{\text{south-}i}$), north ($F_{\text{north-}i}$) or is not migrating ($F_{\text{non-}i}$), as the weighted means of F_{ij} across j bird species. Weighting was done by the interaction weight w_{ij} of each pairwise interaction. Hence, F_i values represent the fraction of the total interaction weight of plant species dispersed by birds with distinct migratory states ($F_{\text{south-}i} + F_{\text{north-}i} + F_{\text{non-}i} = 1$; see Extended Data Fig. 2).

Statistical analyses

Four out of the 81 plant species (*Crataegus monogyna*, *Hedera hibernica*, *Rosa canina* and *Rubus fruticosus*) actually represented operational taxonomic units in certain networks due to the local occurrence of congeneric species whose seeds did not allow unambiguous species-level identification (*Crataegus laevigata*, *Hedera maderensis*, other *Rosa* and other *Rubus* species, respectively). In these cases, we used the name of the most common species to match

the species name across networks in order to use plant species as random factor in mixed models and match a unique tip label in the plant phylogeny (see below).

All generalized linear mixed models (GLMMs) described below were fitted using the R package *glmmTMB* (v. 0.2.3)⁹⁴ and the significance of fixed effects (P -values of Type II Wald χ^2 -tests) was computed using the ‘Anova’ function of the R package *car* (v. 2.1-6)⁹⁵.

Seed-dispersal interactions

We fitted GLMMs to test whether the migration direction (southward or northward), the biome (Mediterranean or temperate), and the interaction between these two fixed factors were significantly associated with (i) the proportion of plant species (prevalence) interacting with birds during migration ($n = 434$ observations), (ii) the frequency of seed-dispersal interactions with birds during migration (whenever these interactions occurred; non-zero F_i) out of the total interaction weight, and (iii) the number of bird species dispersing each plant species during migration (whenever interactions during migration occurred; non-zero values); $n = 260$ observations in (ii) and (iii). Importantly, the prevalence and frequency of interactions with migrants were not interrelated in both migrations (Supplementary Methods). All models included network identity and plant species nested within network as random factors (random intercepts) to account for the repeated measures per network (different plant species) and per plant species within networks (same plant interacting with birds migrating southward and northward). Prevalence among plant species was modelled as a Bernoulli-distributed variable with logit link function ($1: F_i > 0; 0: F_i = 0$). Frequency ($F_i > 0$) was modelled as a mixed-effects beta regression with logit link function where the dispersion parameter ϕ of the beta distribution was allowed to vary in response to the interactive effects of direction and biome ($\Delta\text{AIC} = -25$ relative to a model with fixed ϕ)⁹⁶. For modelling purposes, we transformed F_i values as follows: $F_i' = (F_i (n - 1) + 0.5)/n$, where n is the total number of observations⁹⁶. This transformation compresses the closed interval ($0 \leq y \leq 1$) within the open interval ($0 < y < 1$)

because the values modelled by beta distribution are defined on the latter⁹⁶ (range of $F_i > 0$: 0.0009–1; range of F_i' : 0.0020–0.9988); the estimated means and 95% confidence intervals reported in the article (Fig. 3b) were previously back-transformed ($F_i = (F_i' n - 0.5)/(n - 1)$). The number of bird species per plant was modelled as a Poisson-distributed variable with log link function.

Phylogenetic signal in plants

We tested for the presence of phylogenetic signal in the plant species means across networks regarding their interaction frequency (including zeros) with birds migrating southward and northward, for all plant species ($n = 81$) and separately for species in Mediterranean and temperate networks ($n = 53$ and 45 , respectively). We calculated plant species means across networks because many plant species participated in several networks (mean = 2.7, range = 1–12), either from the same or different biomes. For example, *Cornus sanguinea* participated in six temperate networks, *Myrtus communis* in four Mediterranean networks, and *Crataegus monogyna* in 12 networks from both biomes. We extracted information about the phylogenetic relatedness of the plants present in the study networks from a dated phylogeny of seed plants (Spermatophyta)⁹⁷ with a backbone based on Magallón et al.⁹⁸. The tree was prepared by dropping tips other than the 81 plant species of interest using the R package *ape* (v. 5.3)⁹⁹; the resulting tree contained one polytomy, which was resolved randomly using the function ‘multi2di’. Phylogenetic signal was assessed through Pagel’s λ ¹⁰⁰, a statistic that varies between 0 (phylogenetic independence) and 1 (species’ traits covary in direct proportion to their shared evolutionary history under a Brownian motion model of quantitative trait evolution)¹⁰¹. Intermediate values of λ indicate that traits have evolved according to a process in which the effect of phylogeny is weaker than in the Brownian model¹⁰¹. Pagel’s λ seems strongly robust to polytomies and suboptimal branch-length information¹⁰². Significant phylogenetic signal ($\lambda > 0$) is calculated through a likelihood ratio

test comparing the likelihood of the model fitted to the data (observed λ) to that of a model in which λ was fixed to 0¹⁰¹. These analyses were performed using the R package *phytools* (v. 0.6-99)¹⁰³. As a complementary analysis, we also tested for phylogenetic signal in seed-dispersal phenology since the frequency of interactions with migrant birds is ultimately related to fruiting phenology (see details in Extended Data Fig. 3).

Migratory birds

We fitted GLMMs to test whether the migration direction, the biome, and the interaction between these two fixed factors were significantly associated with the number of migratory bird species in the study networks dispersing plants during migration, and with the proportion of Palearctic and Afro-Palearctic species. The species richness was modelled as a Poisson-distributed variable with log link function and the proportion of Palearctic species as a Bernoulli-distributed variable with logit link function (1: Palearctic; 0: Afro-Palearctic; note that the proportion of both migrant types are fully interdependent). Network identity was included as a random factor (random intercepts) to account for the repeated measures within networks ($n = 26$ observations in each case, i.e., ‘network–direction’ combinations). We also assessed whether the relevance of Palearctic and Afro-Palearctic migrants varied between migrations and biomes. To do so, we calculated the frequency of interactions with Palearctic and Afro-Palearctic birds during migration in each network out of the total interaction weight with all migrant birds during both southward and northward migrations (e.g. $f_{\text{Palearctic}} = W_{\text{Palearctic}} / W_{\text{all migrants}}$; where $W_{\text{all migrants}}$ is the total interaction weight with all migrants per network, thus, $W_{\text{all migrants}} = W_{\text{Palearctic}} + W_{\text{Afro-Palearctic}}$). For this analysis, we used only data from Palearctic migrants ($f_{\text{Palearctic}}$, $n = 26$ observations, i.e., ‘network–direction’ combinations) because frequencies from both migrant types are fully interdependent ($f_{\text{Palearctic}} + f_{\text{Afro-Palearctic}} = 1$). We fitted a GLMM to test whether the migration direction, the biome, and their interaction were significantly associated with the interaction frequency with Palearctic migrants. This

model was as a mixed-effects beta regression with logit link function⁹⁶, where the dispersion parameter ϕ of the beta distribution was allowed to vary in response to the additive effects of direction and biome ($\Delta\text{AIC} = -29$ relative to a model with fixed ϕ). For modelling purposes, we transformed values for beta regression as explained above (range of $f_{\text{Palaearctic}}$: 0.3818–1.0; range of $f_{\text{Palaearctic}}'$: 0.3841–0.9904); the estimated means reported in the article (Fig. 4b) were also back-transformed as explained above. Network identity was included as random factor (random intercepts) to account for the repeated measures within networks.

Finally, we used ‘species strength’, a species-level network metric¹⁰⁴, to identify the most relevant bird species dispersing seeds during each migration. Species strength is the sum of plant dependencies (relative interaction frequencies) on each bird species, therefore, it quantifies a bird species’ relevance across all the fleshy-fruited plant community¹⁰⁵. We calculated species strength of migratory birds ($n = 24$ species) using the R package *bipartite* (v. 2.13)¹⁰⁴ in sub-networks of the original networks that only included seed-dispersal interactions either during southward or northward migration (sub-networks of red or blue links in Fig. 2c, respectively), where strength quantifies a bird species’ relevance as seed disperser during each migration. We then obtained the cumulative species strength (sum across sub-networks) per direction and biome combinations (Mediterranean-south, Mediterranean-north, temperate-south, temperate-north). This way, very high cumulative values can only be found in migratory bird species with high strength values in multiple networks per biome. We used nonparametric Kendall’s rank correlations to test whether, in each biome, the cumulative species strength in the southward and northward sub-networks were correlated, which would indicate that bird species generally display a proportional role in both migrations (Extended Data Fig. 5). Besides, we used Kendall’s rank correlations to test whether, for each migration, the cumulative species strength in the Mediterranean and

temperate sub-networks were correlated, which would indicate that bird species generally display a proportional role in both biomes (Extended Data Fig. 5).

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Acknowledgements The ‘Molecular Ecology Laboratory’ (LEM–EBD–CSIC; ISO9001:2015 and ISO14001:2015 certifications) and the ‘Research Unit of Biodiversity’ (UO–CSIC–PA) provided logistical support for molecular analyses. We thank Leticia Viesca and Eduardo Cires for laboratory assistance and Juan M. Varela for the bird illustrations. **Funding:** Barcoding data were obtained within an Individual Fellowship from the Marie Skłodowska-Curie Actions (H2020-MSCA-IF-2014-656572: MobileLinks) and supported by a GRUPIN grant from the Regional Government of Asturias (IDI/2018/000151). ‘King Jaume I’ awarded to AT supported data collation during two postdoctoral contracts. J.P.G.-V. is supported by a Spanish ‘Ramón y Cajal’ fellowship (RYC-2017-22095) and a grant from the Spanish MICINN (PID2019-104922GA-I00 / AEI / 10.13039/501100011033). B.R. is supported by a Spanish ‘Juan de la Cierva Incorporación’ fellowship (IJCI-2017-33475). R.H. is funded by the Portuguese Foundation for Science and Technology (UID/BIA/04004/2020). B.I.S. is supported by a Royal Commission for the Exhibition of 1851 Research Fellowship. W.J.S. is funded by Arcadia.

Author contributions J.P.G.-V. conceived the study. J.P.G.-V., J.A., J.M.A., R.S.B., T.B., G.E.-A., N.F., D.G., J.C.I., P.J., P.K., W.J.S. and E.V. obtained data of seven new seed-dispersal networks within the EU project ‘MOBILELINKS’. J.M.A. and J.C.I. also conducted the molecular analyses for these networks. L.P.d.S. and R.H. provided data of one unpublished network. P.J. provided data of two published networks. B.R., J.P.G.-V. and A.T. gathered data on fruiting phenology and bird migrations; J.P.G.-V., B.R., J.A. and B.I.S. analyzed the data; J.P.G.-V. wrote the first manuscript draft and all authors worked on the final version.

Competing interests The authors declare no competing interests.

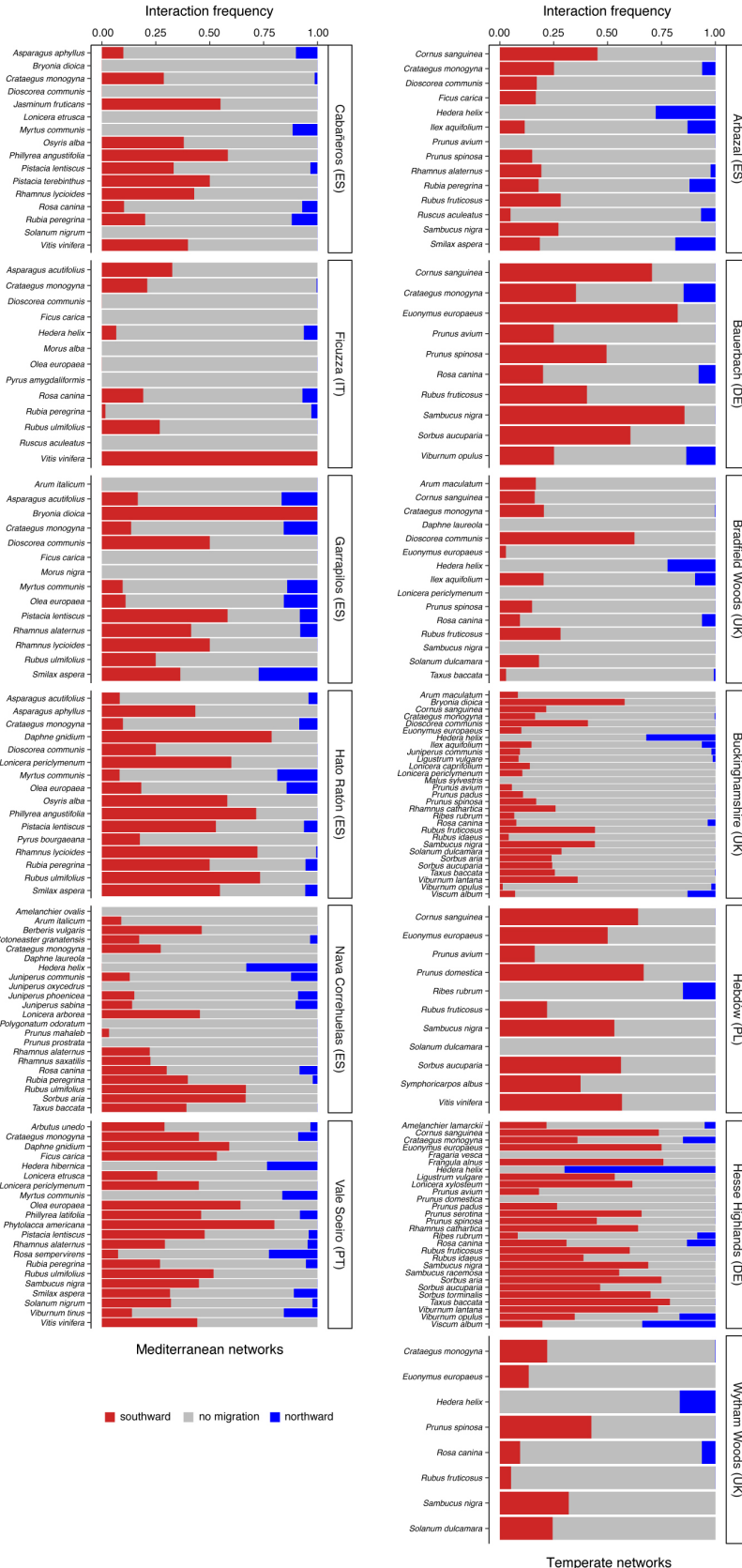
Data availability

All data used in the analyses are available through the Dryad Digital Repository (<https://doi.org/10.5061/dryad.15dv41nx3>). The dated phylogeny of seed plants (Spermatophyta) used to obtain our phylogenetic tree is available through GitHub (https://github.com/FePhyFoFum/big_seed_plant_trees/releases). Data on bird body weight used for size classification (Supplementary Figure 2) were obtained from EltonTraits 1.0 available through Figshare (<https://dx.doi.org/10.6084/m9.figshare.c.3306933>).

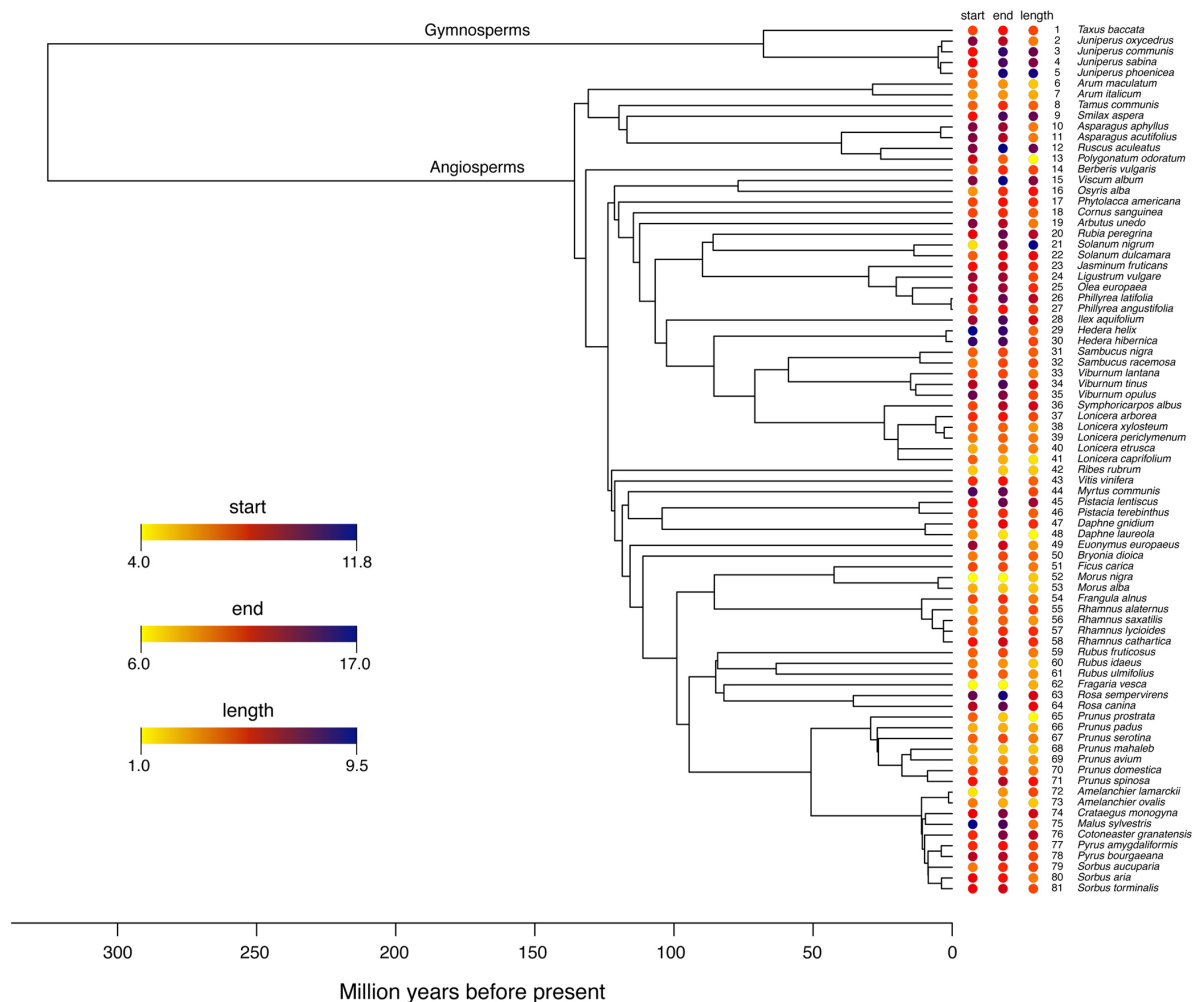
Code availability

The R scripts used to generate all results and figures are available through the Dryad Digital Repository (<https://doi.org/10.5061/dryad.15dv41nx3>).

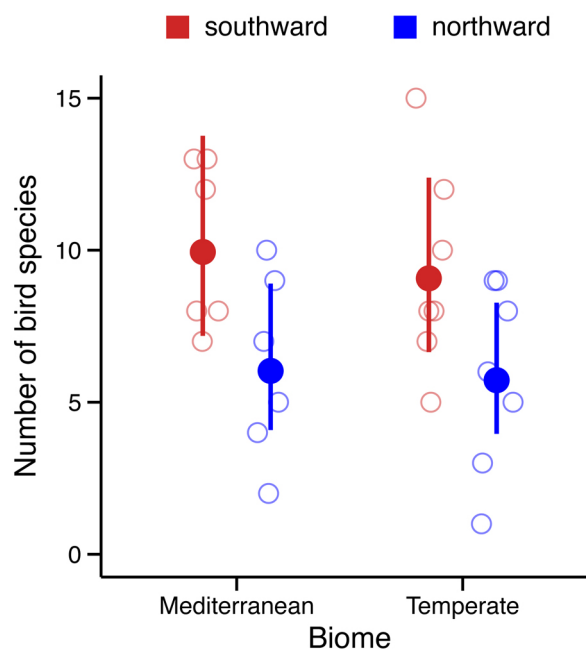
Extended Data Fig. 2 | Estimated interaction frequencies (F_i , relative weights) of plant species within each study network with birds migrating northward (blue), southward (red) or non-migrating (grey). Each panel represents a seed-dispersal network. The upper row of panels includes temperate networks, whereas the lower row includes Mediterranean networks (DE: Germany; ES: Spain; IT: Italy; PL: Poland; PT: Portugal; UK: United Kingdom).



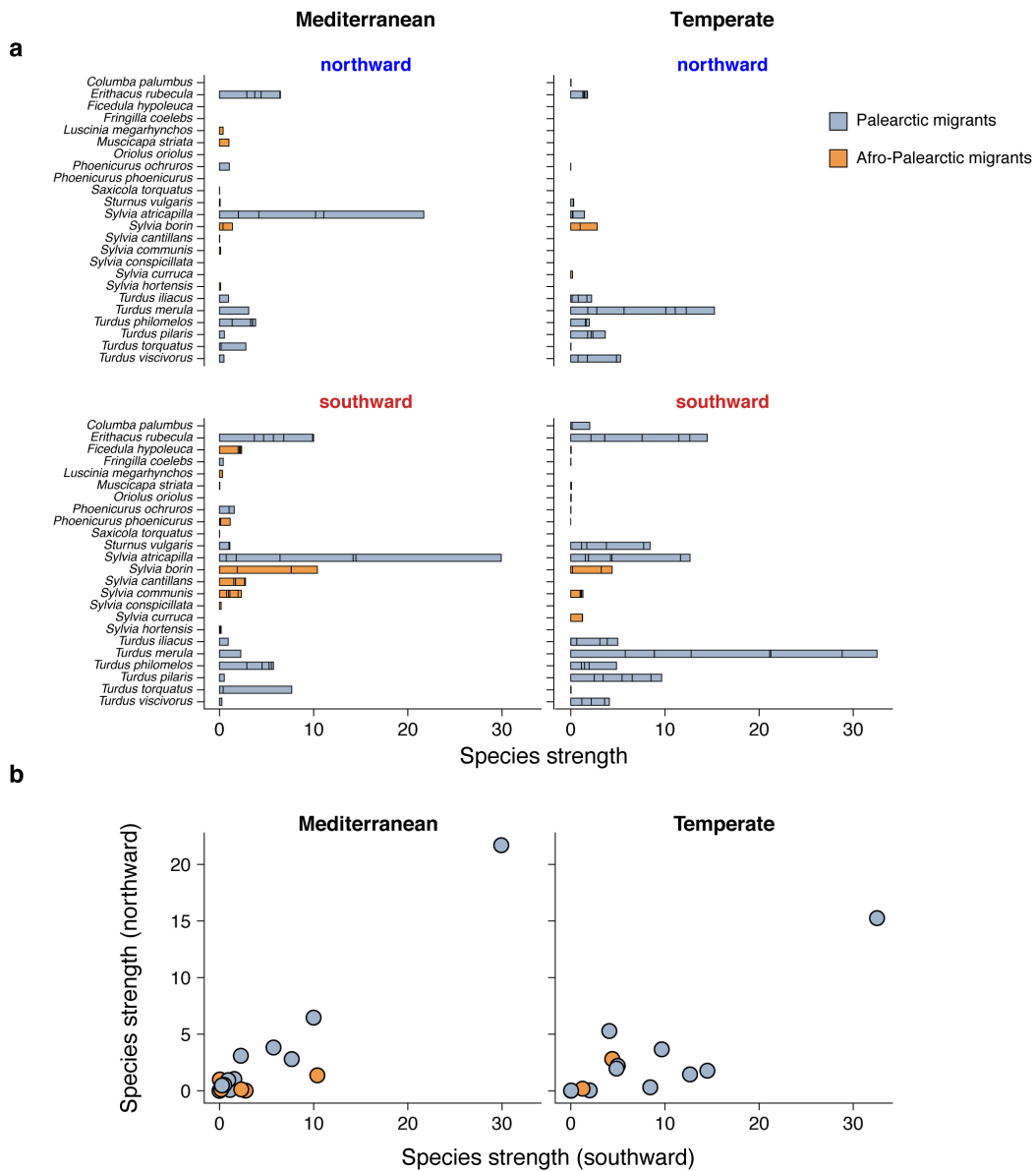
Extended Data Fig. 3 | Variables of the seed-dispersal phenology across the phylogenetic tree of plants. Phylogenetic signal was tested in plant species means across networks in start and end dates (D_{start} and D_{end}), as well as in length ($D_{\text{length}} = D_{\text{end}} - D_{\text{start}}$) of the seed-dispersal period ($n = 81$ plant species) by means of Pagels' λ , as described in section 'Statistical analyses – Phylogenetic signal in plants' of the Methods. The three phenological variables showed significant phylogenetic signal (D_{start} : $\lambda = 0.800$, $P = 0.0103$; D_{end} : $\lambda = 0.781$, $P = 0.0015$; D_{length} : $\lambda = 0.419$, $P = 0.0343$). To test for phylogenetic signal we previously calculated species-level means for D_{start} , D_{end} and D_{length} across bioclimates (see Extended Data Fig. 6). For this reason, we assessed the amount of variance in these phenological variables accounted for by bioclimate as compared to that accounted for by species through linear-mixed models (LMMs) that included 'bioclimate' as fixed factor and 'plant species' as random factor to account for the repeated measures per species (LMMs). Bioclimate only accounted for a minor fraction of variance (1–3%) in D_{start} , D_{end} and D_{length} , as shown by the marginal R^2 values (variance explained by fixed effects; $R^2_{\text{LMM}(m)} = 0.028$, 0.01 and 0.023 respectively). In contrast, the high conditional R^2 values (variance explained by both fixed and random effects; $R^2_{\text{LMM}(c)} = 0.780$, 0.845 and 0.643, respectively) indicated that plant species accounted for most variance in the three phenological variables. LMMs were fitted with the R package package *lme4* (v. 1.1-19)¹⁰⁶.



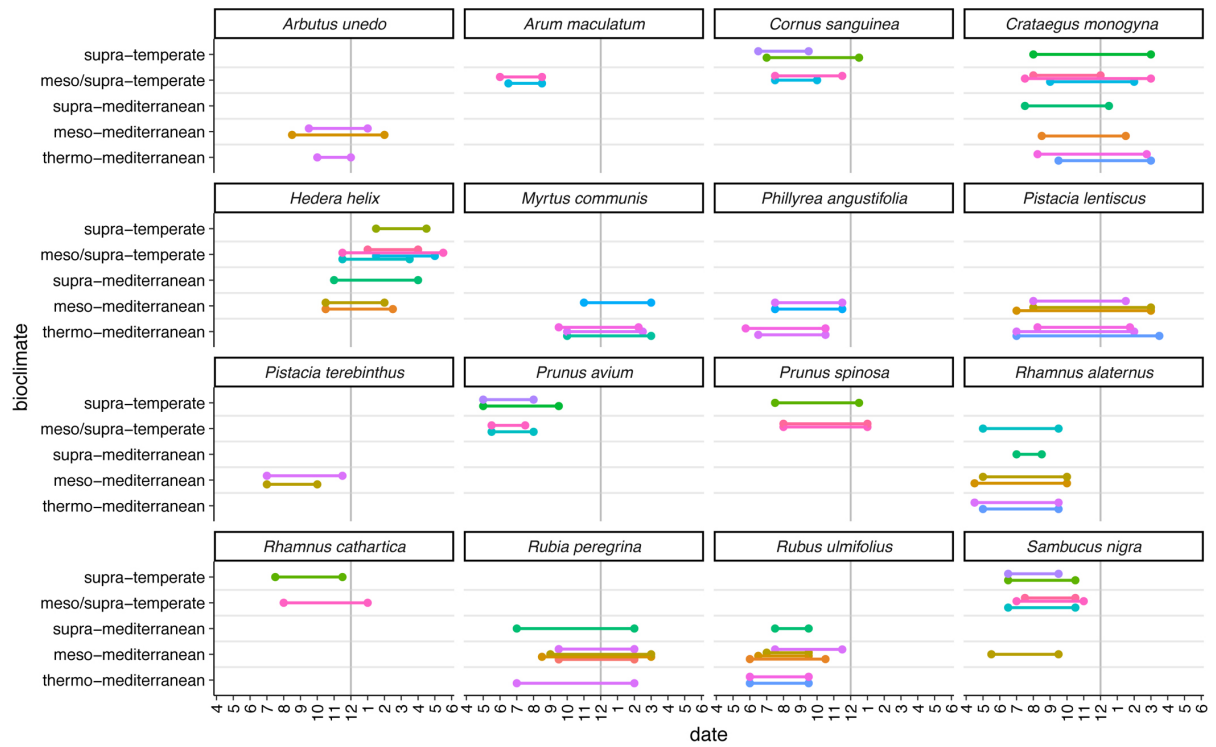
Extended Data Fig. 4 | Number of migratory bird species interacting with plants during migration per network in relation to migration direction (southward or northward) and biome (Mediterranean or Temperate). Large dots and bars denote means \pm 95% confidence intervals estimated by a linear mixed model, whereas circles denote values for each seed-dispersal network ($n = 26$ observations, 13 networks \times 2 directions). Only migration direction had significant effects on the number of migratory bird species interacting with plants during migration in the GLMM (Poisson family and log link function) testing the effects of ‘migration direction’ (Wald- $\chi^2 = 11.08$, $P = 0.0009$), ‘biome’ (Wald- $\chi^2 = 0.17$, $P = 0.6789$), and their interaction (Wald- $\chi^2 = 0.02$, $P = 0.8921$). Model estimates \pm se: intercept = 2.297 ± 0.156 ; direction (northward) = -0.500 ± 0.208 ; biome (temperate) = -0.091 ± 0.215 ; direction (northward) \times biome (temperate) = 0.039 ± 0.288 ; ‘southward’ and ‘Mediterranean’ were used as the reference categories (intercepts) for the factors direction and biome. A mean of 9.5 bird species per community dispersed plants during their southward migration, but only 5.9 species did so during the northward migration.



Extended Data Fig. 5 | (A) Bird-species strength accumulated across seed-dispersal sub-networks between plants and birds migrating southward or northward, in Mediterranean and temperate biomes; species strength quantifies a bird species' relevance across all the fleshy-fruited plant community¹⁰⁵ ($n = 24$ species). Note that some bird species have stacked values from multiple sub-networks, while other species only participated in a single sub-network. **(B)** The cumulative species strength in the 'southward' and 'northward' sub-networks were significantly correlated in the Mediterranean (Kendall's $\tau = 0.396$, $P = 0.0129$) and the temperate biome ($\tau = 0.588$, $P = 0.0006$), indicating that bird species generally display a proportional role in both migrations. However, the cumulative species strength in the Mediterranean and temperate biome were not correlated, neither in the northward ($\tau = 0.276$, $P = 0.1089$) and southward sub-networks ($\tau = 0.263$, $P = 0.0764$); correlation between left and right panels in (A). These results indicate discordance between biomes in the identity of bird species contributions to community-wide seed dispersal during each migration. Pearson's r yielded qualitatively similar results, with higher coefficient values in the significant correlations ($r = 0.946$ and 0.847).



Extended Data Fig. 6 | Bioclimate-level plant phenology from multiple sources. Subset of 16 out of the 81 plant species present in the study networks illustrating how, in many cases, we obtained data on seed-dispersal phenology from multiple sources for the same ‘plant species–bioclimate’ combination. Colour codes denote different data sources. A vertical grey line divides the calendar year.



Extended Data Table 1 | Characteristics of the European seed-dispersal networks studied.

N	Country	Network name	Source	Sampling type	Biome	Bioclimate	Latitude	Longitude	Years (n)	N_{plant}	N_{bird}	N_{int}
1	Spain	Hato Ratón	A	Mist-netting	Mediterranean	thermo-	37.1804	-6.3240	1981–1983 (2)	16	17	120
2	Spain	Nava Correhuelas	A	Observations	Mediterranean	supra-	37.9409	-2.7927	1997–1999 (2)	22	21	111
3	Spain	Garrapilos	B	DNA-barcoding	Mediterranean	thermo-	36.6589	-5.9493	2013–2015 (2)	14	21	56
4	Spain	Cabañeros	B	DNA-barcoding	Mediterranean	meso-	39.3213	-4.2896	2016–2017 (1)	16	14	44
5	Spain	Arbazal	B	DNA-barcoding	temperate	thermo/meso-	43.4313	-5.4971	2016–2017 (1)	14	14	52
6	Portugal	Vale Soeiro	C	Mist-netting	Mediterranean	meso-	40.3127	-8.4035	2012–2018 (6)	21	13	76
7	Italy	Ficuzza	B	DNA-barcoding	Mediterranean	meso-	37.8923	13.3749	2016–2017 (1)	13	12	30
8	UK	Buckinghamshire	D	Observations	temperate	meso/supra-	51.8910	-0.9120	1980–1985 (5)	29	19	204
9	UK	Wytham Woods	E	Observations	temperate	meso/supra-	51.7667	-1.3333	1979–1980 (1)	8	8	24
10	UK	Bradfield Woods	B	DNA-barcoding	temperate	meso/supra-	52.1808	0.8239	2016–2017 (1)	15	11	36
11	Germany	Hesse Highlands	F	Observations	temperate	supra-	51.3957	8.9427	1997–1999 (2)	28	18	128
12	Germany	Bauerbach	B	DNA-barcoding	temperate	supra-	50.7950	8.8230	2016–2017 (1)	10	9	30
13	Poland	Hebdów	B	DNA-barcoding	temperate	supra-	50.1429	20.4274	2016–2017 (1)	11	16	38

N_{plant} , N_{bird} and N_{int} denote the number of plant species, bird species and plant-bird interactions in each network. Network biomes obtained from ^{47,48}; network bioclimates obtained from ⁴⁸. Source: (A) P. Jordano⁴⁹; (B) J.P. González-Varo *et al.* (EU project MOBILELINKS, this study); (C) L.P. da Silva and R. H. Heleno (this study); (D) B. Snow and D. Snow⁵⁰; (E) A.E. Sorensen²⁷; (F) H. Stiebel and F. Bairlein⁵¹

Extended Data Table 2 | List of bird and plant species of the 13 study networks.

Bird species list		Plant species list			
Bird species	Bird family	Plant species	Plant family	Plant species	Plant family
<i>Alectoris rufa</i>	Phasianidae	<i>Amelanchier lamarckii</i>	Rosaceae	<i>Prunus avium</i>	Rosaceae
<i>Columba palumbus</i>	Columbidae	<i>Amelanchier ovalis</i>	Rosaceae	<i>Prunus domestica</i>	Rosaceae
<i>Corvus corax</i>	Corvidae	<i>Arbutus unedo</i>	Ericaceae	<i>Prunus mahaleb</i>	Rosaceae
<i>Corvus corone</i>	Corvidae	<i>Arum italicum</i> †	Araceae	<i>Prunus padus</i>	Rosaceae
<i>Corvus monedula</i>	Corvidae	<i>Arum maculatum</i> †	Araceae	<i>Prunus prostrata</i>	Rosaceae
<i>Cyanistes caeruleus</i>	Paridae	<i>Asparagus acutifolius</i>	Asparagaceae	<i>Prunus serotina</i>	Rosaceae
<i>Cyanopica cooki</i>	Corvidae	<i>Asparagus aphyllus</i>	Asparagaceae	<i>Prunus spinosa</i>	Rosaceae
<i>Dendrocopos major</i>	Picidae	<i>Berberis vulgaris</i>	Berberidaceae	<i>Pyrus amygdaliformis</i>	Rosaceae
<i>Emberiza calandra</i>	Emberizidae	<i>Bryonia dioica</i> †	Cucurbitaceae	<i>Pyrus bourgaeana</i> *	Rosaceae
<i>Erethacus rubecula</i>	Muscicapidae	<i>Cornus sanguinea</i>	Cornaceae	<i>Rhamnus alaternus</i>	Rhamnaceae
<i>Falco tinnunculus</i>	Falconidae	<i>Cotoneaster granatensis</i>	Rosaceae	<i>Rhamnus cathartica</i>	Rhamnaceae
<i>Ficedula hypoleuca</i>	Muscicapidae	<i>Crataegus monogyna</i>	Rosaceae	<i>Rhamnus lycioides</i>	Rhamnaceae
<i>Fringilla coelebs</i>	Fringillidae	<i>Daphne gnidium</i>	Thymelaeaceae	<i>Rhamnus saxatilis</i>	Rhamnaceae
<i>Gallinula chloropus</i>	Rallidae	<i>Daphne laureola</i>	Thymelaeaceae	<i>Ribes rubrum</i>	Grossulariaceae
<i>Garrulus glandarius</i>	Corvidae	<i>Euonymus europaeus</i>	Celastraceae	<i>Rosa canina</i>	Rosaceae
<i>Lanius excubitor</i>	Laniidae	<i>Ficus carica</i>	Moraceae	<i>Rosa sempervirens</i>	Rosaceae
<i>Luscinia megarhynchos</i>	Muscicapidae	<i>Fragaria vesca</i> †	Rosaceae	<i>Rubia peregrina</i> ‡	Rubiaceae
<i>Muscicapa striata</i>	Muscicapidae	<i>Frangula alnus</i>	Rhamnaceae	<i>Rubus fruticosus</i>	Rosaceae
<i>Oriolus oriolus</i>	Oriolidae	<i>Hedera helix</i> ‡	Araliaceae	<i>Rubus idaeus</i>	Rosaceae
<i>Parus major</i>	Paridae	<i>Hedera hibernica</i> ‡	Araliaceae	<i>Rubus ulmifolius</i>	Rosaceae
<i>Phasianus colchicus</i>	Phasianidae	<i>Ilex aquifolium</i>	Aquifoliaceae	<i>Ruscus aculeatus</i>	Asparagaceae
<i>Phoenicurus ochruros</i>	Muscicapidae	<i>Jasminum fruticans</i>	Oleaceae	<i>Sambucus nigra</i>	Adoxaceae
<i>Phoenicurus phoenicurus</i>	Muscicapidae	<i>Juniperus communis</i>	Cupressaceae	<i>Sambucus racemosa</i>	Adoxaceae
<i>Pica pica</i>	Corvidae	<i>Juniperus oxycedrus</i>	Cupressaceae	<i>Smilax aspera</i> ‡	Smilacaceae
<i>Picus sharpei</i>	Picidae	<i>Juniperus phoenicea</i>	Cupressaceae	<i>Solanum dulcamara</i> †	Solanaceae
<i>Picus viridis</i>	Picidae	<i>Juniperus sabina</i>	Cupressaceae	<i>Solanum nigrum</i> †	Solanaceae
<i>Saxicola torquatus</i>	Muscicapidae	<i>Ligustrum vulgare</i>	Oleaceae	<i>Sorbus aria</i>	Rosaceae
<i>Sitta europaea</i>	Sittidae	<i>Lonicera arborea</i>	Caprifoliaceae	<i>Sorbus aucuparia</i>	Rosaceae
<i>Streptopelia decaocto</i>	Columbidae	<i>Lonicera caprifolium</i> ‡	Caprifoliaceae	<i>Sorbus torminalis</i>	Rosaceae
<i>Sturnus unicolor</i>	Sturnidae	<i>Lonicera etrusca</i> ‡	Caprifoliaceae	<i>Symphoricarpos albus</i>	Caprifoliaceae
<i>Sturnus vulgaris</i>	Sturnidae	<i>Lonicera periclymenum</i> ‡	Caprifoliaceae	<i>Dioscorea communis</i> †	Dioscoreaceae
<i>Sylvia atricapilla</i>	Sylviidae	<i>Lonicera xylosteum</i>	Caprifoliaceae	<i>Taxus baccata</i>	Taxaceae
<i>Sylvia borin</i>	Sylviidae	<i>Malus sylvestris</i>	Rosaceae	<i>Viburnum lantana</i>	Adoxaceae
<i>Sylvia cantillans</i>	Sylviidae	<i>Morus alba</i>	Moraceae	<i>Viburnum opulus</i>	Adoxaceae
<i>Sylvia communis</i>	Sylviidae	<i>Morus nigra</i>	Moraceae	<i>Viburnum tinus</i>	Adoxaceae
<i>Sylvia conspicillata</i>	Sylviidae	<i>Myrtus communis</i>	Myrtaceae	<i>Viscum album</i>	Santalaceae
<i>Sylvia curruca</i>	Sylviidae	<i>Olea europaea</i>	Oleaceae	<i>Vitis vinifera</i> ‡	Vitaceae
<i>Sylvia hortensis</i>	Sylviidae	<i>Osyris alba</i>	Santalaceae		
<i>Sylvia melanocephala</i>	Sylviidae	<i>Phillyrea angustifolia</i>	Oleaceae		
<i>Sylvia undata</i>	Sylviidae	<i>Phillyrea latifolia</i>	Oleaceae		
<i>Turdus iliacus</i>	Turdidae	<i>Phytolacca americana</i> †	Phytolaccaceae		
<i>Turdus merula</i>	Turdidae	<i>Pistacia lentiscus</i>	Anacardiaceae		
<i>Turdus philomelos</i>	Turdidae	<i>Pistacia terebinthus</i>	Anacardiaceae		
<i>Turdus pilaris</i>	Turdidae	<i>Polygonatum odoratum</i> †	Asparagaceae		
<i>Turdus torquatus</i>	Turdidae				
<i>Turdus viscivorus</i>	Turdidae				

We followed taxonomy from the ‘Birds of the World’ (birdsoftheworld.org)⁷⁸ and the Smith & Brown⁹⁷ phylogenetic tree (ALLMB), respectively.

* *Pyrus bourgaeana*, the Iberian wild pear, was not present in Smith & Brown⁹⁷ but ‘World Flora Online’ (www.worldfloraonline.org) considers this species as a synonym of *P. communis* auct. iber. We thus matched *P. bourgaeana* to *P. communis* in the phylogenetic tree to test for phylogenetic signal.

† denotes ‘herbs’; ‡ denotes ‘woody vines’; the rest of species are trees and shrubs.

Extended Data Table 3 | Significance of the fixed factors ‘migration direction’ (D), ‘biome’ (B), and their interaction in generalized linear mixed models (GLMMs) testing effects on seed-dispersal interactions of plants with migrating birds.

Fixed-effects	(i) Proportion of plant species (Binomial, logit link)		(ii) Frequency of seed-dispersal interactions (Beta, logit link)		(iii) Number of bird species per plant (Poisson, log link)	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Hypothesis testing						
Direction (D)	51.02	2.0 × 10⁻¹⁶	159.60	2.0 × 10⁻¹⁶	5.75	0.0165
Biome (B)	0.09	0.7612	0.21	0.6452	0.67	0.4142
D × B	7.03	0.0080	6.51	0.0107	1.26	0.2623
Conditional model	Estimate ± se		Estimate ± se		Estimate ± se	
Intercept	1.414 ± 0.310		-0.418 ± 0.207		1.004 ± 0.125	
D (northward)	-1.734 ± 0.368		-1.842 ± 0.164		-0.307 ± 0.124	
B (temperate)	0.714 ± 0.426		-0.322 ± 0.274		0.085 ± 0.168	
D × B	-1.310 ± 0.494		0.642 ± 0.251		0.194 ± 0.173	
Dispersion model	Estimate ± se		Estimate ± se		Estimate ± se	
Intercept	-		1.028 ± 0.140		-	
D (northward)	-		1.874 ± 0.266		-	
B (temperate)	-		0.754 ± 0.198		-	
D × B	-		-1.575 ± 0.389		-	
Random effects	Variance		Variance		Variance	
Plant species: Network	0.368		3.4 × 10 ⁻⁹		0.157	
Network	0.077		0.174		0.052	

(i) Proportion of plant species interacting with birds during migration (Fig. 2a; $n = 434$ observations), (ii) frequency of seed-dispersal interactions with birds during migration whenever these interactions occurred (non-zero frequencies; $n = 260$ observations) out of the total interaction weight (Fig. 2b), and (iii) number of bird species dispersing each plant species during migration whenever these interactions occurred ($n = 260$ observations) (Fig. 2c). Family and link functions are shown in parentheses. All models included network identity and plant species nested within network as random factors to account for the repeated measures at these levels. Note that model (ii) also includes a dispersion model because the dispersion parameter ϕ of the beta distribution was allowed to vary in response to the interactive effects of direction and biome⁹⁶. *P*-values (two-sided) < 0.05 and significant model estimates ($P < 0.05$) are shown in bold.

In all models, ‘southward’ and ‘Mediterranean’ were used as the reference categories (intercepts) for the factors Direction (D) and Biome (B).

Extended Data Table 4 | Significance of the fixed factors ‘migration direction’ (D) and ‘biome’ (B), and their interaction in generalized linear mixed models (GLMMs) testing effects on (i) the proportion of migratory bird species that were Palearctic migrants, and in (ii) the network-level frequency of seed-dispersal interactions with Palearctic migrants.

Fixed-effects	(i) Proportion of migratory bird species that were Palearctic migrants (Binomial, logit link)		(ii) Interaction frequency during migrations with Palearctic migrants (Beta, logit link)	
	χ^2	<i>P</i>	χ^2	<i>P</i>
Hypothesis testing				
Direction (D)	7.98	0.0047	32.47	2.0 × 10⁻¹⁶
Biome (B)	9.14	0.0025	12.98	0.0003
D × B	0.11	0.7458	7.12	0.0076
Conditional model	Estimate ± se		Estimate ± se	
Intercept	0.034 ± 0.363		1.188 ± 0.449	
D (northward)	1.004 ± 0.466		2.508 ± 0.503	
B (temperate)	1.429 ± 0.534		2.219 ± 0.531	
D × B	0.268 ± 0.825		-1.516 ± 0.568	
Dispersion model	Estimate ± se		Estimate ± se	
Intercept	–		1.318 ± 0.560	
D (northward)	–		3.404 ± 0.994	
B (temperate)	–		2.936 ± 0.742	
Random effects	Variance		Variance	
Network	0.336		0.088	

Family and link functions are shown in parentheses. Models included network identity as random factor to account for the repeated measures within networks ($n = 26$ observations, 13 networks × 2 directions). We only used data from Palearctic migrants because the frequencies from both migrant types are fully interdependent (Figs. 3a, 3b). Model (ii) also includes a dispersion model because the dispersion parameter ϕ of the beta distribution was allowed to vary in response to the additive effects of direction and biome⁹⁶. *P*-values (two-sided) < 0.05 and significant model estimates ($P < 0.05$) are shown in bold. Results for the species richness of all migrant species pooled are provided in Extended Data Fig. 4.

In all models, ‘southward’ and ‘Mediterranean’ were used as the reference categories (intercepts) for the factors Direction (D) and Biome (B).