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 through long-distance seed dispersal[3,4]. However, seeds may be consistently dispersed towards cooler or warmer latitudes depending on whether the fruiting period of a plant species coincides with northward or southward migrations. Here we assess the potential of plant communities to keep pace with climate change through 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. Most of the plant species (86%) in these communities are dispersed by birds migrating south, whereas only 35% are dispersed by birds migrating north; the latter subset is phylogenetically clustered in lineages that have fruiting periods that overlap with the spring migration. Moreover, the majority of this critical dispersal service northwards is provided by only a few Palaearctic migrant species. 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, and thus affect 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 that they can tolerate (known as their climatic envelope)[5]. 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 on their dispersal capacities[5,7,9,10]. Tackling this issue is key for understanding and predicting the effects of climate change on biological communities and the ecosystem functions that they mediate, including those that affect human welfare and even climate itself (via vegetation shifts)[1,11].

Plants are the cornerstone of terrestrial ecosystems, but 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 owing to climate change[6,12], whereas dispersal within species ranges allows the immigration of genotypes from warm-adapted populations to cooler areas that are becoming warmer[13]. 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 plants[14–17]. Although 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; however, we need a better mechanistic understanding of these less frequent—yet highly relevant—seed-dispersal events[19]. Migratory birds have recently been identified as possible suppliers of these dispersal events[3,4], because these migrants can transport viable seeds over tens or even hundreds of kilometres in short time periods[3,20,21]. The most notable evidence comes from the Canary Islands in the Atlantic Ocean, where about 1.2% of birds caught in migration by Eleonora's falcons (*Falco eleonorae*) were found to carry seeds in their guts from the mainland, over 170 km away[20]. 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 seeds[24], and large-scale patterns of

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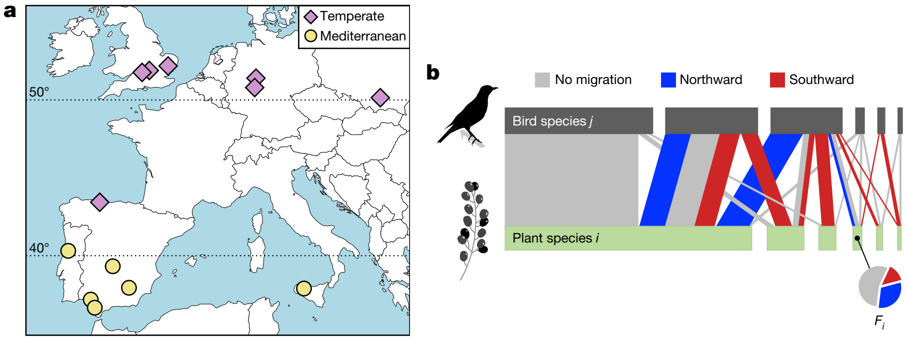

Fig. 1 | Location of the 13 European seed-dispersal networks we studied, and network with bird–plant interactions in relation to bird migration. a, Study sites in Portugal, Spain, UK, Germany, Italy and Poland. Symbols denote the biome of the locations (Mediterranean or temperate). **b**, Hypothetical 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 the interaction frequency values out of the total interaction weight of each plant species *i* that was with birds migrating southwards or northwards or with non-migrating birds.

plant genetic structure along migratory routes[25] (Supplementary Discussion 1). Although such dispersal events seem rare, they are numerically compensated for by the fact that billions of birds migrate every year worldwide through seasonal and directional displacements that are highly predictable in space and time[26].

In the Northern Hemisphere, birds typically migrate towards the Equator in autumn (postnuptial migration) and towards the North Pole in spring (prenuptial 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). The relationship between migration directionality, plant phenology and dispersal potential towards cooler latitudes has, to our knowledge, been overlooked to date, despite this being crucial to predict the ability of plants to track climate change[5,6,11]. In this Article, we provide an assessment of the potential of European plant communities to keep pace with climate change through long-distance seed dispersal towards cooler latitudes. We combined data on fruiting phenology and bird migration with information on 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 that account for a mean of 35% of species in temperate forests and 44% in Mediterranean woodlands[29].

We used data on seed-dispersal networks (that is, local communities of interacting bird and plant species) with links that describe the presence and intensity of pairwise interactions[30]; in this case, the quantity of seeds of each plant species that is 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%), and the remainder were herbs (Extended Data Table 2).

In each network, we partitioned each bird–plant interaction according to the migratory state of the bird: migrating southwards, migrating northwards 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) (Methods). Then, for each plant species *i*, we calculated the fraction of its total interaction weight (F_i) that corresponds to interactions with each of the migratory states of the birds (Fig. 1b, Extended Data Fig. 2). These calculations considered whether bird populations were full migrants or partial migrants, in which a fraction of the population migrates and the rest stays as residents[26] (Methods).

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 (southward or northward) (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 potential for plants to be dispersed towards cooler latitudes, because these biomes differ in fruiting seasonality: Mediterranean woodlands are characterized by longer fruiting seasons[29], 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 southwards, whereas only about one third (35%) are dispersed by northward-migrating birds (direction: $P < 0.001$) (Fig. 2a, Extended Data Table 3). This trend was consistent across biomes, but was less pronounced in Mediterranean (80% and 42% for southward and northward migrations, respectively) than in temperate communities (89% and 29% for southward and northward migrations, respectively) (interaction of biome × direction, $P = 0.008$) (Fig. 2a, Extended Data Table 3). The sums of these percentages are greater than 100% because interactions with southward- and northward-migrating birds are not mutually exclusive (Fig. 1b), and many plant species are dispersed during both migrations (Extended Data Fig. 2, 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, Extended Data Table 3). This trend was also consistent across biomes, but was more pronounced in Mediterranean communities (40% and 9% for southward and northward migrations, respectively) than in temperate communities (32% and 13% for southward and northward migrations, respectively) (interaction of direction × biome, $P = 0.011$) (Fig. 2b). Finally, plants were dispersed by more bird species migrating southwards than northwards (estimated mean = 2.9 and 2.3 species per plant, respectively; direction, $P = 0.017$), a small but consistent difference across biomes (Fig. 2c, Extended Data Table 3). Importantly, these results were not an artefact of analysing networks that were 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 winter[29], when migratory birds move southwards[26].

We further tested whether closely related plant species tend to have similar seed-dispersal interactions with birds migrating southwards or

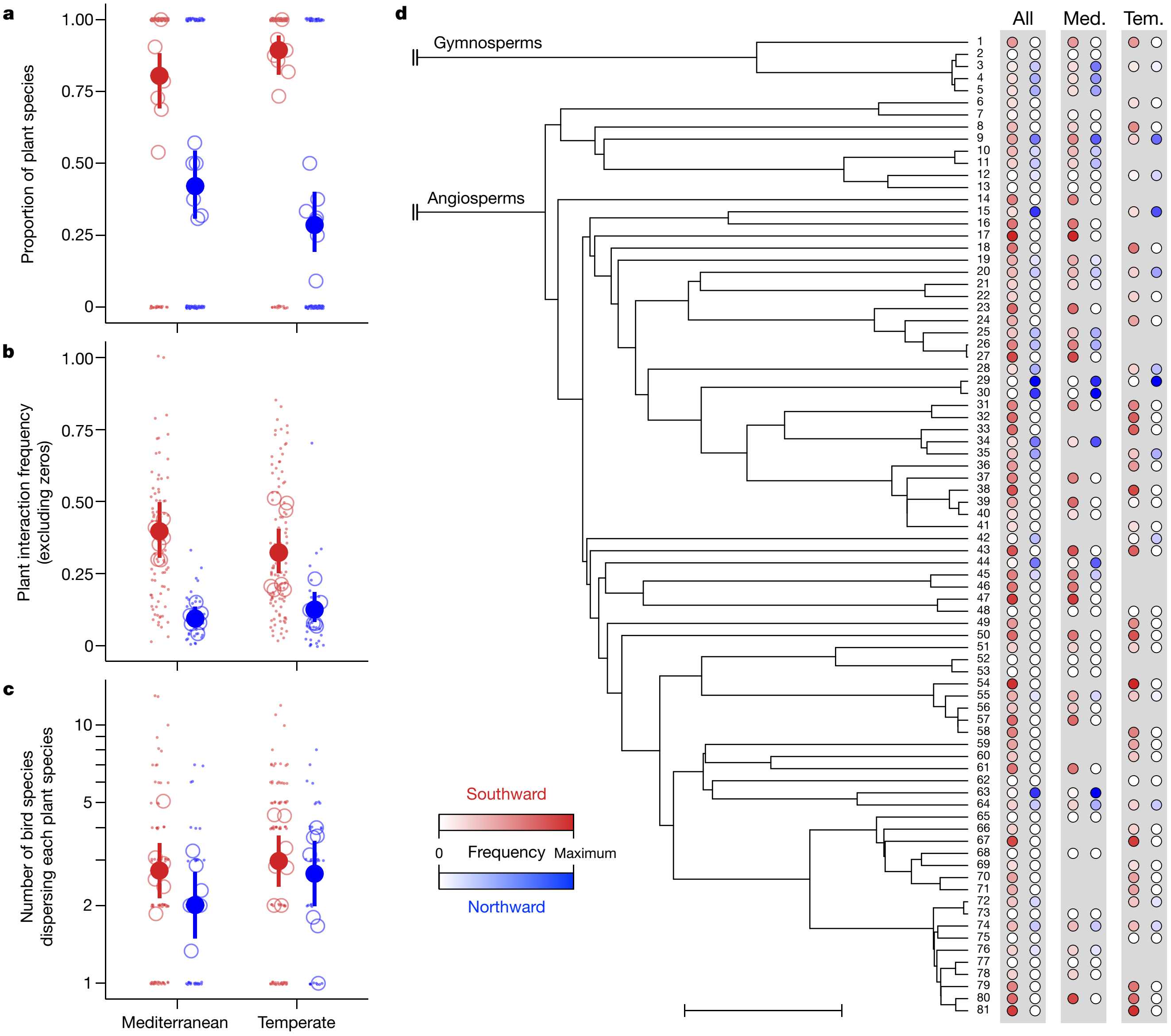

Fig. 2 | Seed-dispersal interactions of plants with migratory birds in relation to southward and northward migration and Mediterranean or temperate biome. **a**–**c**, Large dots and bars denote means ± 95% confidence intervals estimated by generalized linear mixed models predicting the proportion of plant species interacting with birds during migration ($n = 434$ observations from 13 networks across plant species and directions) (**a**), the frequency of interactions with migrating birds when these occurred (zeros excluded) ($n = 260$ observations), out of the total seed-dispersal interactions (**b**), and the number of bird species dispersing each plant species ($n = 260$ observations) (**c**). Circles denote mean values for each seed-dispersal network; tiny dots denote plant-level data. **d**, Dated phylogeny of the fleshy-fruited plants in the studied networks, with the root at 325 million years ago (shown in Extended Data Fig. 3). Scale bar, 50 million years. 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 southwards or northwards (red and blue colour gradients, respectively) calculated across all networks (all) and, separately, for Mediterranean (Med.) and temperate (tem.) networks (maximum frequency means in all, Mediterranean and temperate, respectively: southward = 0.80, 0.80 and 0.76; northward = 0.30, 0.23 and 0.34).

northwards. The rationale is that the fruiting period of plants shows a phylogenetic signal[31] and can thus be related to the phenological overlap with seasonal migrations (Extended Data 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 (specifically, the start and end dates, and the period length) (Extended Data Fig. 3). Accordingly, plant lineages that are frequently dispersed by northward-migrating birds are characterized by long fruiting periods (for example, *Juniperus* spp.; labels 3–5 in Fig. 2d) or late fruiting periods that extend until the spring of the next calendar year (for example, *Hedera* spp.; labels 29–30 in Fig. 2d). By contrast, plant lineages that are not dispersed by northward migrants are characterized by short fruiting periods between summer and early winter (for example, *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

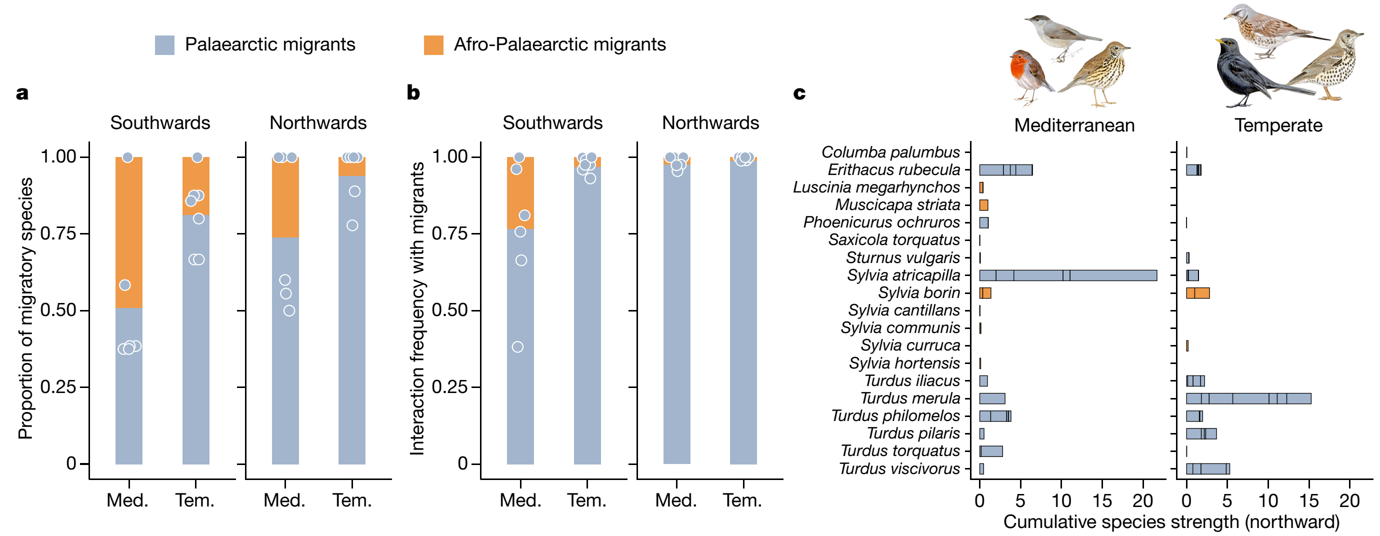

Fig. 3 | Relevance of Palaearctic and Afro-Palaearctic migratory birds dispersing seeds during their southward and northward migration in Mediterranean and temperate communities. a, Mean proportion of Palaearctic (grey) and Afro-Palaearctic (orange) species (wintering ranges in Europe and Africa north of the Sahara, and in sub-Saharan Africa, respectively) dispersing seeds while migrating, in relation to migration direction (southwards (left) or northwards (right)) and biome (Mediterranean or temperate). **b**, Mean relative contributions of Palaearctic and Afro-Palaearctic migrants to network-level interaction weight with migratory birds during their southward (left) and northward (right) migrations in Mediterranean and temperate communities. Circles in **a**, **b** denote network-level observations for Palaearctic migrants. **c**, Relevance of bird species for seed dispersal towards cooler latitudes across Mediterranean (left) and temperate (right) fleshy-fruited plant communities, measured as the cumulative strength of bird species in subnetworks of interactions between plants and birds migrating northwards (blue links in Fig. 1b). Species strength quantifies the relevance of a bird species across the whole plant community; high cumulative values are found in bird species with high strength values in several subnetworks within each biome. Bird drawings represent the three most relevant species in each biome (from left to right, *E. rubecula*, *S. atricapilla*, *T. philomelos*, *T. merula*, *T. pilaris* and *T. viscivorus*). Illustrations by Juan M. Varela.

climate change is clustered in particular 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 functions[32] and community composition at higher trophic levels[33,34].

European migratory birds can be classified into two distinct groups according to their migratory strategy: Palaearctic migrants winter in southern Europe and northern Africa, whereas Afro-Palaearctic migrants winter in sub-Saharan Africa[26]. In addition, both groups differ in their population trends; in contrast to Palaearctic migrants, Afro-Palaearctic 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). However, most of these species were Palaearctic migrants (Fig. 3a), particularly during the northward migration (mean = 87%; direction, $P = 0.005$) and in temperate communities (mean = 89%; biome, $P = 0.003$) (Extended Data Table 4). Furthermore, we found that both types of migrant 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 (Methods)). Palaearctic migrants accounted for almost all interaction frequency (Fig. 3b), particularly during the northward migration (mean = 98%; direction, $P < 0.001$) (Extended Data Table 4). Palaearctic migrants were also significantly more relevant in temperate (mean = 98%) than in Mediterranean communities (mean = 87%; biome, $P < 0.001$), in which Afro-Palaearctic birds had a more important role—particularly when migrating southwards (interaction of direction × biome, $P = 0.008$) (Extended Data Table 4). 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 (about 5) of Palaearctic migrant species per locality. This stronger role of Palaearctic migrants can be explained by their occurrence in Europe during the winter (when invertebrates are scant and fruits abound) and their earlier spring migration northwards[37].

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 the relevance of a bird species for community-wide seed dispersal towards cooler latitudes (Methods). To do so, we used subnetworks of the original networks that included only interactions during northward migrations (blue links in Fig. 1b). Then, we obtained the cumulative species strength per biome as the sum of species strengths across Mediterranean and temperate subnetworks (Fig. 3c). Results showed that a few Palaearctic 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%; and song thrush, 9%). Across temperate communities, the blackbird (*Turdus merula*) was prominently the most relevant species, followed by the mistle thrush (*Turdus viscivorus*) and the fieldfare (*Turdus pilaris*) (Fig. 3c); these thrushes accounted for 69% of cumulative strength (blackbird, 44%; mistle thrush, 15%; and fieldfare, 10%). Thus, bird species did not have similar relevance in both biomes (Extended Data Fig. 5). Notably, 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 communities[38]. 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 in the Mediterranean Basin (estimated over 1 million individuals of each species killed per year[41]).

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 of 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 models[24]. Such data are expected to come during this decade, as we are witnessing a revolution in next-generation GPS tags that will enable the tracking of small frugivorous birds with unprecedented spatiotemporal resolution[42].

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 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 with a relevance that 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 Hemisphere[26]. 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 change[1]. 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.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-03665-2.

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Methods

No statistical methods were used to predetermine sample size. Randomization and blinding do not apply to our study, as we did not conduct experiments.

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 in which 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 ($n = 7$) biomes of Europe[47,48] (Fig. 1a and 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 metres above sea level) in which agricultural fields surround the remnant vegetation. The single exception is the 'Nava Correhuelas' network, which is located on a well-preserved Mediterranean mountain at an elevation of 1,600 metres. 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 analysis[52] (as described in 'Methods for the new network data'). 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 in which the bird behaves as a legitimate seed disperser (swallowing the fruit and defecating or regurgitating viable seeds), discarding pulp-pecking and seed-predation interactions[53].

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 prenuptial and postnuptial migration periods of all migratory birds; the single exception was the network from ref. [27], 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 networks[54–56] 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 analyses of variance (ANOVAs) $\log_{10}[n] \sim$ 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 (as described in 'Methods for the new network data'. Yet, in networks based on feeding observations, interaction weights were originally expressed as number of bird visits to focal plants[53]. 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 ($R^2_{\mathrm{GLMM}(m)} = 0.924$) 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. In cases in which 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 (as described in 'Seed-dispersal phenology' and 'Migrant types and phenology of bird migrations'), 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 a part of our phenological data was based on the presence of seeds dropped by birds in seed traps or during mist netting (as described in 'Methods for the new network data').

Methods for the new network data

Authorship of the eight 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 km^2) located in Spain, UK, Germany, Italy and Poland (Extended Data Table 1). Six of these plots were sampled for one year (2016–2017) and one plot 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[61]. Seed traps were 0.22-m^2 plastic trays covered with wire mesh to prevent postdispersal 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 (as described below in this section). The route used to survey the seed traps was also used as a 1-m wide single fixed belt transect (range 2,630–9,110 m length, mean 4,410 m) to search for bird-dispersed seeds and quantify seed rain in canopy-free open interspaces, where bird-mediated seed rain is less likely[61]. Individual seeds or droppings with seeds were sampled for DNA barcoding 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 particular plant species; for example, 40–50% of the hyper-abundant *Pistacia lentiscus* seeds in Garrapilos during its fruiting peak[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 Supplementary Methods. Resulting sequences were identified at the species level based on best sequence matches in the 'BARCODE OF LIFE DATA' identification system (BOLD[62]) (www.boldsystems.org), typically at a 98–100% similarity (Supplementary Fig. 1). We successfully identified the disperser species of 2,991 samples (that is, 2,991 sequences; 123–1,753 per network) including 3,014 interaction events between a bird–plant species pair, and containing

4,812 seeds (144–2,193 per network); overall 3,234 samples containing 5,181 seeds were analysed, 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 J.P.G.-V.) and pictures from a guide of seeds of European fleshy-fruited species that includes plants from the Mediterranean and temperate biomes[58]. The exception were 11 samples for which initial identification was not possible and for which we conducted DNA-barcoding analysis using chloroplast MaturaseK gene (*matK*)[63] (detailed laboratory protocols are provided in 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 BLAST[64]; (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. Thus, this DNA-barcoding analysis served us to short list and guide visual identification (further details are provided in Supplementary Methods). All seed samples are stored by J.P.G.-V. at the Laboratory of Botany in the University of Cádiz, 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 $f_{ijk} = n_{\text{DNA-}ijk}/n_{\text{DNA-}ik}$, in which 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 $sr_{ijk} = sr_{ik} \times f_{ijk}$, in which sr_{ik} is average seed rain (seeds per m^2) of plant species i measured in seed traps located beneath perch type k (similar to 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 weight (w_{ij}) of pairwise interactions in these networks, expressed as seeds per m^2.

Vale Soeiro network. Community-wide seed dispersal by frugivorous birds was sampled in a plot of natural woodland of about 0.5 km^2 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 6 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 4,462 bird captures, 1,330 produced droppings with seeds ($n = 3,398$ seeds). Defecated or regurgitated seeds were later extracted and identified by comparison with a reference collection. A quantitative seed-dispersal network was built in which interaction weights (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 zones[66]. We used distinct data sources: published studies[27,50,55,59,67–77], from which information was extracted from figures, tables and text; and our own data associated with the new eight networks that we obtained through fortnightly sampling surveys. Published studies included data on entire fleshy-fruited plant communities (for example, ref. [67]), in some cases associated to the published networks we compiled (for example, refs. [50,59,72]), as well as data on specific taxa (for example, refs. [68,70]). In some cases, we also used personal observations for the phenology of particular plant species at specific bioclimatic zones. From each data source, we obtained the 'start' and the 'end' of the seed-dispersal period (D_{start}–D_{end}) of each plant species. We used a monthly scale (0–12) in which exact values represent the transition between months (for example, 0 = end of December–beginning of January; 1 = end of January–beginning of February; and so on) and half values represent the midpoint within months (for example, 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) (Extended Data Fig. 1). Most phenological data were obtained at a 0.5-month accuracy (about 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 several sources or years for the same plant species at a particular bioclimate (Extended Data Fig. 6). When the same data source included information from different fruiting seasons (for example, refs. [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) 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 according to plant species and network bioclimate.

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), 'Palaearctic migrant' (birds that breed in Europe and winter in southern Europe and Africa north of the Sahara) and 'Afro-Palaearctic migrant' (birds that breed in Europe and winter in sub-Saharan Africa)[26]. Palaearctic migrants are often partial migrants (that is, only a fraction of their populations migrates while the other fraction behaves as resident)[26]. For this reason, we characterized the proportion of migrants (P_{migrants}) in the bird populations of the study networks by means of a semiquantitative 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[79,80,82–91] and our own data). Hence, Palaearctic 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 short periods while migrating (stopover site)[26].

We obtained country-level phenological data for the prenuptial (northward) and postnuptial (southward) migrations of the bird species in the study networks (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 obtained mainly from bird migration atlases of the study networks' countries: Spain and Portugal (Iberia)[79,80], Italy[82,83], UK[84], Germany[86] and Poland[87]. We also obtained data from specific references from Poland[88–91] and websites from recognized ornithological organizations in the case of Spain (www.seo.org/listado-aves-2)[81] and the UK (www.birdtrack.net)[92]. 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_{start}–N_{end} and S_{start}–S_{end}, respectively) from figures, tables and text. All phenological data were obtained at a 0.5-month accuracy (about 2 weeks). Again, we used a monthly scale in which exact values represent the transition between months and half values represent the midpoint within months (as described in '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_{start}–N_{end} and S_{start}–S_{end}), we used migration phenology available for the Western Palaearctic region[85] or at a continental coarse scale (www.eurobirdportal.org). Phenological data were finally incorporated into the network data according to bird species and network country.

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 $O_{\text{south-}ij} = \min(D_{\text{end-}i}, S_{\text{end-}j}) - \max(D_{\text{start-}i}, S_{\text{start-}j})$. Before 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 Extended Data 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 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 northwards as $F_{\text{north-}ij} = P_{\text{migrants-}j} \times O_{\text{north-}ij}/O_{\text{total-}ij}$, and southwards 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 (for example, refs. [27,50,71]) and the local context (for example, ref. [74]).

Finally, for each plant species i in each study network, we calculated the frequency of seed-dispersal interactions during which the birds are migrating south ($F_{\text{south-}i}$), north ($F_{\text{north-}i}$) or are 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 ($F_{\text{south-}i} + F_{\text{north-}i} + F_{\text{non-}i} = 1$) (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 some networks owing to the local occurrence of congeneric species with seeds that did not allow for 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, which allowed us to use plant species as random factor in mixed models and match a unique tip label in the plant phylogeny.

All generalized linear mixed models (GLMMs) described below were fitted using the R package glmmTMB (v.0.2.3)[93] 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)[94].

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 (1) the proportion of plant species (prevalence) interacting with birds during migration ($n = 434$ observations), (2) 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 (3) the number of bird species dispersing each plant species during migration (whenever interactions during migration occurred; non-zero values); $n = 260$ observations in (2) and (3). 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 southwards and northwards). 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 in which the dispersion parameter ϕ of the beta distribution was allowed to vary in response to the interactive effects of direction and biome ($\Delta\mathrm{AIC} = -25$ relative to a model with fixed ϕ)[95]. For modelling purposes, we transformed F_i values as follows: $F_i' = (F_i\,(n-1) + 0.5)/n$, in which n is the total number of observations[95]. 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 latter[95] (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. 2b) were previously back-transformed ($F_i = (F_i'n - 0.5)/n - 1$). The number of migrating bird species that dispersed each plant species 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 (F_i values, including zeros) with birds migrating southwards and northwards, 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 *C. 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)[96] with a backbone based on a previous publication[97]. The tree was prepared by dropping tips other than the 81 plant species of interest using the R package ape (v.5.3)[98]; the resulting tree contained one polytomy, which was resolved randomly using the function multi2di. Phylogenetic signal was assessed through Pagel's λ (ref. [99]), 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)[100]. 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 model[100]. Pagel's λ seems strongly robust to polytomies and suboptimal branch-length information[101]. 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 0[100]. These analyses were performed using the R package phytools (v.0.6-99)[102]. As a complementary analysis, we also tested for phylogenetic signal in seed-dispersal phenology as the frequency of interactions with migrant birds is ultimately related to fruiting phenology (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 Palaearctic and Afro-Palaearctic species. The species richness was modelled as a Poisson-distributed variable with log link function and the proportion of Palaearctic species as a Bernoulli-distributed variable with logit link function (1: Palaearctic; 0: Afro-Palaearctic; 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, that is, 'network–direction' combinations). We also assessed whether the relevance of Palaearctic and Afro-Palaearctic migrants varied between migrations and biomes. To do so, we calculated the frequency of interactions with Palaearctic and Afro-Palaearctic birds on migration in each network out of the total interaction weight with all migrant birds during the southward and northward migrations (for example, $f_{\mathrm{Palaearctic}} = W_{\mathrm{Palaearctic}}/W_{\mathrm{all\ migrants}}$; in which $W_{\mathrm{all\ migrants}}$ is the total interaction weight with all migrating birds per network, thus, $W_{\mathrm{all\ migrants}} = W_{\mathrm{Palaearctic}} + W_{\mathrm{Afro\text{-}Palaearctic}}$). For this analysis, we used only data from Palaearctic migrants ($f_{\mathrm{Palaearctic}}$, $n = 26$ observations, that is, network–direction combinations) because frequencies from both migrant types are fully interdependent ($f_{\mathrm{Palaearctic}} + f_{\mathrm{Afro\text{-}Palaearctic}} = 1$). We fitted a GLMM to test whether the migration direction, the biome and their interaction were significantly associated with the interaction frequency with Palaearctic migrants. This model was as a mixed-effects beta regression with logit link function[95], in which the dispersion parameter ϕ of the beta distribution was allowed to vary in response to the additive effects of direction and biome ($\Delta\mathrm{AIC} = -29$ relative to a model with fixed ϕ). For modelling purposes, we transformed values for beta regression as explained in 'Seed-dispersal interactions' (range of $f_{\mathrm{Palaearctic}}$: 0.3818–1.0; range of $f'_{\mathrm{Palaearctic}}$: 0.3841–0.9904); the estimated means reported in the article (Fig. 3b) were also back-transformed as explained in 'Seed-dispersal interactions'. 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 metric[103], 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 the relevance of a bird species across all the fleshy-fruited plant community[104]. We calculated species strength of migratory birds ($n = 24$ species) using the R package bipartite (v.2.13)[103] in subnetworks of the original networks that only included seed-dispersal interactions either during southward or northward migration (subnetworks of red or blue links in Fig. 1b, respectively), in which strength quantifies the relevance of a bird species as a seed disperser during each migration. We then obtained the cumulative species strength (sum across sub-networks) per direction and biome combinations (Mediterranean–southward, Mediterranean–northward, temperate–southward and temperate–northward). This way, very high cumulative values can only be found in migratory bird species with high strength values in several networks per biome. We used nonparametric Kendall's rank correlations to test whether, in each biome, the cumulative species strength across southward and northward subnetworks 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 across Mediterranean and temperate subnetworks were correlated, which would indicate that bird species generally display a proportional role in both biomes (Extended Data Fig. 5).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

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 Fig. 2) were obtained from EltonTraits 1.0 available through Figshare (https://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).

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Additional information
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