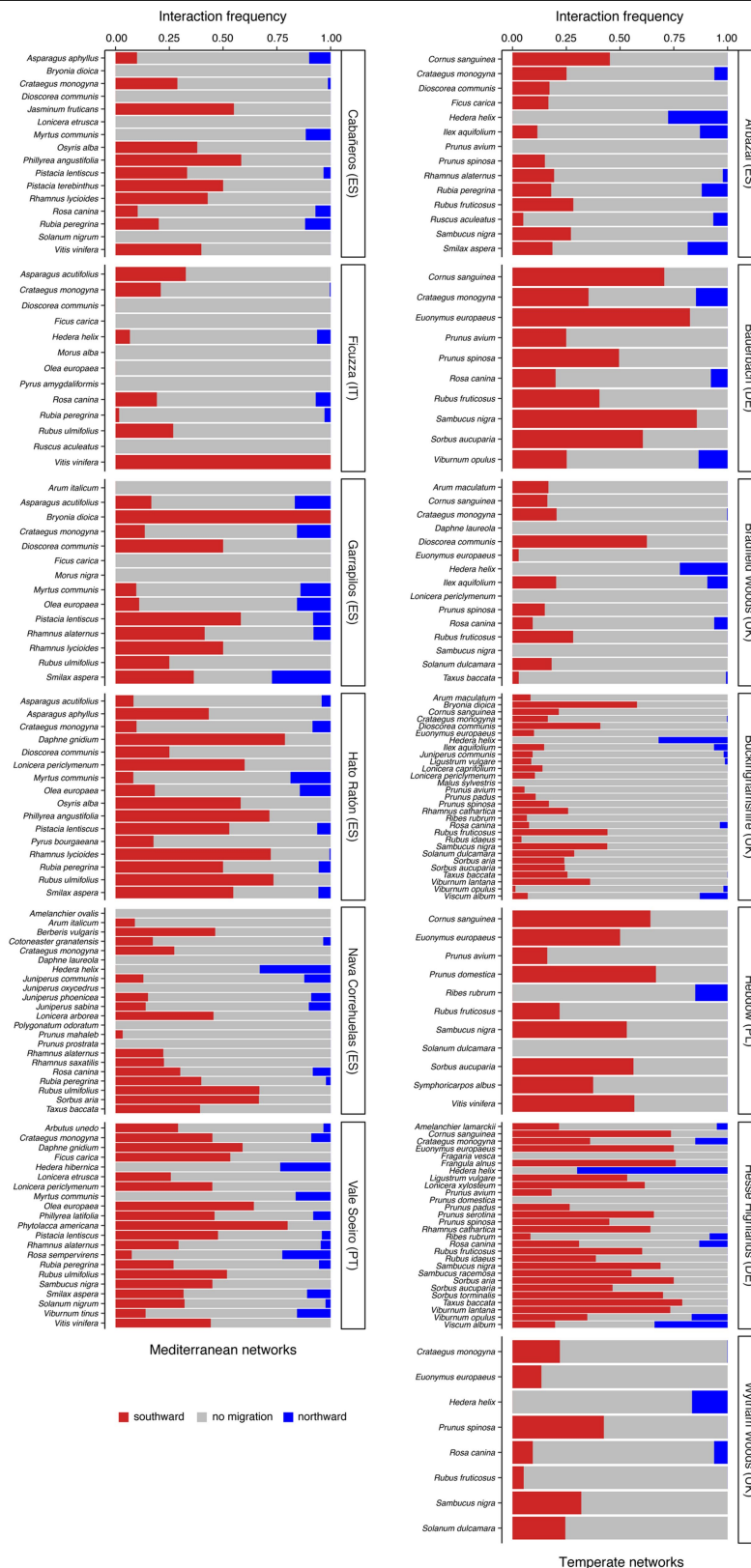


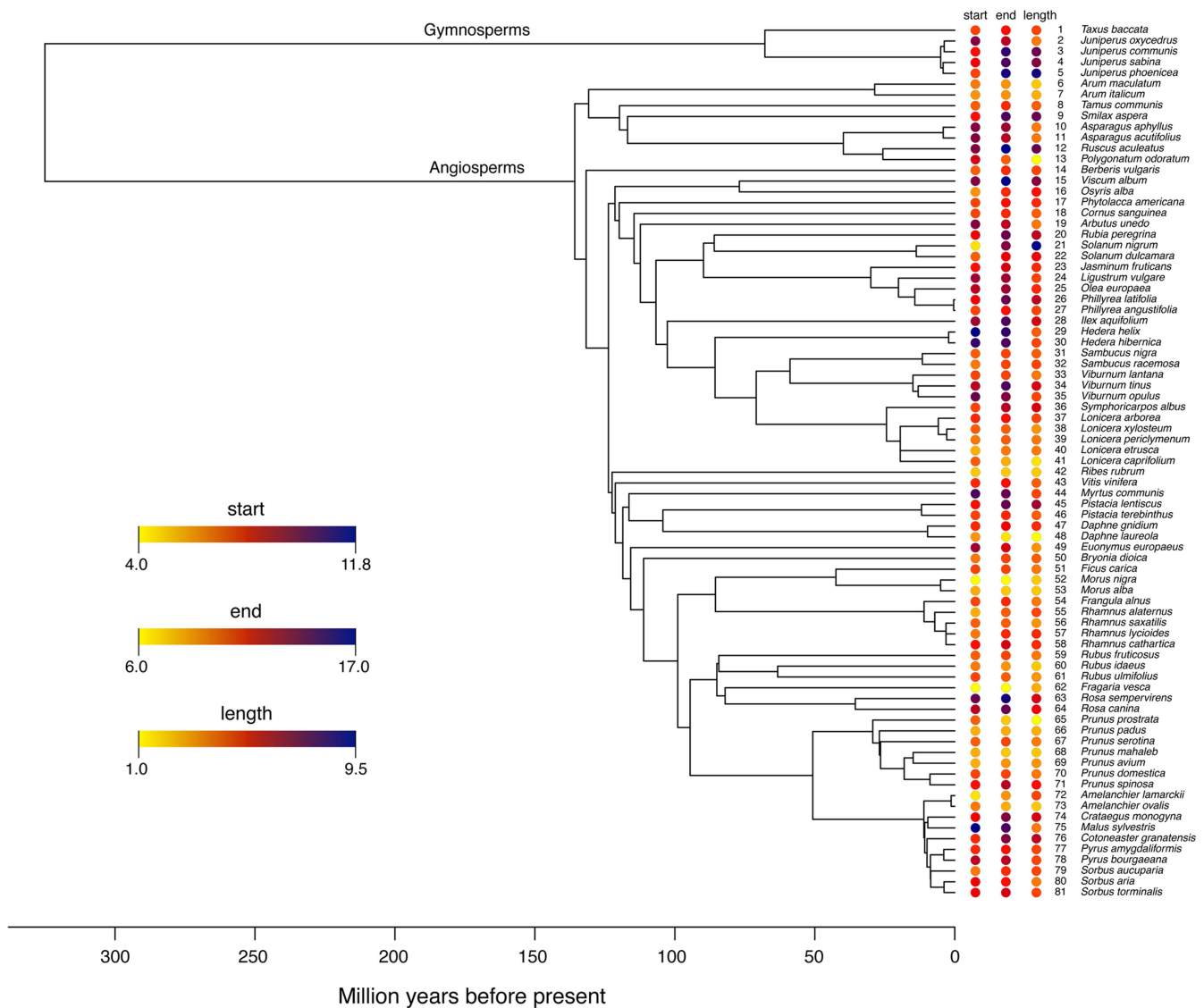
Extended Data Fig. 1 | Conceptual diagrams showing directional patterns of long-distance seed dispersal by migratory birds and phenological overlaps between seed-dispersal periods and bird migrations. a, Yellow and black arrows denote long-distance seed dispersal within and beyond the current range of a plant species, respectively. Seed dispersal mediated by birds migrating south (left), non-migrating birds (centre) and birds migrating north (right). The colour gradient from red to blue represents a climatic gradient from warmer to cooler latitudes (from south to north in the Northern Hemisphere), respectively. In the diagram on the right, seed dispersal within the range is necessary for warm-adapted populations to colonize cooler areas that are warming owing to climate change, whereas seed dispersal beyond the

range is necessary for range shifts. **b,** Three hypothetical examples of phenological overlap between the seed-dispersal period of plant species *i* and bird species *j* while the bird migrates northwards (top), southwards (middle) or during both migrations (bottom). The examples include a wintering migrant with a winter-spring fruiting plant (top); a summer migrant with a summer-autumn fruiting plant (middle); and a transient migrant with an autumn-winter fruiting plant (bottom). In some cases, there is also phenological overlap during non-migration periods. More details on phenological overlaps in relation to the migratory strategy of birds are provided in Supplementary Fig. 3.



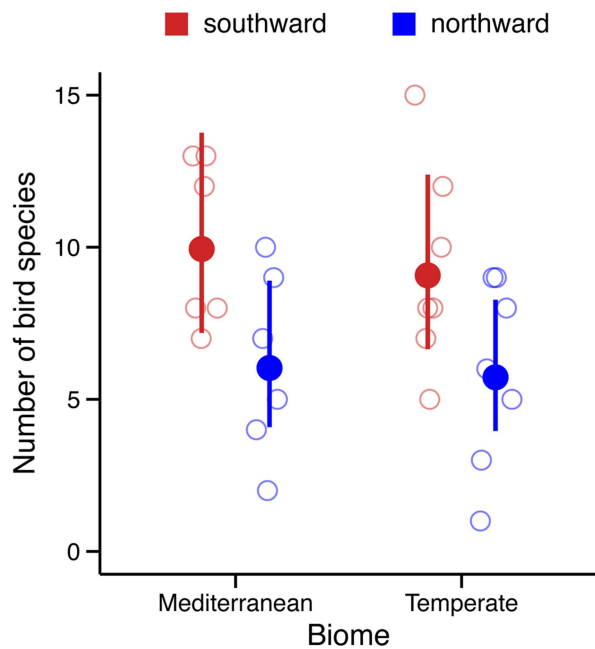
Extended Data Fig. 2 | Estimated interaction frequencies of plant species within each study network with birds migrating northwards, southwards or not migrating. Blue, interactions during northward migration; red, interactions during southward migration; grey, non-migration interactions.

Each panel represents a seed-dispersal network. The left column of panels includes Mediterranean networks, whereas the right column includes temperate networks. DE, Germany; ES, Spain; IT, Italy; PL, Poland; PT, Portugal; UK, United Kingdom.

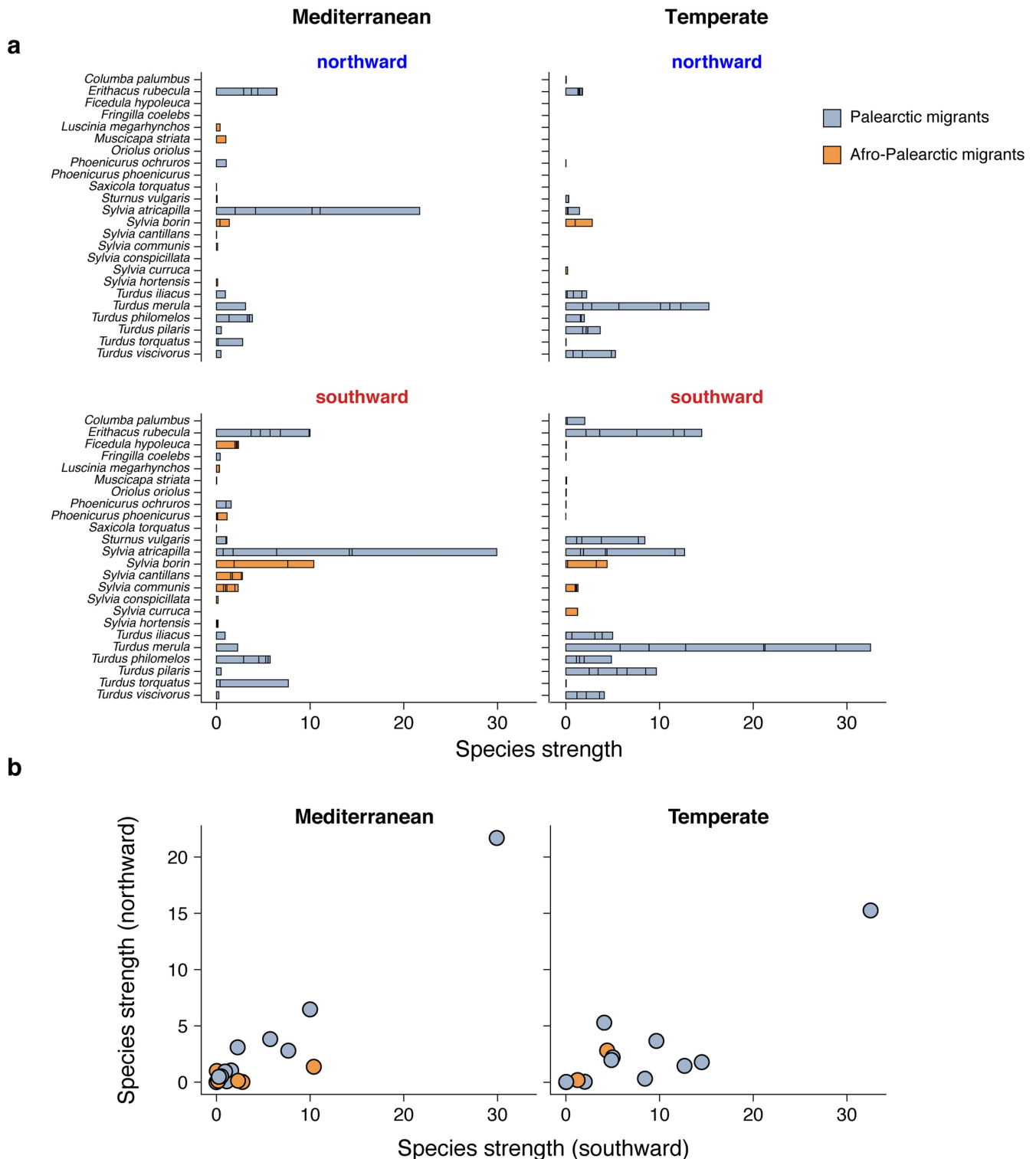


Extended Data Fig. 3 | Variables of the seed-dispersal phenology across the phylogenetic tree of plants. Phylogenetic signal was tested in plant-species means across networks in start and end dates (D_{start} and D_{end}), as well as in length ($D_{\text{length}} = D_{\text{end}} - D_{\text{start}}$) of the seed-dispersal period ($n = 81$ plant species) by means of Pagels' λ , as described in 'Phylogenetic signal in plants' in 'Statistical analyses' (Methods). The three phenological variables showed significant phylogenetic signal ($D_{\text{start}}, \lambda = 0.800, P = 0.0103$; $D_{\text{end}}, \lambda = 0.781, P = 0.0015$; and $D_{\text{length}}, \lambda = 0.419, P = 0.0343$). To test for phylogenetic signal, we previously calculated the species-level means for $D_{\text{start}}, D_{\text{end}}$ and D_{length} across bioclimate (Extended Data Fig. 6). For this reason, we assessed the amount of variance in these phenological variables that is 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. Bioclimate accounted for only a minor fraction of variance (1–3%) in $D_{\text{start}}, D_{\text{end}}$ 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). By 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)¹⁰⁵.

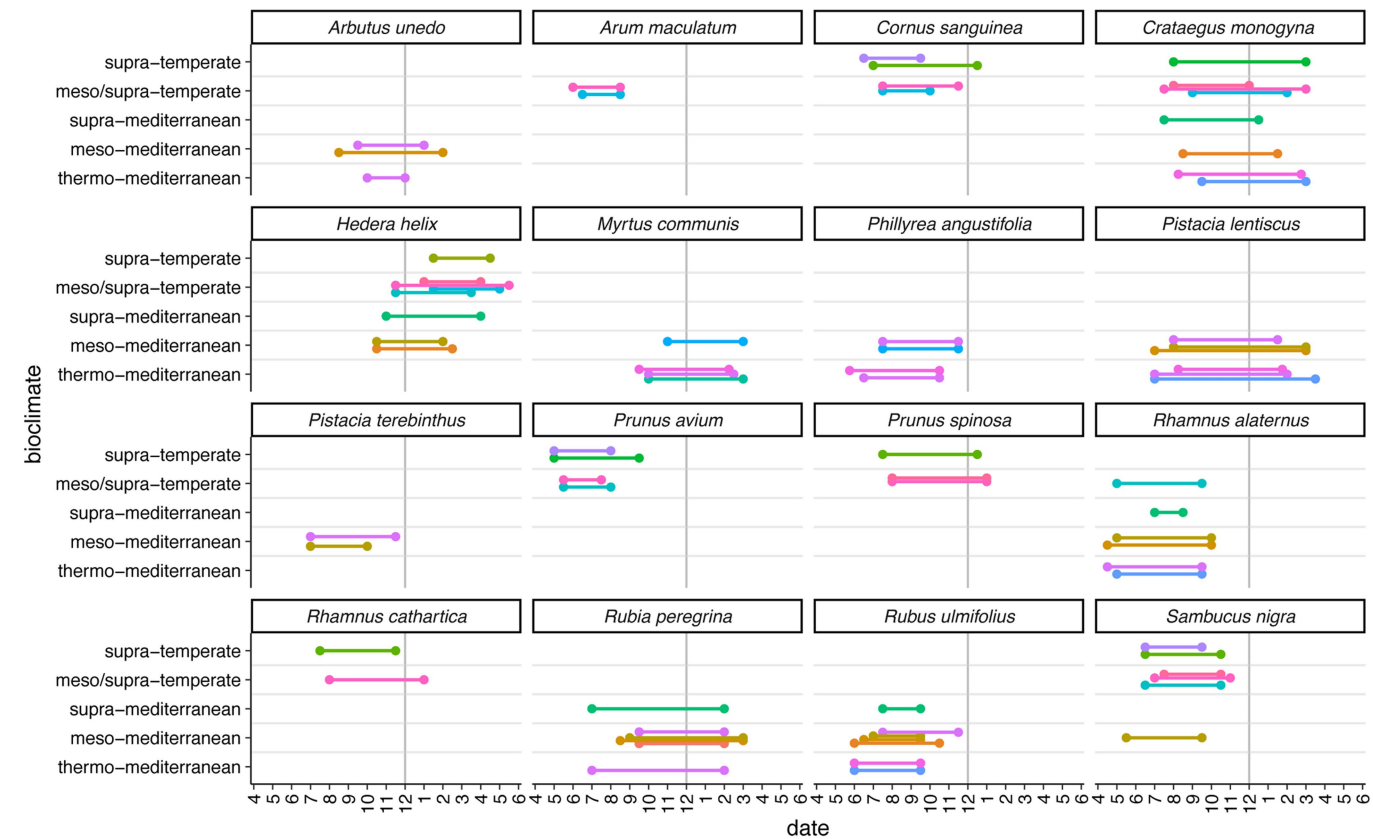


Extended Data Fig. 4 | Number of migratory bird species interacting with plants during migration per network in relation to migration direction and biome. Large dots and bars denote means \pm 95% confidence intervals estimated by a GLMM, whereas circles denote values for each seed-dispersal network ($n = 26$ 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 s.e.: 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, respectively. 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 | Individual and cumulative bird species strengths accumulated across seed-dispersal subnetworks. a, Bird species strength accumulated across seed-dispersal subnetworks between plants and birds migrating southwards or northwards, and in Mediterranean and temperate biomes; species strength quantifies the relevance of a bird species across the entire fleshy-fruited plant community¹⁰⁴ ($n = 24$ species). Some bird species have stacked values from several subnetworks, whereas other species participated only in a single subnetwork. **b,** The cumulative species strength across the southward and northward subnetworks 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 across the northward ($\tau = 0.276$, $P = 0.1089$) nor across the southward subnetworks ($\tau = 0.263$, $P = 0.0764$) (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 several 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 several 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 that we 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, respectively. Network biomes were obtained from refs. ^{47,48}; network bioclimates were obtained from ref. ⁴⁸. Source A is ref. ⁴⁹; source B is this study (EU project MobileLinks); source C is this study (unpublished data provided by L.P.d.S. and R.H.H.); source D is ref. ⁵⁰; source E is ref. ²⁷; and source F is ref. ⁵¹.

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>Erithacus 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 ‘Birds of the World’ (www.birdsoftheworld.org)⁷⁸ for birds and a previously published⁹⁶ phylogenetic tree (ALLMB) for plants. Plants are defined as herbs (†), woody vines (*) or trees and shrubs (all other species).

**Pyrus bourgaeana* (Iberian wild pear) was not present in ref. ⁹⁶ but ‘World Flora Online’ (www.worldfloraonline.org) considers this species as a synonym of *Pyrus communis* auct. iber. We thus matched *P. bourgaeana* to *P. communis* in the phylogenetic tree to test for phylogenetic signal.

Extended Data Table 3 | Significance of the fixed factors migration direction and biome, and their interaction, in 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)	
Hypothesis testing	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
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	

Proportion of plant species interacting with birds during migration ($n = 434$ observations) (i) (Fig. 2a), 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 (ii) (Fig. 2b) and number of bird species dispersing each plant species during migration whenever these interactions occurred ($n = 260$ observations) (iii) (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. 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 biome⁹⁵. *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*), respectively.

Extended Data Table 4 | Significance of the fixed factors migration direction and biome, and their interaction, in GLMMs testing effects on the proportion of migratory bird species that were Palaearctic migrants, and in the network-level frequency of seed-dispersal interactions with Palaearctic migrants

Fixed-effects	(i) Proportion of migratory bird species that were Palaearctic migrants (Binomial, logit link)		(ii) Interaction frequency during migrations with Palaearctic migrants (Beta, logit link)	
Hypothesis testing	χ^2	<i>P</i>	χ^2	<i>P</i>
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 used data only from Palaearctic migrants because the frequencies from both migrant types are fully interdependent (Fig. 3a, b). 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 biome⁹⁵. *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*), respectively.