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SEED DISPERSAL

Evidence of a European seed dispersal crisis

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Seed dispersal is crucial for ecosystem persistence, especially in fragmented landscapes, such as those common in Europe. Ongoing defaunation might compromise effective seed dispersal, but the conservation status of pairwise interactions remains unknown. With a literature review, we reconstructed the first European-wide seed dispersal network and evaluated the conservation status of interactions by assessing each interacting partner's IUCN (International Union for Conservation of Nature) conservation status and population trends. We found that a third of the disperser species and interactions face potential extinction and that 30% of the plant species have most of their dispersers threatened or declining. Our study reveals a developing seed dispersal crisis in Europe and highlights large knowledge gaps regarding the dispersers and conservation status of zoochorous plants, urging further scrutiny and action to conserve the seed dispersal service.

The movement of genetic diversity across space is a fundamental cornerstone of long-term ecosystem functioning and resilience (*1*). For most plants, the dispersal of seeds by either biotic (i.e., animals) or abiotic (e.g., wind) vectors is crucial because it is the only stage of their life cycle when individuals can move (*2*). Seed dispersal is an important ecological function and a key regulating service (*3*), allowing plant species to alter their distributional range, avoid high competition and natural enemies near the mother plant, recover from perturbations, and maintain gene flow between fragmented populations (*4*–*6*). Animal dispersers are thus important ecosystem service providers (*7*), particularly for plants with traits that promote biotic seed dispersal (*8*).

The European landscape has undergone severe transformations in recent millennia, becoming the most fragmented continent on Earth (*9*). Habitat fragmentation due to transportation networks, urbanization, and agriculture poses multiple physical barriers to plant dispersal. These constraints affect gene flow and population dynamics (*10*), being particularly worrying given plants' need to track favorable climatic envelopes because of climate change (*11*). Furthermore, the increasing frequency and intensification of wildfires (*12*) magnifies the importance of seed dispersal for the recolonization of burnt areas (*13*).

In this context, the decline and local extinction of animals—many of which disperse viable seeds—can have profound implications for European plant recruitment (*14*, *15*). It is estimated that 2248 native European plant species (~23% of the European flora) have seeds with specific adaptations for biotic dispersal, growing to 66% for woody species (*8*). Accordingly, the decline of seed dispersers could transform European landscapes into "empty forests" (*16*), creating a plant extinction debt (*17*).

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Surprisingly, despite considerable efforts to conserve European species (*18*, *19*), the conservation of the biotic interactions that hold those species together has received comparatively little attention (*20*). This is unfortunate, as the extinction of interactions often anticipates that of species (*21*). By simultaneously considering the species and the interactions that support them, ecological network analysis provides a critical framework for evaluating how the loss of species and interactions affect community functioning and resilience (*22*). However, and despite the urge to conserve biotic interactions and the ecological functions they provide, we still lack a comprehensive framework to assess the conservation status of biotic interactions (*23*).

Defaunation has raised concerns over animals' capacity to effectively disperse seeds, but generalizations are hindered by a predominance of single-guild studies (*24*, *25*). Consequently, the general conservation status of seed dispersal services remains unevaluated [but see (*11*)]. We address this knowledge gap by assembling a European-wide seed dispersal network. We conducted a systematic literature review in Google Scholar and Web of Science to extract all records of frugivory and seed dispersal interactions by all vertebrates and invertebrates on the European continent. To minimize geographical and taxonomical biases, we performed direct searches for each animal species in English, Portuguese, Spanish, French, German, and Russian. This enabled us to (i) evaluate the conservation status of seed dispersal services in Europe, (ii) identify specific plants and regions particularly vulnerable to dispersal failure, and (iii) develop a general framework to assess the conservation status of biotic interactions.

European frugivory and seed dispersal network

Our literature searches retrieved more than 50,000 publications, including scientific papers, books, grey literature, curated datasets, reports, and personal communications. Information was compiled from 1843 published references (1660–2023). Most (65%) of these publications were in English, with the remaining being written in 25 other languages, namely Russian (10%), Spanish (7%), German (7%), French (4%), Hungarian (2%), and 20 other European languages (5%). Interaction data originated from 38 European countries, including the nine European biomes (Fig. 1). The European frugivory and seed dispersal network had 15,229 distinct plant-animal interactions among 2154 plant species (138 families) and 516 animal species (103 families) (Fig. 2A). Naturally, owing to the broad spatial scale of the study, not all species co-occur.

Eighteen percent of all interactions correspond to records of confirmed seed dispersal (with viable seeds), 57% to records of potential seed dispersal (entire seeds dispersed but viability untested), and 25% to frugivory records without information about seed fate. Frugivory was discarded from further analysis, while the former two were combined and considered hereafter as seed dispersal interactions. Seed predation interactions were not included in this study. Thus, the European seed dispersal network (Fig. 2B) included 11,414 interactions between 1902 plant species and 455 disperser species. The latter included 283 bird species, 85 arthropods, 69 mammals, 11 reptiles, four mollusks, two fish, and one annelid. Most plant and disperser species were native to Europe; however, ~11% of the plants (n = 203) and 8% of the dispersers (n = 35) were introduced, and 0.7% (n = 3) had uncertain origin (Fig. 2B). Introduced plants were excluded from further analyses.

Only 35% of the 1699 native plants included in the network had specific traits to promote biotic seed dispersal. Thirty percent had adaptations to promote abiotic dispersal, and 42% had unspecialized seeds (Fig. 2C). It is widely recognized that even plants without adaptations for biotic dispersal benefit from animal dispersal and that losing dispersers can reduce their dispersal distances (*26*, *27*). However, because these plants do not strictly depend on animals for dispersal, hereafter we focused exclusively on native plants with adaptations for animal dispersal (n = 592). These were dispersed by 398 disperser species through 5030 interactions (Fig. 2D).

Each animal species dispersed on average 13 plant species (median = 4; range 1 to 119). The number of plant species dispersed by each disperser (animal degree) and the importance of each animal species for the plant community (measured as the sum of the dependencies of

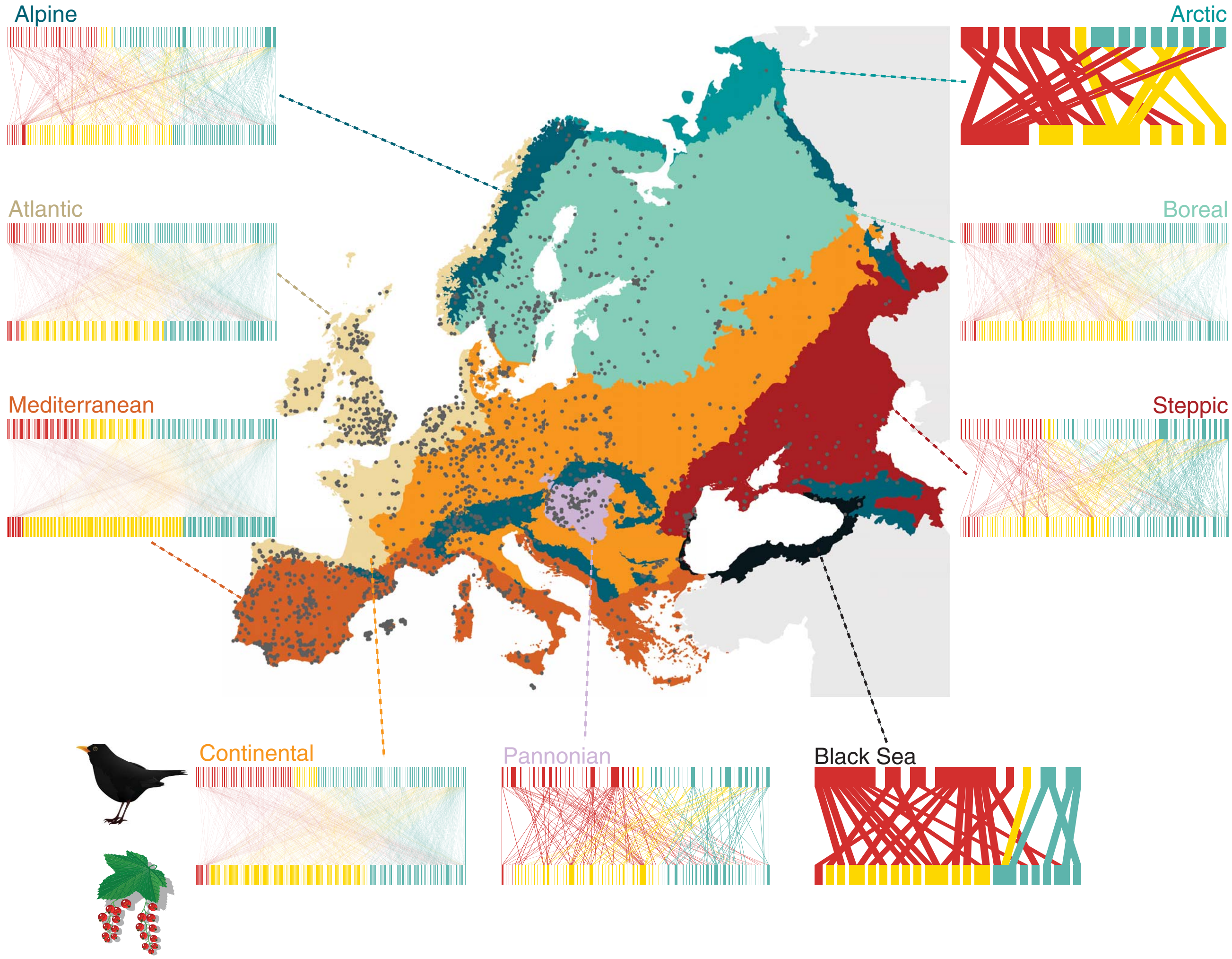


Fig. 1. Seed dispersal interactions across the European biomes. Points represent the location of frugivory and seed dispersal interactions. Networks represent the pairwise interactions between native and introduced seed dispersers (top boxes) and native plant species with biotic seed dispersal syndromes (bottom boxes). Network nodes and interactions are colored according to their conservation status: High Concern (red), Not Evaluated (yellow), and Low Concern (teal).

plant species on each focal disperser, i.e., animal species strength) (*28*) were highly correlated (Kendall correlation test, $n = 398$, $\tau = 0.696$, $P < 0.001$), suggesting that this service is predominantly provided by generalist dispersers, which have a high species strength mainly because they disperse many species. The most important dispersers include abundant and widespread mammals such as red deer (*Cervus elaphus*, 119 plants), wild boar (*Sus scrofa*, 115 plants), red fox (*Vulpes vulpes*, 100 plants), sheep (*Ovis aries*, 99 plants), and birds: blackbird (*Turdus merula*, 105 plants), Eurasian magpie (*Pica pica*, 96 plants), and Eurasian blackcap (*Sylvia atricapilla*, 95 plants).

Each plant species had on average nine dispersers (median = 4; range 1 to 90). The plant species with the most dispersers were elder (*Sambucus nigra*, 90 dispersers), European blueberry (*Vaccinium myrtillus*, 88 dispersers), rowan (*Sorbus aucuparia*, 81 dispersers), sweet cherry (*Prunus avium*, 70 dispersers), crowberry (*Empetrum nigrum*, 69 dispersers), common grape vine (*Vitis vinifera*, 69 dispersers), and red raspberry (*Rubus idaeus*, 65 dispersers). Most plants (63%) had 5 or fewer dispersers, and although plants' dependence on dispersers is highly variable and hard to estimate (*29*), losing any of them could hinder future plant recruitment (*7*). Dispersers' diversity is critical to secure effective seed dispersal services either because animal species provide complementary services (*30*, *31*) or because they promote community redundancy (*32*). Plants with a highly diverse disperser assemblage are then expected to have an advantage in tracking rapidly changing climate, putting additional pressure on plants with reduced dispersal capacity (*33*). Moreover, new plant introductions, often facilitated by climate change, might divert seed dispersal services away from natives (*33*).

Fifty-seven percent of the native plants relied exclusively on native dispersers, 36% were dispersed by native and non-native dispersers, and 7% were dispersed only by non-native animals, whereby the latter can ameliorate but unlikely fully compensate the loss of native dispersers (*34*, *35*).

We found that the European biotic network was highly modular [modularity (M) = 0.41; $P < 0.0001$] and that dispersers were clustered into six distinct modules of densely interacting species (*36*). Eight of the dispersers acted as network hubs (species that are highly connected both within and across modules); 12 acted as module hubs (particularly well connected within their module); 30 acted as connectors (species that have many links with species on other modules); and the remaining animal species were peripherals (species with few interactions).

To estimate the sample coverage of our dataset, we built incidence matrices using individual bibliographic references as sampling units. Although no network is ever fully sampled (*37*), the biotic seed dispersal network

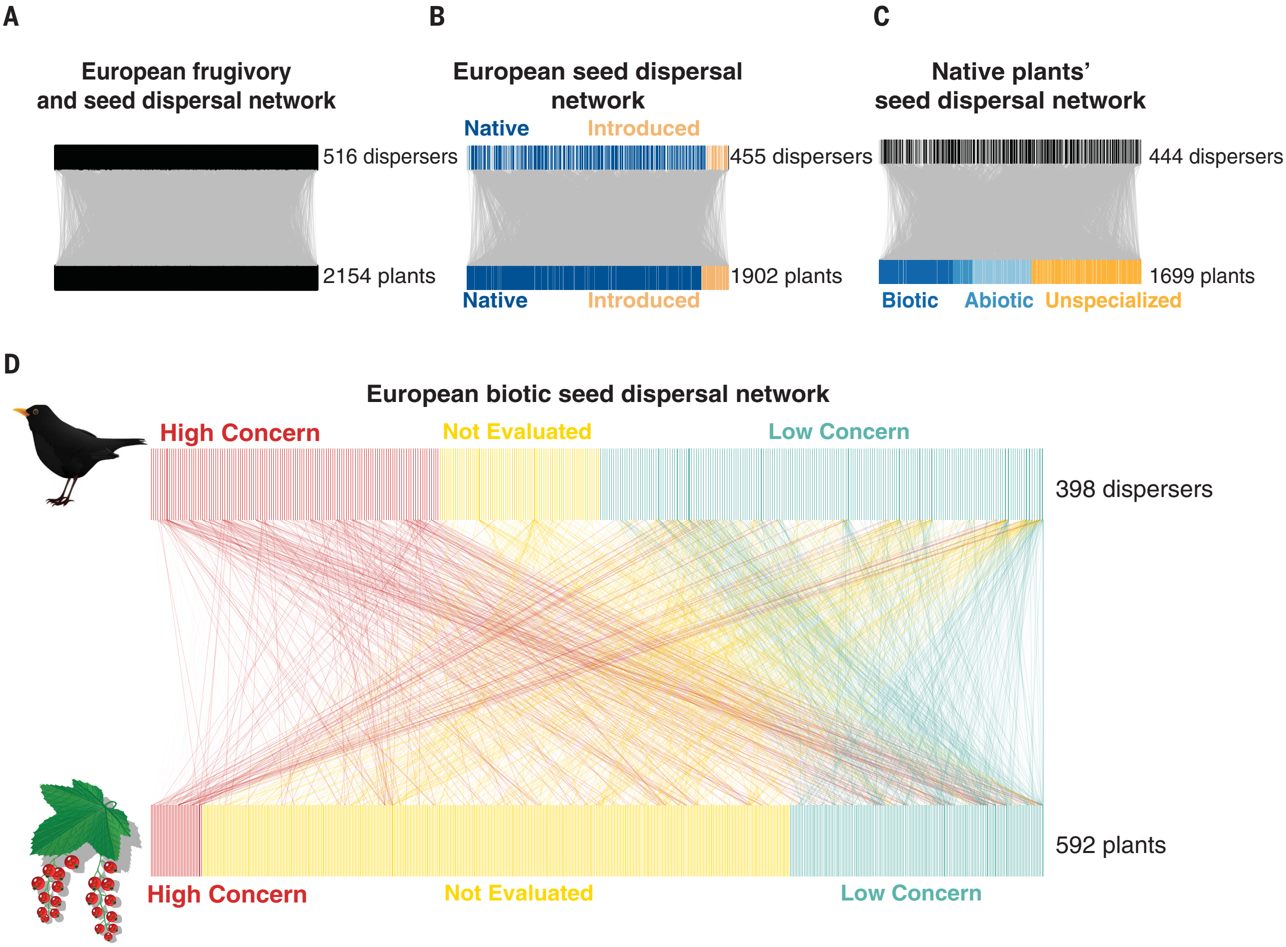


Fig. 2. Visualization of the aggregated European frugivory and seed dispersal networks. Top boxes represent seed dispersers, and bottom boxes represent plant species. (**A**) European frugivory and seed dispersal network, including all records of frugivory and potential seed dispersal independently from the level of confirmation of seed viability (see supplementary materials, materials and methods), but excluding those records where seed predation has been confirmed. (**B**) European seed dispersal network, including only interactions where seed viability has been experimentally confirmed or assumed based on the presence of intact seeds in fecal samples. Nodes with unknown origin are shown in black (top right). (**C**) European native plants' seed dispersal network, representing pairwise interactions between native and introduced seed dispersers and native plant species. Each plant is colored according to the presence of dispersal syndromes, and species with unspecialized diaspores are shown in orange. (**D**) European biotic seed dispersal network, including pairwise interactions between native and introduced dispersers and native plants with biotic dispersal syndromes. Network nodes and interactions are colored according to their conservation status.

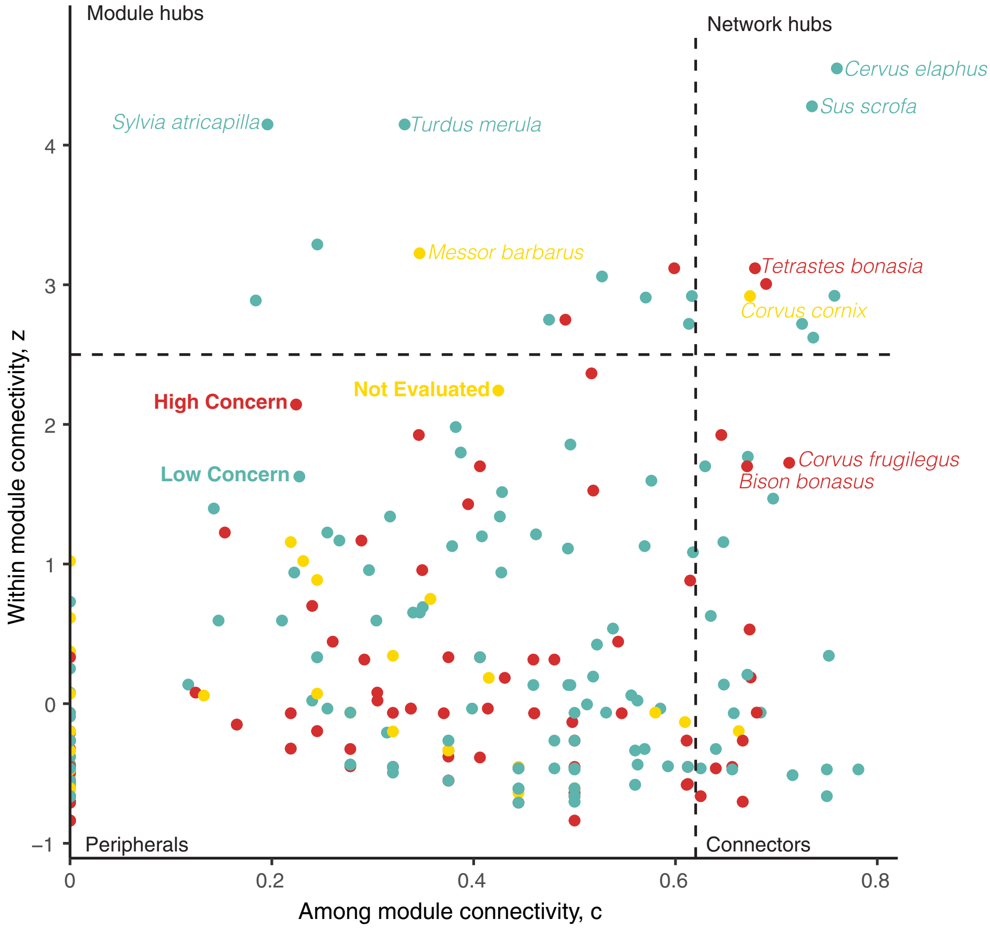
had a very high sample coverage for dispersers (98%), plants (97%), and interactions (83%), which indicates that our review captured the vast majority of the published information on seed dispersal interactions. Sample coverage estimates for each biome varied between 57 to 95% for dispersers, 73 to 95% for plants, and 27 to 75% for interactions (table S1). These estimates exclude only the Arctic and Black Sea biomes because of their small extent and scarcity of studies (table S1). This level of sample coverage was only possible because of the directed literature searches for each animal species, which revealed many diet studies in which seeds are reported (*38*) but not included in specific seed dispersal studies.

Despite such high sample coverage, data are available for only 26% of the ~2248 native plant species with zoochorous traits, highlighting important knowledge gaps in seed dispersal research in Europe. To confirm this, we performed searches for 100 European plant species with zoochorous traits not present in our network (table S2) and found no new interactions, further suggesting that the dispersers of many of these rare and localized species remain unknown. Part of this gap could be explained by the predominant animal-centered nature of seed dispersal research, which should be complemented by plant-centered studies. To check whether this bias could be affecting our capacity to find information, we performed another set of targeted searches for 100 European plant species with zoochorous traits (table S3) already present in our network. Again, we detected no new interactions, which suggests that such bias is intrinsic to the literature but not affecting our capacity to find relevant published information. Therefore, identifying the seed dispersers for many understudied plant species—many of them with restricted and threatened populations—is key, even in one of the most studied continents.

A seed dispersal crisis in Europe

To assess the health of the seed dispersal services in Europe, we first obtained the conservation status and population trends from the International Union for Conservation of Nature (IUCN) Red List (*23*) for all species. Eleven percent of the dispersers were Threatened, 64% Not Threatened, and 25% Not Evaluated (table S4); 43% were Declining (undergoing population declines), 35% were Stable, and 22% were Increasing (tables S4 and S5). We then sorted species into three broader conservation categories by combining their conservation status and population trends: (i) "High Concern" for species listed as Near Threatened, Threatened, or Declining; (ii) "Not Evaluated"

Fig. 3. Distribution of seed disperser species according to their network role regarding the modular structure. Each point represents a disperser species colored according to its conservation status: High Concern (red), Not Evaluated (yellow), and Low Concern (teal).



for Not Evaluated and data-deficient species with unknown population trends; and (iii) "Low Concern" for Not Threatened species with Stable, Increasing, or Unknown population trends. We found that for native plants, 33% of the dispersers were of High Concern, 18% were Not Evaluated, and 49% were of Low Concern (Fig. 2d).

The most important dispersers, in terms of degree (number of partner species) and species strength (a measure of the dependence of mutualistic partners on the focal species), included species of High Concern from several animal groups, including birds (garden warbler *Sylvia borin*, rook *Corvus frugilegus*, and redwing *Turdus iliacus*), mammals (European bison *Bison bonasus*, reindeer *Rangifer tarandus*, and European rabbit *Oryctolagus cuniculus*), reptiles (Lilford's wall lizard *Podarcis lilfordi*), and ants (European red wood ant *Formica polyctena* and Southern wood ant *F. rufa*). Furthermore, all European biomes had at least one-third of their dispersers classified as High Concern (table S6). Lastly, among network hubs, module hubs, and connector species, 32% were of High Concern (Fig. 3). The loss of High Concern dispersers that play essential network roles might accelerate the fragmentation of the network structure (*36*). In turn, dispersal failure due to the loss of dispersers may disrupt plant recruitment, constrain gene flow, reduce genetic and phenotypic plant diversity, and truncate seed dispersal distances, which is particularly worrying given plants' need to track climate change (*7*, *11*).

Only 1% of the biotically dispersed plants were evaluated as Threatened, while 32% were evaluated as Not Threatened, and most (67%) lacked IUCN assessment (table S4). Regarding population trends, 20% of the plant species were Declining, 75% were Stable, and only 5% were Increasing (tables S4 and S5). Therefore, 6% were of High Concern (e.g., English oak *Quercus robur*, French rose *Rosa gallica*, and Lapland buttercup *Ranunculus lapponicus*), 67% were Not Evaluated, and 27% were of Low Concern (Fig. 2D).

Our data shows that most native plant species (n = 357; 60%) had at least one disperser of High Concern and one-third (n = 190; 32%) had at least half of their evaluated dispersers in this category. These are important warning signs for the future of European plants, particularly considering that the seed dispersal service does not stop abruptly when the last disperser goes extinct but gradually erodes as the dispersers' populations decline (*16*, *39*). Indeed, animal species can become functionally extinct well before their actual extinction (*40*, *41*). Although our dataset reveals no documented disperser extinction in the last four centuries, many High Concern species may no longer be effectively delivering the dispersal services compiled here.

We found that Low Concern animals dispersed more native plant species than did Not Evaluated (Tukey test, z = 5.26, P < 0.001) and High Concern dispersers (Tukey test, z = 3.84, P < 0.001) (fig. S1A and table S7). Similarly, Low Concern plants also had more dispersers than did High Concern plants (Tukey test, z = 2.25, P = 0.06) (fig. S1B and table S7). However, we found no differences in species strength between High Concern, Low Concern, and Not Evaluated dispersers (Kruskal-Wallis test, $\chi2$ = 0.99, df = 2, P = 0.611) (fig. S1C), suggesting that High Concern dispersers, many of which with small populations and reduced distributions, are just as important as those of Low Concern, despite the latter being typically more widespread and abundant.

Interaction conservation status

To assess interaction conservation status, we extended the framework developed for species

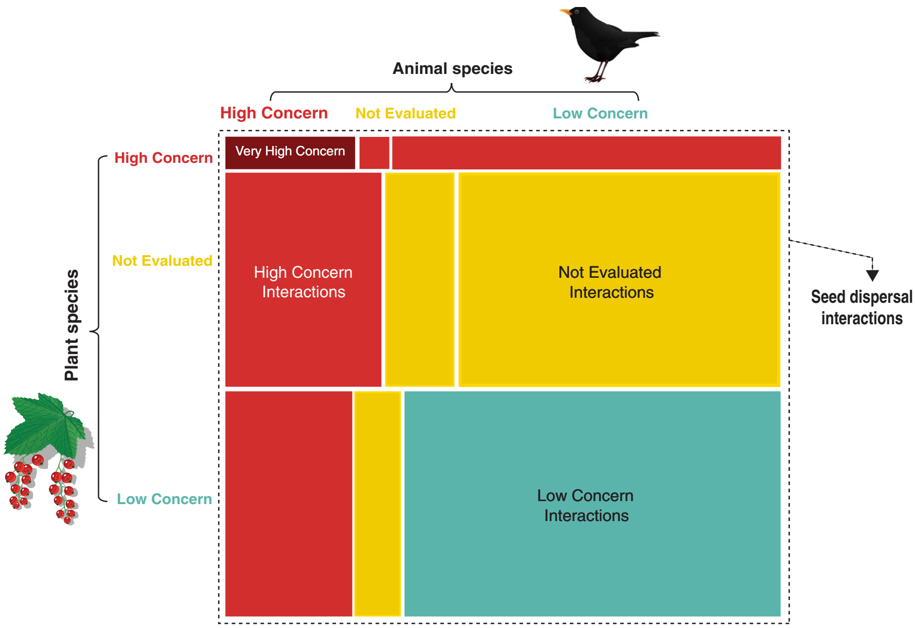


Fig. 4. Proportion of seed dispersal interactions per interaction conservation status. Mosaic plot depicting the proportion of seed dispersal interactions according to their conservation status as defined in supplementary materials, materials and methods: Very High Concern (dark red), High Concern (red), Not Evaluated (yellow), and Low Concern (teal) interactions.

conservation categories to classify every plant-disperser species interaction as: (i) "Very High Concern," if both interacting species were of High Concern; (ii) High Concern, if at least one of the partner species was Threatened or Declining; (iii) Not Evaluated, if at least one partner species was Not Evaluated and the other partner was not of High Concern; and (iv) Low Concern, if both interacting partners were of Low Concern. We found that 2% of the interactions were classified as Very High Concern, 29% as High Concern, 36% as Not Evaluated, and 33% as Low Concern (Fig. 4 and table S8). Our results showed that the proportion of High and Very High Concern interactions (31%) far exceeded that of High Concern species (17%) (χ^2 = 78.40, df = 1, P < 0.001), suggesting that the conservation status of interactions is likely to be a more sensitive and comprehensive indicator of community health than the conservation status of species alone. Indeed, conservation efforts should first concentrate on Very High Concern interactions, which are likely to be disrupted soon. This framework may provide a useful metric for guiding conservation and restoration strategies targeting ecosystem functioning (*42*), while bolstering regional collaboration among ecologists, conservation practitioners, and policy-makers.

Interaction conservation statuses were not homogeneously distributed across the European biomes (χ^2 = 163.39, df = 12, P < 0.001) (table S6). However, all biomes had a sizeable proportion of High Concern interactions, ranging from 25% in the Mediterranean to 54% in the Pannonian, 72% in the Arctic, and 81% in the Black Sea biomes (Fig. 1 and table S6). The high prevalence of threatened interactions in some of the more geographically restricted, understudied, and degraded biomes in Europe (*43*, *44*) clearly highlight the need to understand and protect the interaction networks that support their distinctive species assemblages.

A likely underestimated picture

Despite Europe's strong tradition in natural history, ecological research, and well-structured scientific and conservation communities, there are still critical knowledge gaps limiting our assessment of the health of seed dispersal services. Noticeably, the conservation status of 67% of the zoochorous plant species has not been assessed by the IUCN, and 73% have unknown European-level population trends. However, there is evidence that many of these species are declining, at least regionally (*14*, *45*). For example, 70% of the plant species in Germany have declined in the last 60 years (*46*). This assessment bias is even more evident for invertebrate seed dispersers (mostly ants), 85% of which have still not been assessed by IUCN. This is particularly concerning because recent evidence shows that unassessed species are not a random subset of all species but tend to have restricted ranges and smaller populations, which are likely associated with unfavorable conservation status (*47*). Accordingly, the fraction of unevaluated species likely hides a much larger conservation threat for European dispersers, plants, and seed dispersal interactions (*48*). Additionally, our data revealed a significant difference in the conservation status of the dispersers of native and introduced plants with zoochorous traits (χ^2 = 14.096, df = 2, P < 0.001). Indeed, introduced plants have a higher proportion of Low Concern dispersers than do native plants (table S9), potentially facilitating their spread and exacerbating the competition for resources and seed dispersers for native plants (*33*).

Although our literature search was planned to minimize taxonomical biases, we identified a significant correlation between the number of source references from which their interactions were retrieved (i.e., number of papers with interactions of species i) and both the number of plant species dispersed by each animal and the number of dispersers per plant species (Kendall correlation test, n = 398, τ = 0.674, P < 0.001; n = 592, τ =0. 818, P < 0.001, respectively).

This bias reflects a research bias toward species with socioeconomic importance, broad distributions, high abundance, and large body size, which might blur the real magnitude of the seed dispersal crisis rather than inflating it. This bias is reflected in the high proportion of studies focused on Low Concern dispersers (75%), whereas High Concern dispersers were only reported in 38% of the studies, and Not Evaluated dispersers in 7% (some studies focused on more than one species, whereby the total percentage exceeds 100%). Because data are only available for 26% of the European zoochorous plant species, we performed bootstrap analysis to explore how the estimated proportion of High Concern interactions would vary on the basis of variable subsamples (ranging from 10 to 80%) of our original dataset. This analysis showed that even estimates based on as little as 10% of our full dataset would provide practically similar estimates (fig. S2), supporting the reliability of our estimates.

Conclusions

Despite the consensus about the importance of biotic interactions in general—and seed dispersal in particular—for ecosystem functioning (*1*, *5*), ecologists and land managers still have incomplete knowledge about seed dispersal interactions and their conservation status. We showed evidence of a seed dispersal crisis in Europe that might have started with the Pleistocene megafauna extinctions (*49*) and that presents an uncertain future. This crisis is particularly worrying given that plants need to track rapidly shifting climatic envelopes in a continent strongly affected by habitat fragmentation (*9*). Our study provides compelling evidence for the need to prioritize the study and conservation of seed dispersal interactions that plants— and therefore people— depend upon.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.ado1464
Materials and Methods
Fig. S1 and S2
Tables S1 to S9
References (*51*–*76*)
MDAR Reproducibility Checklist

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Correction (15 October 2024): The corresponding author's email address was entered incorrectly during production as "sarabmendes@gmail.com". This has now been corrected.