Frugivore-mediated seed dispersal in fragmented landscapes: Compositional and functional turnover from forest to matrix

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Seed dispersal by frugivores is a fundamental function for plant community dynamics in fragmented landscapes, where forest remnants are typically embedded in a matrix of anthropogenic habitats. Frugivores can mediate both connectivity among forest remnants and plant colonization of the matrix. However, it remains poorly understood how frugivore communities change from forest to matrix due to the loss or replacement of species with traits that are less advantageous in open habitats and whether such changes ultimately influence the composition and traits of dispersed plants via species interactions. Here, we close this gap by using a unique dataset of seed-dispersal networks that were sampled in forest patches and adjacent matrix habitats of seven fragmented landscapes across Europe. We found a similar diversity of frugivores, plants, and interactions contributing to seed dispersal in forest and matrix, but a high turnover (replacement) in all these components. The turnover of dispersed seeds was smaller than that of frugivore communities because different frugivore species provided complementary seed dispersal in forest and matrix. Importantly, the turnover involved functional changes toward larger and more mobile frugivores in the matrix, which dispersed taller, larger-seeded plants with later fruiting periods. Our study provides a trait-based understanding of frugivore-mediated seed dispersal through fragmented landscapes, uncovering nonrandom shifts that can have cascading consequences for the composition of regenerating plant communities. Our findings also highlight the importance of forest remnants and frugivore faunas for ecosystem resilience, demonstrating a high potential for passive forest restoration of unmanaged lands in the matrix.

DNA barcoding | community ecology | habitat fragmentation | species interactions | trait-based ecology

Anthropogenic destruction and fragmentation of natural habitats have transformed terrestrial ecosystems globally (1–3). Remnant habitats typically persist as relatively natural patches embedded in a matrix of anthropogenic land covers (4), mainly agricultural fields, rangelands, industrial areas, and urban settlements (2). The capacity of species to disperse through such a matrix underpins the functional connectivity of populations and communities (5), and enables the colonization of unoccupied and regenerating habitat patches after disturbance (6, 7). Dispersal is thus a cornerstone process for community assembly in fragmented landscapes (8, 9).

Across the world's biomes, many plants, particularly woody ones, produce fleshy fruits and rely on frugivorous animals for their seed dispersal (10). In this mutualism, frugivores consume fleshy fruits, transport seeds in their guts, and deposit them in suitable conditions for germination (11), generating spatial patterns of seed rain (12) that influence the assembly of early-regenerating plant communities (13). Species that transfer propagules within and across disturbed habitats are termed "mobile links" (14). Hence, frugivores operate as mobile links in fragmented landscapes when they actively move between habitats and transport seeds within and across the matrix (15). This way, frugivores maintain landscape-scale connectivity and favor the colonization of matrix habitats (15), which is crucial for plant community dynamics (16) and ecosystem resilience after land-use changes (7, 13, 15, 17). Yet, we know little about mobile-link functions within diverse frugivore assemblages and their consequences for the dispersal of plant communities in fragmented landscapes (but see ref. 13). At the community level, interactions between multiple frugivore and plant species comprise networks of seed-dispersal interactions (18). These networks are characterized by interaction redundancy and complementarity (19). That is, although most plant species in a community share some frugivores with others (redundancy), they typically interact with different subsets of the whole frugivore assemblage (complementarity) owing to morphological traits or spatiotemporal occurrence (20) as well as frugivore preferences (21) that constrain interactions between plants and frugivores. Thus, one would expect a differential capacity of plant species within communities to be

Significance

Many plants rely on frugivorous animals for seed dispersal. In fragmented landscapes, frugivore communities can change from forest to matrix due to species loss or replacement in open anthropogenic habitats, and such changes have potential consequences for the plants they disperse. We report a similar diversity of frugivores, plants, and interactions contributing to seed dispersal in forest and matrix habitats from seven fragmented landscapes across Europe. However, we found a substantial turnover of both species and interactions. This turnover entailed functional changes toward larger and more mobile frugivores in the matrix that dispersed taller, larger-seeded plants with later fruiting periods. Our study provides a trait-based understanding of frugivore-mediated seed dispersal in anthropogenic landscapes and can inform ecological restoration.

dispersed through the matrix whenever frugivore species differ in their role as mobile links (Fig. 1).

Frugivore species do in fact operate unequally as mobile links because they respond differently to the open anthropogenic matrix: While some species avoid it, the matrix is an important or even the main habitat for other species (15). Such response diversity (22) generates changes in species composition (i.e., beta diversity) between forest remnants and the matrix due to the loss or replacement (i.e., losses and gains) of frugivore species (23) and to changes in their relative abundances (15). Frugivore responses to the matrix are driven by response traits that determine sensitivity to disturbance (24). For example, wing morphology is related to flight efficiency and predicts the ability of bird species to cross deforested areas (25). Generally, response traits are not randomly distributed but clustered in certain phylogenetic lineages or taxonomic groups of frugivores (26). Importantly, response traits of frugivores are also effect traits for mobile-link functions because they determine the potential for seed dispersal through the matrix (24). Ultimately, these taxonomic and functional responses are expected to cascade into the community of dispersed plants via pairwise interactions (Fig. 1 B and C). Certain plant traits will be favored or hindered in the matrix whenever they influence pairwise interactions with frugivores (i.e., matching traits, ref. 24). Moreover, changes in communities of dispersed plants can also be influenced by the presence of fruiting plants in the matrix acting as seed sources, often cultivated or grown as ornamentals (27) (Fig. 1C). Indeed, exotic plants are typically more prevalent in the matrix, where they can be successfully dispersed by frugivores (28, 29). However, there is a major gap of empirical research jointly addressing these taxonomic and functional changes at the community level, accounting for species, interactions and traits. This is largely explained by methodological constraints to link the seeds arriving to forest and matrix with the frugivore species that dispersed them (15, 30). Notably, the few available studies tackling some of these questions used indirect evidence by combining information on diet and perch use to infer avian seed dispersal (e.g., ref. 13).

Here, we seek a comprehensive understanding of community-level changes in frugivore-mediated seed dispersal from forest to matrix. To do so, we sampled frugivore-dispersed seeds in seven fragmented landscapes across Europe year-round, covering the entire fruiting period of all plant species. Then, we used DNA barcoding to identify the frugivore species responsible for the seed-dispersal events (30). This technique has the advantage of identifying frugivores (thus, plant–frugivore interactions) at seed deposition sites, once the dispersal function is completed (30). First, we assessed differences between forest and matrix in local diversity (i.e., alpha diversity) of frugivore species, seed species, and pairwise interactions contributing to community-wide seed dispersal. We also evaluated differences between forest and matrix in the functional complementarity of interactions, that is, the degree of dependence of seed diversity on frugivore diversity (24). Then, we assessed how much of the beta diversity between forest and matrix was accounted for by turnover (i.e., replacement ref. 31) of species and interactions. Finally, we tested for differences between forest and matrix in the contributions to community-wide seed dispersal of the most important frugivore families and for differences in frugivore and plant traits. Our general hypothesis was that frugivore-mediated seed dispersal through fragmented landscapes is shaped by the turnover of frugivore species and traits from forest to matrix (scenario of Fig. 1C).

Results

DNA-barcoding analysis identified 43 frugivore species to be responsible for the dispersal of the seeds sampled in the study landscapes: 40 species belonging to 14 bird families and three mammal species belonging to two families of the Order Carnivora (*SI Appendix*, Table S3). We identified an average of 16 disperser species per landscape (range = 11 to 22). The seeds sampled included 48 (operational) species (44 species, three species aggregates, and one cultivated variety) belonging to 25 families (*SI Appendix*, Table S4); on average, there were 14 species per landscape (range = 11 to 16). From seed and frugivore identifications, we obtained a total of 240 unique interactions between species pairs, on average, 57 per landscape (range = 44 to 83). Bird-mediated seed rain sampled in seed traps was significantly higher in forest than in matrix (mean = 19.3 and 8.8 seeds per m^2, respectively) and two orders of magnitude higher than mammal-mediated seed rain sampled in transects. The latter was nonsignificantly different between forest and matrix (mean = 0.15 and 0.09 seeds per m^2, respectively; see *SI Appendix*, Fig. S4).
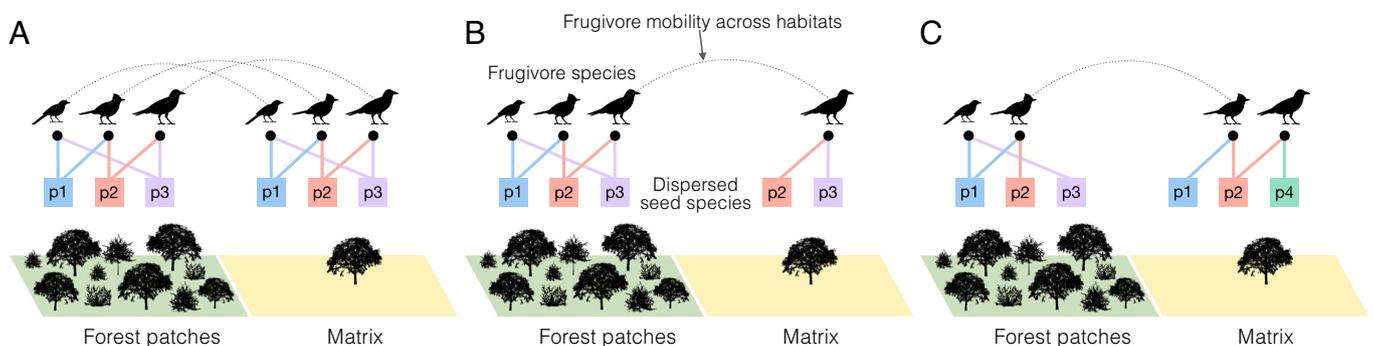

Fig. 1. Conceptual diagram showing seed-dispersal (deposition) networks within forest patches and in the surrounding matrix of a fragmented landscape, illustrating three hypothetical scenarios (*A–C*) regarding frugivore mobility across habitats. In these networks, upper nodes are different frugivore species (black dots with silhouettes), lower nodes are different seed species (colored and labelled squares), and links connecting nodes (colored lines) are seed-dispersal services of frugivore species to plant species in each habitat. Dotted lines denote frugivore mobility across habitats. (*A*) All frugivore species move across habitats leading to similarity between forest and matrix in frugivore contributions and seed-rain composition (null hypothesis). (*B* and *C*) Only a fraction of the frugivore community move across habitats and, consequently, dissimilarity in seed-rain composition between habitats could be driven by (*B*) the loss of frugivore species and their interactions from forest to matrix; or alternatively (*C*) by a turnover (replacement) of frugivore species and their interactions. Note that seeds from some plant species ("p3" and "p4") are only deposited either in forest or matrix because they are dispersed by frugivore species that do not move across habitats ("p4" represents an ornamental exotic species of the matrix). The taxonomic differences between forest and matrix in (*B* and *C*) could be associated to changes in traits (response traits) of both frugivores and plants. These toy examples only focus on changes in species composition, but changes can also affect the relative contributions of both species and interactions.

Alpha Diversity and Interaction Complementarity in Forest and Matrix. We found no significant differences between forest and matrix in mean species richness of frugivores contributing to seed rain (11.3 and 12.9 species, respectively; $\chi^2 = 0.71$, $P = 0.401$; Fig. 2). However, mean Hill–Shannon was significantly higher in the matrix (5.9 species) than in the forest (4.7 species; $\chi^2 = 6.03$, $P = 0.014$; Fig. 2). Regarding the seeds, we found no significant differences between forest and matrix in mean species richness (11.7 and 9.9 species, respectively; $\chi^2 = 1.12$, $P = 0.291$) or mean Hill–Shannon (4.7 and 5.0 species, respectively; $\chi^2 = 0.293$, $P = 0.589$) (Fig. 2). Similarly, pairwise interactions did not differ between forest and matrix in terms of mean richness (30.1 and 26.3 interactions, respectively; $\chi^2 = 1.82$, $P = 0.178$) or mean Hill–Shannon (12.3 and 12.1 interactions, respectively; $\chi^2 = 0.03$, $P = 0.870$) (Fig. 2). However, despite these similar levels in interaction diversity, we found that seed-dispersal networks were more complementary (less redundant) in the matrix (mean $H_2' = 0.65$) than in the forest (mean $H_2' = 0.50$; $\chi^2 = 7.97$, $P = 0.005$)

(Fig. 3; see all networks in *SI Appendix*, Fig. S5). Details on these models can be found in *SI Appendix*, Table S6.

Landscape-Scale Beta Diversity. We found substantial levels of landscape-scale beta diversity of frugivores and seeds between forest and matrix (mean Jaccard = 0.44 and 0.47, respectively), and high levels of interaction beta-diversity (mean Jaccard = 0.73) (Fig. 2). Remarkably, beta diversity of seeds was positively related to that of frugivores (*SI Appendix*, Fig. S6). Beta diversity was mostly driven by the turnover of species and interactions. Indeed, the turnover component accounted on average for 88% of beta diversity of frugivores, 59% of beta diversity of seeds, and 93% of beta diversity of pairwise interactions (Fig. 2). When considering the quantitative contributions to seed rain, we found a high proportional dissimilarity between forest and matrix in the contributions of frugivore species and pairwise interactions (mean = 0.58 and 0.67, respectively), which doubled that found for the contribution of seed species (mean = 0.34) (Fig. 2).
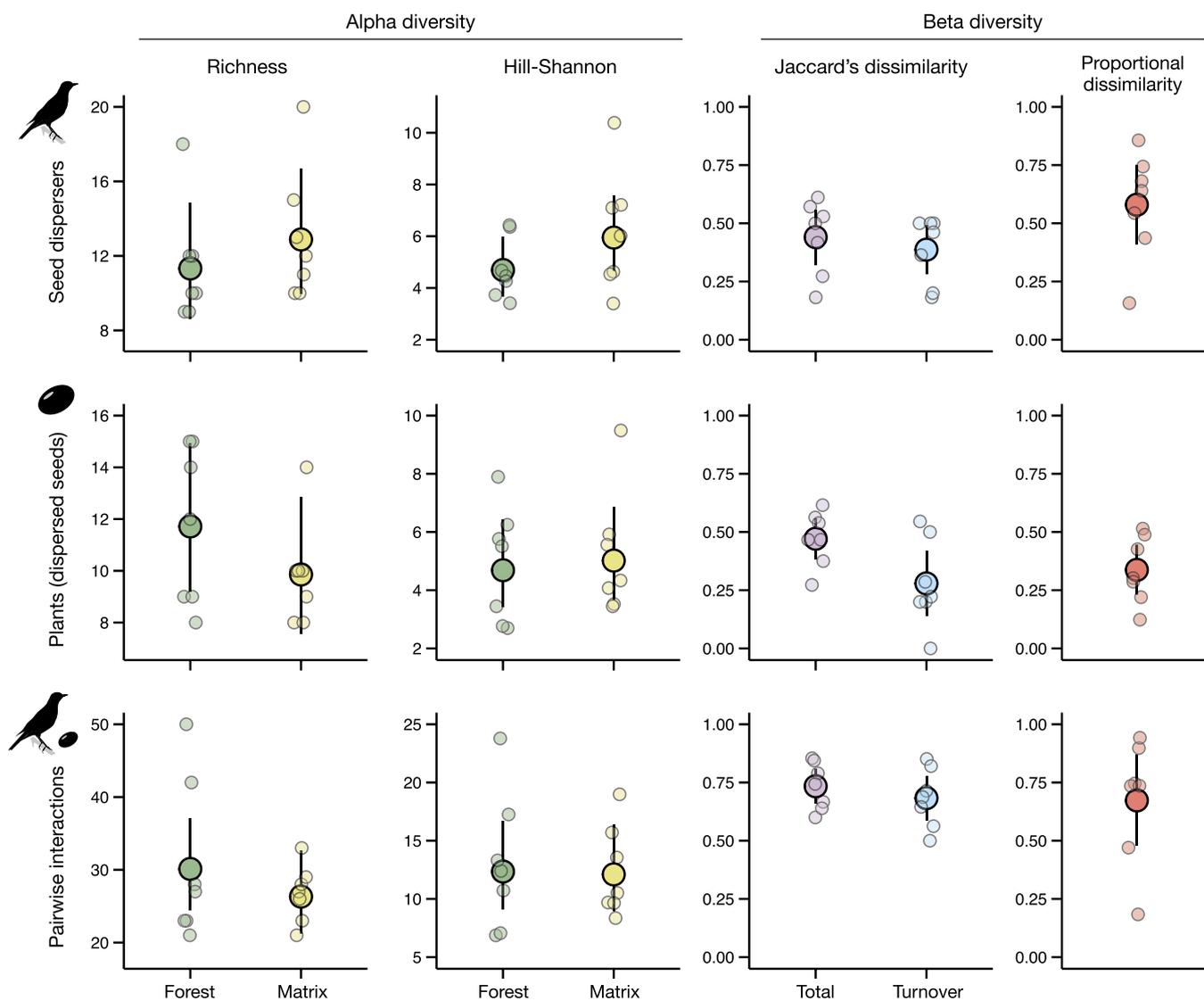

Fig. 2. Patterns in alpha and beta diversity of frugivore species contributing to seed rain (*Top* row of panels), dispersed seed species (*Central* row of panels), and pairwise interactions between frugivore and seed species (*Bottom* row of panels). Alpha diversity in forest and matrix is expressed in terms of richness and Hill–Shannon (note the different scales for the *y* axis). According to Chao et al. (32), Hill–Shannon can be interpreted as the effective number of common species (or pairwise interactions). Large circles with error bars denote back-transformed means ± 95% CI estimated by GLMMs testing differences between habitats, whereas small circles denote observed values. Beta diversity between forest and matrix of each study landscape is expressed in terms of Jaccard's compositional dissimilarity (differentiating between the total dissimilarity and that due to turnover) and proportional dissimilarity (which accounts for differences in relative contributions) of species and pairwise interactions. Large circles and error bars denote dissimilarity means ± 95% CI, whereas small circles denote values per landscape.
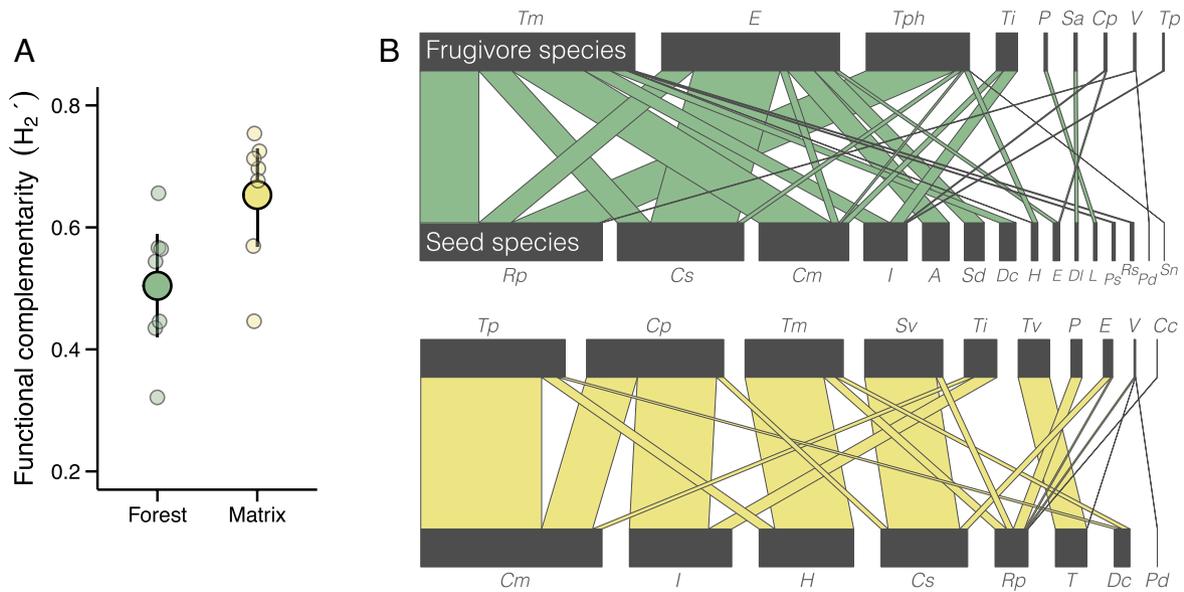
Fig. 3. (*A*) Functional complementarity (complementary specialization index H_2') of seed dispersal networks sampled in the forest and matrix of the study landscapes. Large circles with error bars denote back-transformed means ± 95% CI estimated by a GLMM testing differences between habitats, whereas small circles denote observed values. (*B*) Seed-dispersal networks sampled in the forest (*Top*) and matrix (*Bottom*) of the Bradfield-Woods landscape (United Kingdom) illustrating interaction patterns associated with distinct degrees of H_2' ($H_{2'\,forest}$ = 0.435; $H_{2'\,matrix}$ = 0.754). In each network, the nodes from the higher level are frugivore species (*Cc: Curruca communis; Cp: Columba palumbus; E: Erithacus rubecula; P: Phasianus colchicus; Sa: Sylvia atricapilla; Sv: Sturnus vulgaris; Ti: Turdus iliacus; Tm: T. merula; Tp: T. pilaris; Tph: T. philomelos; Tv: T. viscivorus; V: Vulpes vulpes*), whereas the nodes from the lower level are seed species (*A: Arum maculatum; Cm: Crataegus monogyna/laevigata; Cs: Cornus sanguinea; Dc: Discorea communis; Dl: Daphne laureola; E: Euonymus europaeus; H: Hedera helix; I: Ilex aquifolium; L: Lonicera periclymenum; Pd: Prunus domestica; Ps: Prunus spinosa; Rp: Rubus plicatus/caesius; Rs: Rosa* sp.; *Sd: Solanum dulcamara; Sn: Sambucus nigra; T: Taxus baccata*). Horizontal width of nodes and links is proportional to the seed-rain density contributed by species and pairwise interactions, respectively.

Contributions to Seed Rain by Frugivore Families. Six bird families accounted for most of the mean relative contribution to seed rain across the study landscapes, both in forest (0.978) and matrix (0.968; Fig. 4); mammals accounted for a minor contribution (0.008), which was evenly distributed between habitats (*SI Appendix,* Fig. S7). We found no significant differences between forest and matrix in the mean relative contributions of Turdidae (0.508 and 0.468, respectively, the highest contribution in both habitats; χ^2 = 0.33, *P* = 0.565) and Corvidae (0.045 and 0.074, respectively; χ^2 = 1.06, *P* = 0.304) (Fig. 4 *A* and *B*). Yet, the mean contributions of

Muscicapidae and Sylviidae were significantly higher in forest than in matrix (Muscicapidae: 0.184 and 0.052, respectively, χ^2 = 16.02, *P* = 10^{-4}; Sylviidae: 0.140 and 0.072, respectively, χ^2 = 6.28, *P* = 0.012) (Fig. 4 *C* and *D*); in Muscicapidae, this was mostly mediated by *Erithacus rubecula* (*SI Appendix,* Fig. S7). Conversely, the mean contributions of Columbidae and Sturnidae were significantly higher in matrix than in forest (Columbidae: 0.061 and 0.011, respectively, χ^2 = 7.04, *P* = 0.008; Sturnidae: 0.169 and 0.003, respectively, χ^2 = 26.65, *P* = 2 ×10^{-16}) (Fig. 4 *E* and *F*); the contribution of Sturnidae was nearly 60 times higher. Details on these models can be
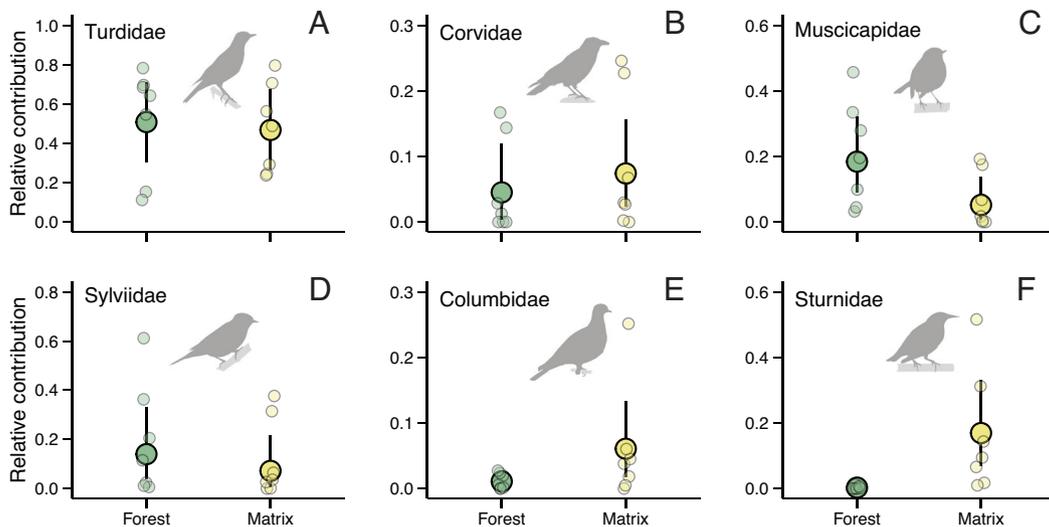
Fig. 4. Relative contribution to community-wide seed rain in forest and matrix of the six main frugivore families: (*A*) Turdidae, (*B*) Corvidae, (*C*) Muscicapidae, (*D*) Sylviidae, (*E*) Columbidae and (*F*) Sturnidae. These families accounted for an average across landscapes of ~98% and ~97% of seed-rain in forest and matrix, respectively. Large circles with error bars denote back-transformed means ± 95% CI estimated by GLMMs, whereas small circles denote observed values. Note the different scales for the *y* axis.

found in *SI Appendix*, Table S7. We obtained similar results from a Principal Component Analysis on the contribution of these families (*SI Appendix,* Table S8).
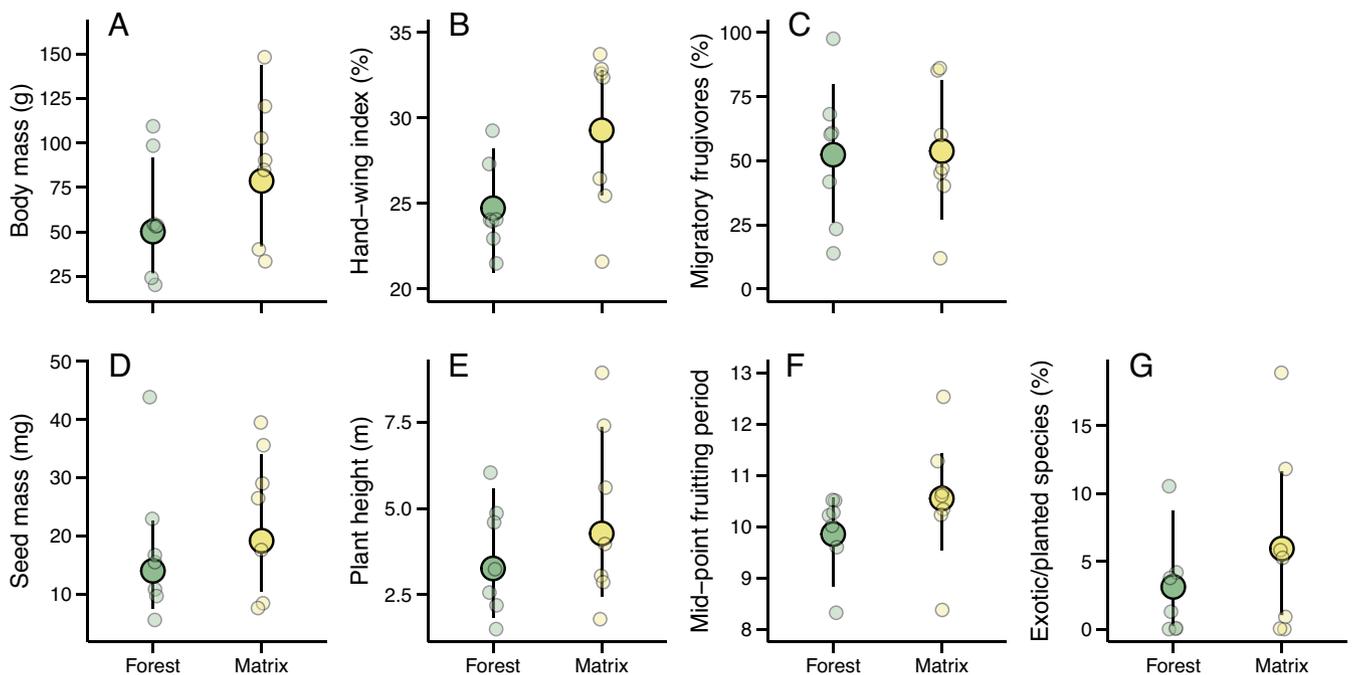
Community-Weighted Mean (CWM) Traits of Frugivores and Plants. The CWM body mass of frugivores contributing to seed rain was higher in matrix (78.6 g) than in forest (50.2 g), as well as the CWM hand-wing index of birds (29.3% and 24.7%, respectively) (Fig. 5 *A* and *B*); >99.6% of the posterior distribution of the matrix effect on both traits were above zero (*SI Appendix,* Fig. S8). In summary, frugivores in the matrix were on average larger and more mobile than those in the forest. The CWM percentage of migratory frugivores contributing to seed dispersal was almost the same in forest and matrix (52.3% and 53.8%, respectively; Fig. 5*C* and *SI Appendix,* Fig. S8). This was mostly driven by the dominanance of Palearctic migrants because the small contribution of Afro-Palearctic migrants was higher in matrix than in forest (*SI Appendix,* Fig. S7).

Regarding the CWM plant traits, seed mass and plant height of the dispersed seed communities were both higher in matrix (19.2 mg and 4.3 m) than in forest (14.0 mg and 3.3 m; Fig. 5 *D* and *E*); 94% and 97% of the posterior distribution for the matrix effect on both traits, respectively, was above zero (*SI Appendix,* Fig. S8). Importantly, the differences within landscapes between forest and matrix in seed mass and plant height were positively related to differences in frugivore size (*SI Appendix,* Fig. S6). Moreover, CWM midpoint date of fruiting periods was later in matrix (10.5) than in forest (9.9; Fig. 5*F*); 96% of the posterior distribution of the matrix effect was above zero (*SI Appendix,* Fig. S8). Finally, the mean percentage of exotic or planted species in the seed rain of the matrix (5.9%) doubled that of the forest (3.1%; Fig. 5*G*), but only 86% of the posterior distribution for the matrix effect was above zero (*SI Appendix,* Fig. S8).

Discussion

Understanding how ecological functions respond to global change is a major challenge in ecology, especially when functions are mediated by complex interacting communities (24, 33, 34). However, theoretical frameworks addressing this issue have mainly focused on the loss of species and functions under environmental changes (24, 34, 35), paying little attention to the importance of compositional and functional turnover. Here, we report no or little change between forest and matrix in the alpha diversity of frugivores, plants, and interactions contributing to seed rain in fragmented landscapes across Europe, but an important turnover in all these components (scenario of Fig. 1*C*). The turnover leads to an increased complementarity in the matrix, where the seed-dispersal services of frugivore species are less redundant. In addition, we show that the turnover is related to response traits (mainly body size and mobility) that are largely shared by frugivores from the same taxonomic group. Importantly, the compositional and functional turnover toward larger and more mobile frugivores in the matrix cascades into plant traits via pairwise interactions because it is related to changes in matching traits of the dispersed plant communities, such as seed size and plant height (*SI Appendix,* Fig. S6). These findings provide a trait-based understanding of how frugivore assemblages complementarily contribute to functional connectivity and potentially shape plant community dynamics across habitat boundaries in fragmented landscapes.

Compositional and Functional Turnover of Species and Interactions. Our findings of similar alpha diversity of frugivores contributing to seed rain in forest and matrix due to species turnover are in line with those reported for the wild olive tree (*Olea europaea* var. *sylvestris*) in southern Spain (15). Hence, our results from multiple plant–frugivore communities and across a large geographical area verify that seed dispersal through

Fig. 5. Community-Weighted Mean (CWM) traits of frugivores (*A–C*) and plants (*D–G*) contributing to community-wide seed rain in the forest and matrix of the study landscapes. (*A*) Body mass of all frugivores, (*B*) hand-wing index (HWI) of avian frugivores; (*C*) percentage of frugivores that are migratory; (*D*) seed mass, (*E*) plant height; (*F*) mid-point date of the fruiting period (monthly scale); and (*G*) percentage of "exotic/planted" species in the seed rain. Large circles with error bars denote medians ± 95% credible intervals of posterior distributions obtained by means of generalized joint attribute models fitted separately to frugivore and plant traits; small circles denote observed CWM values. Values in (*A*) and (*D*) are back-transformed (log$_{10}$-transformation). Proportions are expressed as percentages in (*C*) and (*G*).

fragmented landscapes is complementarily mediated by frugivores behaving either as matrix avoiders, matrix frequenters, or matrix dwellers (15). These behaviors determine within-habitat and cross-habitat dispersal: Seeds dispersed in the matrix can arrive from both the forest and the fine-grained vegetation of the matrix (15, 36), and the same is expected to happen in the forest (i.e., some seed arrival from the matrix; 15). Importantly, frugivore behavior can be explained by differences in habitat specificity and mobility (25, 37), which in turn are related to specific response traits (24). Indeed, frugivores were larger and had higher flight efficiency in the matrix than in the forest. Taxonomically, these traits were associated with specific avian families: Sylviidae and Muscicapidae (mostly *Erithacus rubecula*; *SI Appendix*, Fig. S7), small birds (10 to 22 g) with contributions biased toward the forest; and Columbidae and Sturnidae, larger birds (77 to 490 g) with contributions strongly biased toward the matrix. Thrushes (Turdidae) and corvids (Corvidae) are medium- and large-sized birds (61 to 570 g) that contributed evenly to seed rain across habitats. This general pattern is nicely exemplified in Fig. 3*B* showing how seed dispersal in the Bradfield Woods is mainly mediated by thrushes (*Turdus merula* and *T. philomelos*) and European robins (*E. rubecula*), whereas in the surrounding matrix, it is mainly mediated by thrushes (*T. pilaris* and *T. merula*), wood pigeons (*Columba palumbus*), and common starlings (*Sturnus vulgaris*). The highest and even contribution of thrushes to seed dispersal in forest and matrix stresses their paramount potential for providing mobile-link functions across habitats (see ref. 15).

Four movement types can be distinguished in mobile organisms: dispersal, migration, home-range movements, and nomadism (16). The prevalence of these movements varies seasonally and can influence mobile-link functions (36). We found a similar proportion of migrant frugivores contributing to seed rain in forest and matrix. In central and southern Europe, Palearctic migrants disperse seeds during long periods that include migration and wintering (i.e., local movements, ref. 38), whereas Afro-Palearctic migrants mostly disperse seeds transiently during migration (39). The latter could explain why the contribution of Afro-Palearctic migrants to seed rain was biased toward the matrix while that of Palearctic migrants was similar in both habitats (*SI Appendix*, Fig. S7). In sum, frugivore traits that influence their movement in fragmented landscapes, namely body size, flight efficiency and—to a lower extent—migratory strategy, have a predictive value on their mobile-link functions across habitats.

The changes between forest and matrix in frugivore contributions are congruent with those found in the seed communities they dispersed. On the one hand, compositional beta diversity of frugivore and seed species were positively related (*SI Appendix*, Fig. S6). On the other hand, some changes in plant traits of the dispersed seeds were related to changes in frugivore traits: The larger and more mobile frugivores of the matrix dispersed larger seeds from taller plants (*SI Appendix*, Fig. S6). The relationship with plant height likely reflects the ability of larger and more mobile birds to access to tall plants as high-canopy foragers (40). Our results support the expectation that plant traits influencing pairwise interactions (matching traits) with frugivores are also traits that respond to the open anthropogenic matrix (24). We also found that plants dispersed in the matrix had a later fruiting period than those dispersed in the forest, which could be explained by a relatively higher seed rain in the forest in early summer, when forest birds are breeding, hence not performing dispersal, nomadic, or migratory movements (16, 36). Finally, exotic and planted species generally occur in anthropogenic habitats, and this can explain their higher contribution to seed dispersal in the matrix. Indeed, a large fraction of seeds dispersed in the matrix is expected to come from the fine-grained vegetation of the matrix (15) in the form of isolated plants, hedgerows, and gardens.

Plant–frugivore interactions exhibited a higher beta diversity and turnover between forest and matrix than those of frugivore and seed species. This makes sense considering the joint changes in frugivore and seed communities. Importantly, the proportional dissimilarity between forest and matrix of seed species was smaller than that of frugivore species and much smaller than that of pairwise interactions. In other words, the seed communities dispersed in forest and matrix were quantitatively more similar than the frugivore communities that dispersed them. Again, this is nicely exemplified in Fig. 3*B*, which shows how *Cornus sanguinea* and *Crataegus monogyna/laevigata*, two of the main seed species dispersed in the Bradfield-Woods landscape, are dispersed by distinct frugivore species in forest and matrix. Interestingly, apart from this complementarity across habitats, we found a higher degree of interaction complementarity in the matrix and hence a lower redundancy of seed-dispersal services (Fig. 3). A plausible explanation is a lower dependence on fruit diet among the highly omnivorous frugivores of the matrix, in the way that they feed on fewer fruit species because they consume fruits during specific periods of the year (41). Importantly, the higher complementarity in the matrix means that the dispersed seed communities would be more sensitive to fluctuations in frugivore populations (e.g., increases, declines, extinctions) than in the forest (24).

Implications and Generalizations. The way frugivores disperse seeds through fragmented landscapes is expected to shape the dynamics of fleshy-fruited plant communities within and beyond the forest edges. This requires effective dispersal that leads to plant recruitment (42), which can take place in forest patches as well as in abandoned or unmanaged lands of the matrix (7, 28, 29, 43). Hence, the seed-rain patterns reported here should influence seedling and sapling communities. Yet, the number of seeds needed for recruitment is negatively related to seed size; few large seeds or many small seeds are needed to produce a sapling (44). This means that the differences in CWM seed mass between forest and matrix reported here could amplify at the seedling and sapling stages. This could explain why some large-seeded species like the wild olive tree or the black cherry (*Prunus serotina*) easily recruit in the matrix of Mediterranean and temperate landscapes (15, see ref. 29).

The broad geographical coverage of the study ensures the generalization of our findings, not only across Europe but also to regions where seed dispersal is mostly mediated by small and medium-sized birds. Most of our landscapes were sampled for 1 y but interannual variability in fruit production can be substantial within and between species (45). Our findings on the matrix effects on frugivore and plant traits in multiple communities (i.e., beyond particular species or sites) suggest that our results should be consistent across years, as reported in other plant–frugivore assemblages (17, 19). However, the degree of deforestation and the matrix type deserve consideration before extrapolating our results to other contexts. Our study landscapes included forest patches, the matrix included isolated trees, and our sampling was conducted within a few hundred meters from the forest edge (Fig. 6*B* and *SI Appendix*, Fig. S2). The turnover of frugivores reported here is expected to increase when entering into the matrix, at farther distances from forest edges (15, 46). In fact, the cross-habitat movements of birds tend to decrease in more deforested landscapes (47). Hence, matrix dwellers like starlings (*Sturnus* sp.) and wood pigeons must play a major role as seed dispersers in the matrix of highly deforested landscapes (15). Another consideration is that our study landscapes had open
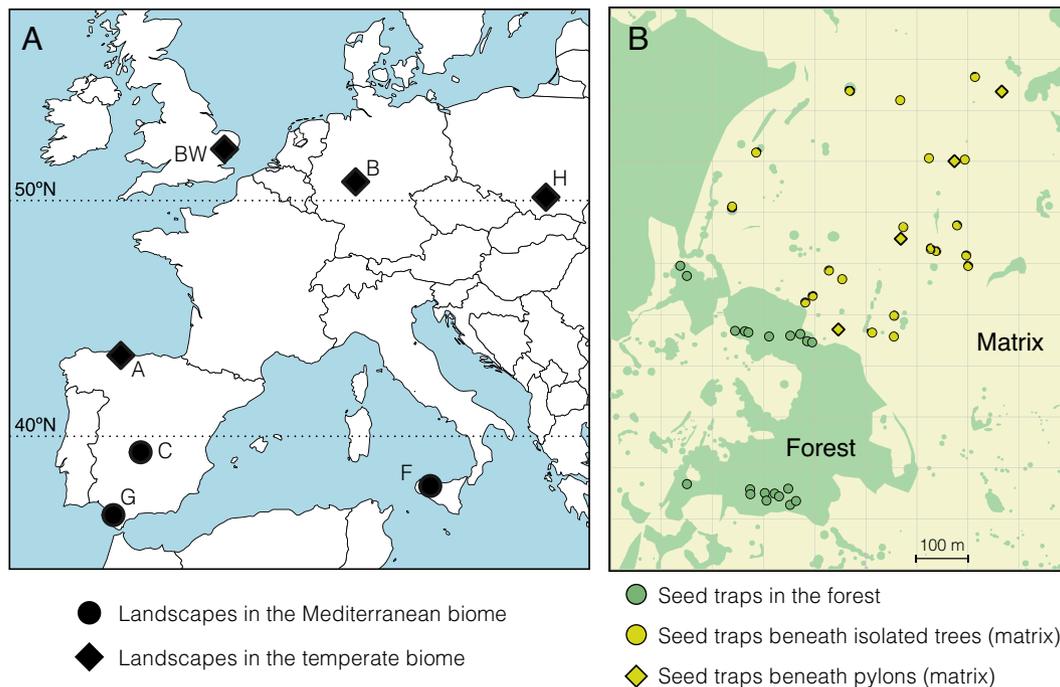
Fig. 6. (A) Location of the seven study landscapes across Europe: Spain (A: Arbazal; C: Cabañeros; G: Garrapilos), United Kingdom (BW: Bradfield Woods), Germany (B: Bauerbach), Italy (F: Ficuzza), and Poland (H: Hebdów). (B) One of the study landscapes (Arbazal) illustrating the sampling design for sampling avian seed dispersal in seed traps placed beneath trees and shrubs within a forest patch (n = 20 to 24 in each landscape), and beneath isolated trees and electricity pylons (i.e., natural and artificial perching sites for birds) in the surrounding agricultural matrix (n = 20 to 34 in each landscape); landscape map produced in QGIS v.3.26.1 (QGIS Development Team 2022) by digitizing satellite images. Additionally, the routes we fortnightly used to survey the seed traps were considered as two fixed belt transects (1-m wide and 560 to 4,030-m length in the forest and 1,610 to 5,080-m length in the matrix of each landscape) where we sampled mammalian seed dispersal (i.e., scats with seeds) and complemented our sampling of avian seed dispersal.

agricultural matrices and the degree of frugivore turnover depends on matrix type (23). For instance, suburban matrices with gardens are expected to be a softer matrix for frugivores (46), which may reduce the degree of frugivore turnover from forest patches. Urban matrices are also expected to increase the contribution of ornamental garden plants to community-wide seed dispersal (27). Although the contribution of exotic seeds was small in the study landscapes, our results unveil mechanisms underlying plant invasions: Nonnative seeds are mainly dispersed by matrix-dwelling frugivores from and toward the matrix (15, 28).

Our findings highlight the importance of both the biodiversity reservoirs of forest remnants and the mobile-link functions of frugivore faunas for ecosystem resilience in fragmented landscapes. Finally, our study provides useful knowledge for the restoration of unmanaged agricultural lands, revealing a high potential for passive forest restoration of fleshy-fruited plants in matrices with isolated trees and at short distances from forest edges (<300 m) (48). Hence, active restoration efforts should focus on planting isolated trees (if lacking) as focal areas for recovery (49) as well as on those plant species that poorly disperse and establish through the matrix—frugivores will bring many others available in forest remnants.

Methods

For a fully detailed version of methods, please see *SI Appendix*, Appendix S1.

Study Design. We conducted our study in forest and matrix of seven fragmented landscapes distributed across the Mediterranean and temperate biomes of Europe (Fig. 6A). Thus, our study comprised a paired design as we sampled in paired habitats within landscapes (Fig. 1). The study landscapes ranged from 1 to 3.8 km², were located between 45 and 630 m asl. (*SI Appendix*, Table S1), and comprised one or a few forest patches surrounded by an agricultural matrix of arable land and/or cattle pastures with isolated trees (Fig. 6B). Hereafter, we refer to these two main habitats within each landscape as "forest" and "matrix," respectively.

All forest patches and the isolated trees were dominated by broadleaved species (*SI Appendix*, Appendix S1a and Table S1). Six of these landscapes were studied for 1 y (June 2016 to June 2017) and one landscape (Garrapilos, southern Spain) for 2 complete years (October 2013 to October 2015). Thus, our sampling covered the entire fruiting periods of all local fleshy-fruited species.

Sampling Frugivore-Mediated Seed Dispersal. We sampled community-wide seed dispersal by frugivores in the forest and matrix of the study landscapes using seed traps and fixed transects (*SI Appendix*, Appendix S1b). Through both sampling methods, we can obtain seed-rain densities (number of seeds per unit area) and sample defecated or regurgitated seeds for subsequent DNA barcoding analysis (see next section) to identify the frugivore species responsible for seed dispersal (15, 30). For seed traps, we used 0.22-m² plastic trays covered with wire mesh to prevent post-dispersal seed predation. We placed 20 to 24 seed traps in the forest of each landscape (n = 146 across landscapes), beneath the canopy of different trees and shrubs not bearing fleshy fruits (*SI Appendix*, Table S1 and Fig. S1). In the matrix, we placed 20 to 34 seed traps per landscape (n = 178 across landscapes), of which 20 to 29 were beneath the canopy of isolated trees without fleshy fruits and, in six of the seven landscapes, 4 to 5 were under different electricity/telephone pylons (Fig. 6B and *SI Appendix*, Appendix S1b, Table S1, and Fig. S1). In the forest, distances from seed traps to the nearest forest edge ranged from 1 to 254 m (most distances were under 100 m), whereas in the matrix, distances ranged from 4 to 438 m (most distances were <300 m) (*SI Appendix*, Fig. S2). Across landscapes, we monitored a total of 324 seed traps (n = 40 to 58 per landscape). The fact that all seed traps were placed beneath trees and shrubs (or structures) not bearing fleshy fruits implied that all seeds arriving to them were dispersed by birds horizontally away from their source plants. We monitored the seed traps through periodic surveys (fortnightly) in which we sampled bird-dispersed seeds for DNA-barcoding analysis and counted the number of seeds of different plant species to calculate seed-rain densities (i.e., seeds per m²). Additionally, we used the routes adopted for periodically surveying the seed traps as fixed belt transects (1-m wide), whose length ranged between 560 and 4,030 m in the forest (10,540 m across landscapes) and between 1,610 and 5,080 m in the matrix (20,340 m across landscapes). We monitored a total of 2,630 to 9,110-m² of belt transects per landscape fortnightly, where we also

searched for frugivore-dispersed seeds (mainly by mammals) and sampled them for subsequent DNA-barcoding analysis.

Frugivore and Seed Identification. We used DNA barcoding analysis of the mitochondrial cytochrome c oxidase subunit I (COI) gene to identify the animal species responsible for the seed-dispersal events, as DNA of animal origin can be extracted from the surface of defecated or regurgitated seeds (30). We sampled individual seeds or droppings with seeds found in seed traps and transects into sterile tubes, which were labelled and stored in a freezer at −20 °C until DNA extraction. Detailed information on the procedures for DNA barcoding analysis can be found in *SI Appendix*, Appendix S1c. Resulting sequences were identified at the species level based on best sequence matches in the "BARCODE OF LIFE DATA" identification system (BOLD; 50) (www.boldsystems.org), typically at a 98 to 100% similarity (see Supplementary Figure S1 in ref. 51). We analyzed 3,313 samples containing 15,260 seeds of which we successfully identified the frugivore species in 3,063 samples (127 to 1,771 per landscape) containing 14,683 seeds (245 to 9,917 per landscape; see *SI Appendix*, Table S2). We obtained an overall identification success of 92.5% (i.e., PCR failure occurred in 7.5% of samples). The 3,063 samples included 3,093 interaction events between "frugivore–seed" species pairs because some samples (droppings) contained multiple seed species.

After the extraction of animal DNA, 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 (52). The exceptions were the seed species of 11 samples for which we used DNA-barcoding analysis to shortlist and guide visual identification (*SI Appendix*, Appendix S1c).

Seed-Dispersal Networks in Forest and Matrix. We obtained seed-dispersal networks for the forest and matrix of the study landscapes by using the interaction-level seed rain (sr_{ij}) as the weight of pairwise interactions (expressed as seeds per m^2) between each plant species i and each frugivore species j (e.g., ref. 51). Briefly, we used DNA barcoding identifications to calculate the relative contribution (f_{ij}) of each frugivore species j to the seed-rain density of each plant species i in the forest and matrix of the study landscapes. We did so separately for avian and mammalian frugivores using data from seed traps (birds) and transects (mammals), respectively. We then estimated the seed-rain density of plant species i dispersed by frugivore species j in forest and matrix as $sr_{ij} = sr_i \times f_{ij}$, where sr_i is the mean seed-rain density (seeds per m^2) of plant species i measured in seed traps or transects. In the case of seed traps, we did this process by weighting by the proportion of seed traps in the matrix placed beneath natural (canopy) and artificial (pylons) perches. We then merged data from seed traps and transects to obtain seed deposition networks with sr_{ij} values as interaction weights. Detailed information on this procedure can be found in *SI Appendix*, Appendix S1d.

Animal and Plant Traits. We obtained trait data for the frugivore and plant species identified in the study landscapes as detailed in *SI Appendix*, Appendix S1e. We focused on traits that are expected to act as response traits, determining sensitivity to the open anthropogenic matrix, and/or as effect traits, favoring the realization of seed-dispersal interactions (24, 40). For frugivores, we focused on three traits: body mass, hand-wing index of birds (HWI = 100 × Kipp's distance/wing length), and migratory status. Body mass is typically both a response and an effect trait because it is related to susceptibility to defaunation and capacity to disperse large seeds over long distances (e.g., ref. 53). The HWI is a measure of wing pointedness, a proxy for wing aspect ratio and flight efficiency in birds and is positively related to flight strength and ability to cross open habitats (25, 54). We obtained species-level mean body mass and mean HWI of birds from the AVONET database (55). For mammals, we obtained species-level mean body mass from EltonTraits 1.0 (56). The migratory status of frugivore species characterizes whether their occurrence in the landscape is permanent or seasonal and, thus, can be related to their movement patterns (16). However, Palearctic migrants (birds that winter in southern Europe and northern Africa) are often partial migrants, that is, only a fraction of their populations migrates while the other fraction behaves as resident; all Afro-Palearctic migrants (birds that winter in sub-Saharan Africa) are fully migratory (51). We used published information characterizing the proportion of migrants ($P_{migrants}$) in the frugivorous bird species at the study landscapes ($P_{migrants}$ can vary geographically within species) by means of a semiquantitative variable ranging from 0 (residents) to 1 (full

migrants) (51). All identified mammals (foxes and martens) were nonmigrant species, thereby $P_{migrants} = 0$.

For plants, we focused on four traits: seed mass, plant height, fruiting phenology, and origin in the study landscapes. The first three traits are traits directly involved in interactions with frugivores through morphological trait matching or through spatial and temporal overlap (20). The fourth trait characterizes whether the species occurrence in the landscape is natural or anthropogenic (i.e., exotic and planted plants), which we consider to be a proxy of dispersal from cultivated, ornamental, and invasive plants of the matrix (27–29) (Fig. 1C). We obtained species-level individual seed mass (mg) from Torroba Barlmori *et al.* (52) for most species (70%) and from other sources for the remaining species (*SI Appendix*, Table S5). We obtained species-level plant height from the TRY database (57) for most species (60%) and from other sources for the remaining species (*SI Appendix*, Table S5). Regarding the fruiting phenology, we used the bioclimate-level data on start and end fruiting dates (d_{start}–d_{end}) obtained by González-Varo et al. (51) for the plant species and bioclimate of the study landscapes. The dates were obtained on a monthly scale (0–12) where exact values represent the transition between months and half values represent the midpoint within months (for example, 1 = end of January–beginning of February; 1.5 = mid-February). We calculated the midpoint fruiting period as $d_{mid} = (d_{start} + d_{end})/2$. Finally, we used a Bernoulli-distributed variable to classify the seed species according to the origin of their adult plants in each landscape (1: exotic or planted; 0: wild and native).

Statistical Analyses.

General analytical approach. We fitted generalized linear mixed models (GLMMs) to test for differences between forest and matrix in different response variables using the R package *glmmTMB* v.1.1.3 (58). All GLMMs included "habitat type" as fixed factor and "landscape identity" as random factor (random intercepts) to account for the repeated (paired) measures per landscape ($n = 14$ observations from seven landscapes). We selected family distributions and link functions according to the nature of the response variables and, when these were suitable to different distributions (e.g., $y \sim$ Gamma and $y \sim$ Normal), according to model selection based on the lowest values of the Akaike information criterion corrected for small sample sizes (AICc). We obtained AICc values with the R package *MuMIn* v.1.46.0 (59). 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.3.0-12 (60). We used the R package *emmeans* v.1.7.3 to obtain estimated marginal means from the GLMMs for forest and matrix on the original scale. All analyses were conducted in R v.4.1.2 (61).

Alpha and beta diversity of species and interactions. We first tested for differences between forest and matrix in alpha diversity of frugivore species contributing to seed rain, dispersed seed species, and pairwise plant–frugivore interactions (Fig. 1). We obtained two Hill diversity metrics: richness (s = number of species or interactions) and Hill–Shannon ($e^{-\sum_{i=1}^{s} p_i \log(p_i)}$) (32, 62), where p_i is the relative contribution to community-wide seed rain of each frugivore species, seed species, or pairwise interactions. While richness is very sensitive to rare species and interactions, Hill–Shannon can be interpreted as the effective number of equally common species or interactions (32). We followed the rarefaction and extrapolation method proposed by Chao et al. (63) to estimate sample coverage and sampling completeness (*SI Appendix*, Fig. S3). There were no significant differences between forest and matrix both in sample coverage and sampling completeness of species and interactions (*SI Appendix*, Fig. S3), indicating that our results on alpha diversity were not biased by sampling differences between habitats. We used Poisson GLMMs with log link function for richness and Gamma GLMMs with log link function to model Hill–Shannon. We also analyzed beta diversity between the forest and matrix of the study landscapes in species and interactions contributing to community-wide seed rain. We used Jaccard's index to estimate dissimilarity in qualitative terms and a proportional dissimilarity index to estimate dissimilarity when accounting for relative contributions. We used the R package *betapart* v.1.5.6 (64) to obtain the total Jaccard's beta diversity and its turnover component, which accounts for compositional differences caused by replacements (31). We calculated proportional dissimilarity as 1–the proportional similarity index (PS; 65); i.e., as $1 - \sum_{i=1}^{n} \min(p_{i\text{-forest}}, p_{i\text{-matrix}})$, where for n species/interactions, $p_{i\text{-forest}}$ and $p_{i\text{-matrix}}$ are the relative contributions of species/interaction i in forest and matrix, respectively.

Complementarity of seed-dispersal interactions. We tested for differences in functional complementarity of seed-dispersal interactions in forest and matrix. Specifically, we obtained the complementary specialization H_2' index (a network-level metric) using the R package *bipartite* v.2.17 (66). H_2' quantifies to what extent interaction frequencies deviate from random interactions that are proportional to species' total frequencies (67). H_2' ranges from 0 (maximum redundancy) to 1 (maximum complementarity) and, thus, it is a direct measure of functional segregation and an inverse measure of niche overlap (68). In our case, it represents the degree to which frugivorous animals complementarily specialize on different plant species as fruiting resources and the degree to which plants complementarily rely on different frugivore species as their seed dispersal agents. Importantly, H_2' can be understood as the extent to which the diversity of dispersed seeds relies on the diversity of frugivores (24). H_2' is quite robust to biases induced by differences in species richness, thus, in network size (67, 69). Indeed, we only report raw values of H_2' because these were virtually identical to null-model corrected values (difference ≤0.0003 in Δ-corrected values; see ref. 41) using a Patefield model with 1,000 replicates (66). We used a mixed-effects beta regression (GLMM) with logit link function to model H_2' because it ranges from 0 to 1, like proportions derived from continuous numbers (see ref. 70).

Contributions to seed rain by frugivore families. We tested for differences between forest and matrix in the contribution of the most important frugivore families to community-wide seed rain (i.e., those contributing on average to ≥5% of dispersed seeds either in the forest or matrix across study landscapes) using mixed-effects beta regression with logit link function. Relative contributions of frugivore families (p_f) were proportions calculated as the quotient between the seed rain contributed by family f and the total seed rain. For modelling purposes, we transformed p_f values whenever they included 0 or 1 as follows: $p_f' = (p_f[n-1] + 0.5)/n$, in which n is the total number of observations (70). This transformation compresses the closed interval ($0 \leq p_f \leq 1$) within the open interval ($0 < p_f' < 1$) because the values modelled by the beta distribution are defined on the latter (70). The estimated means and 95% CI were back-transformed for presentation ($p_f = [p_f' n - 0.5]/[n - 1]$). We fitted models with fixed dispersion parameter ϕ of the beta distribution and with variable ϕ in response to the habitat type to check whether the latter improved model fit according to ΔAICc (70). We also analysed the contribution of the six main frugivore families in a complementary way, by testing differences between forest and matrix in the principal components of a Principal Component Analysis.

CWM traits of frugivores and plants. We evaluated differences between forest and matrix in frugivore and plant traits. First, we calculated community-weighted means (CWMs) of frugivore and plant traits in the forest and matrix of each study landscape using the relative contribution of species to community-wide seed rain. CWMs were calculated as $\sum_{j=1}^{n} p_j \times t_j$ for frugivore traits and as $\sum_{i=1}^{n} p_i \times t_i$ for plant traits, where p_j is the relative contribution of frugivore species j to community-wide seed rain, p_i is the relative abundance of plant species i in the community-wide seed rain, and t_j and t_i are trait values of frugivore and plant species, respectively (71). Note that t_j and t_i were obtained at the species level in some cases (e.g., body mass or plant height) and at a bioclimatic/regional level in others (e.g., $P_{migrants}$ or fruiting phenology). Prior to CWM calculations, frugivore body mass, seed mass, and plant height were $\log_{10}$-transformed due to positively skewed distributions. We used a joint-distribution modelling approach to evaluate the response of frugivore and plant traits to habitat type because it accommodates both variation and covariation between CWMs that are obtained from the same weights (72). Specifically, we fitted two "trait response models" sensu Clark (72), one for frugivores and another for plants, by means of generalized joint attribute modelling using with the R package *gjam* v.2.6.2 (73). In these models, a multivariate normal distribution is fitted by means of Gibbs sampling (Bayesian approach) to vectors of CWMs at different locations in response to "habitat type" (forest *vs*. matrix), our location-level predictor variable. The models also included "landscape identity" as a random factor. For modelling purposes, percentages (CWM hand-wing index) were transformed into proportions, and data on CWM mid-point fruiting period were divided by 10 ($x' = x/10$) to reduce differences in scale (73). For CWMs describing proportions, we used priors truncating intercept estimates (i.e., habitat = "forest") within the [0, 1] interval. We ran 60,000 Gibbs steps and obtained 50,000 after a burn-in of 10,000 steps. We checked for convergence of Gibbs chains by visualizing the trace plots of estimated parameters.

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