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Trophic and spatial complementarity on seed dispersal services by birds, wild mammals, and cattle in a Mediterranean woodland pasture

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ABSTRACT

Most earth surfaces have undergone intensive land-use changes, creating habitat mosaics. Seed dispersal by animals is a crucial process in such mosaics, but community-wide studies comparing the functional complementarity and response to man-imposed habitat heterogeneity are rare. Here, we investigate the trophic and spatial seed dispersal networks underpinning a strong, woody vegetation expansion over a pastureland inside the largest forest remnant in western Sicily, Italy. Over two fruiting seasons, we surveyed transects in three distinct biomes within our study area: forest, pastureland, and unpaved road. In total, we collected 659 feces and tested for differences in defecation patterns and seed rain density of birds, wild mammals, and cattle. We also tested the degree of trophic and spatial specialization and modularity using a network approach. Overall, birds dispersed 1208 seeds/ha of nine plant species, including six exclusive. Mammals dispersed 679 seeds/ha from four wild species, three of which also dispersed by birds, and 38 seeds/ha of three cultivated species. In turn, mammals dispersed exclusively the seeds of wild pear (*Pyrus amygdaliformis*), the most abundant tree in the woodland pasture. Cattle only dispersed wild pear, but accounting for 56% of the dispersed seeds. Seed rain densities were significantly higher in woodland pastures than in forests. However, almost of half the seeds dispersed by cattle and red fox were deposited on unpaved roads. While both trophic and spatial networks were more specialized than expected, we did detect distinct modules. Our study demonstrated the magnitude of the effects of man-made habitat heterogeneity on seed dispersal services, giving baseline information for restoration programs as well as high nature value pastureland management strategies.

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1. Introduction

Anthropogenic land use changes have greatly affected natural environments, resulting in a mosaic of habitats with different arrays of species assemblages (Galetti and Dirzo, 2013; Pausas and Millán, 2019). Such mosaics currently occupy 40% of the world surface and can range from overgrazed and degraded areas that possess little vegetation cover and animal diversity to heterogeneous mosaics of agricultural fields and natural vegetation inhabited by richer biodiversity and are recognized as “high nature value systems” (Campedelli et al., 2018; Levers et al., 2018; Paracchini et al., 2008; Práválie et al., 2017). Another source of direct and indirect land-use changes within these mosaics are linear developments such as roads and firebreaks (Rendall et al., 2021; Suárez-Esteban et al., 2016). Unpaved roads (i.e. soft linear developments - SLD) are almost ubiquitous in rural environments, and are also common inside protected areas. While SLDs have been associated with facilitating movement for some species (cite), this trend is not universal, with some species completely avoiding such structures (Rendall et al., 2021; Suárez-Esteban et al., 2013a). Seed dispersal is a crucial process in sustaining biodiversity and molding the demographic patterns of plants, by linking populations and communities across landscapes (Emer et al., 2018; Jordano et al., 2011). Seed dispersal also underpins ecosystem functioning and is crucial in subsidizing ecosystem services (Schleuning et al., 2015). Seed dispersal by animals (i.e. zoochory) is the dominant mechanism for up to 65% of the Mediterranean plant species (Jordano, 2000; La Mantia et al., 2019). Wild birds and mammals are usually the main seed dispersers of these plant species (García, 2016; Herrera, 1989; Lopez-Bao and Gonzalez-Varo, 2011). However in anthropogenic mosaics, domestic mammals may play an important role as seed dispersers as they usually compose the bulk of biomass within defaunated environments, and may also be present within protected areas (Bianchetto et al., 2015). Despite domestic mammals’ negative impacts on natural vegetation (e.g. overbrowsing, trampling), they may eat fruits and disperse intact seeds in suitable habitats. Nonetheless, their potential compensatory role as seed dispersers is poorly documented for woody species (Aschero and García, 2012; Malo et al., 2000; Reid and Ellis, 1995). Beyond the typical diet differences (i.e. trophic level) between birds and mammals (both wild and domestic), variations in their behavior lead to different responses to the landscape configuration, and consequently to their seed dispersal services (i.e. spatial level). For example, some wild mammals (e.g. red fox) tend to be less restrictive in using agricultural matrix, while many frugivorous birds tend to concentrate their activity in forests, woody patches and in natural or artificial perches (Herrera and García, 2009; La Mantia et al., 2019; Pausas et al., 2006). In turn, domestic animals tend to have fewer restrictions in habitat use and often spill over from pasturelands to forests. Wild animal’s behavior towards SLD also varies, from total avoidance to strong preference (Lopez-Bao and Gonzalez-Varo, 2011; Suárez-Esteban et al., 2013b), but little is known regarding domestic animals. While trophic seed dispersal networks reveal the pair-wise relationships between frugivores and plants, spatial networks represent the link between the trophic network and the environment, thereby showing at which extent the different landscapes features (e.g. different habitats or human-made structures) receive the different species composing the overall seed rain. Therefore, habitat-use variations coupled with site-specific mosaic configuration and species assemblages can shape both trophic and spatial seed dispersal networks, ultimately determining the degree of functional redundancy or complementarity of seed dispersal services (Bueno et al., 2013; Miguel et al., 2018; Perea et al., 2013).

Few studies have compared the redundancy or complementarity in seed dispersal services provided by birds and wild mammals within the same spatio-temporal scale (Acosta-Rojas et al., 2019; Jordano et al., 2007; Santos et al., 1999), and even fewer have assessed these services for domestic animals (Escribano-Avila et al., 2014). Moreover, the structural properties of trophic and spatial networks have only recently been investigated in a community-wide perspective (Rumeu et al., 2020), and the potential of SLD to attract seed rain is poorly quantified (Suárez-Esteban et al., 2016). Many low-use agricultural areas in Europe exhibit a mosaic of pastures, woodlands and SLD, whose heterogeneity conditions species composition of plants and frugivores. Understanding the functioning of seed dispersal assemblages using trophic and spatial networks is essential for assessing the effectiveness of passive and active restoration of woody communities based on the rewiring of ecological interactions. This is also important for gauging the potential of sustainable management of extensive pastures, especially in the context of high nature value agro-silvo-pastoral systems (Campedelli et al., 2018; Costa et al., 2018; Fedriani et al., 2018). Here, our main objective is to unravel the trophic and spatial seed dispersal networks underpinning a strong woody vegetation expansion over a pastureland in the last decade (Bueno et al., 2020b). We aimed to answer the following questions: (1) what is the quantitative and qualitative contribution of birds and mammals (wild and domestic) seed dispersal to such woody vegetation expansion? (2) Are SLDs acting as seed rain “magnets” in comparison with forests and pasturelands? (3) at which extent do the spatial and trophic networks vary in specialization and modularity? We predict that birds and mammals foster vegetation expansion through complementary seed dispersal services, emerging from specialization and modularity in the trophic network. We also expect that SLD will concentrate an important fraction of the seed rain, although generated only by a sub-set of the seed disperser assemblage, contributing to a higher degree of specialization and modularity in the spatial seed dispersal network. Finally, we expect that domestic mammals (cattle) will provide relevant seed dispersal service due to the particular vegetation composition (i.e. abundance of wild pear), albeit they will not compensate wild mammal’s seed dispersal services both at the trophic (due to fewer species dispersed) and spatial levels (due to higher seed deposition on the WP).

2. Materials and methods

2.1. Study site

Our study was conducted in the “Bosco della Ficuzza, Rocca Busambra, Bosco del Cappelliere e Gorgo del Drago” natural reserve (hereafter FBCD), a 7397 ha protected area comprising the last large remnant of forest in western Sicily (Badalamenti et al., 2017; Gianguzzi and La Mantia, 2004). Inside FBCD, our study site was in a woodland pasture of 160 ha surrounded by forest remnants at the

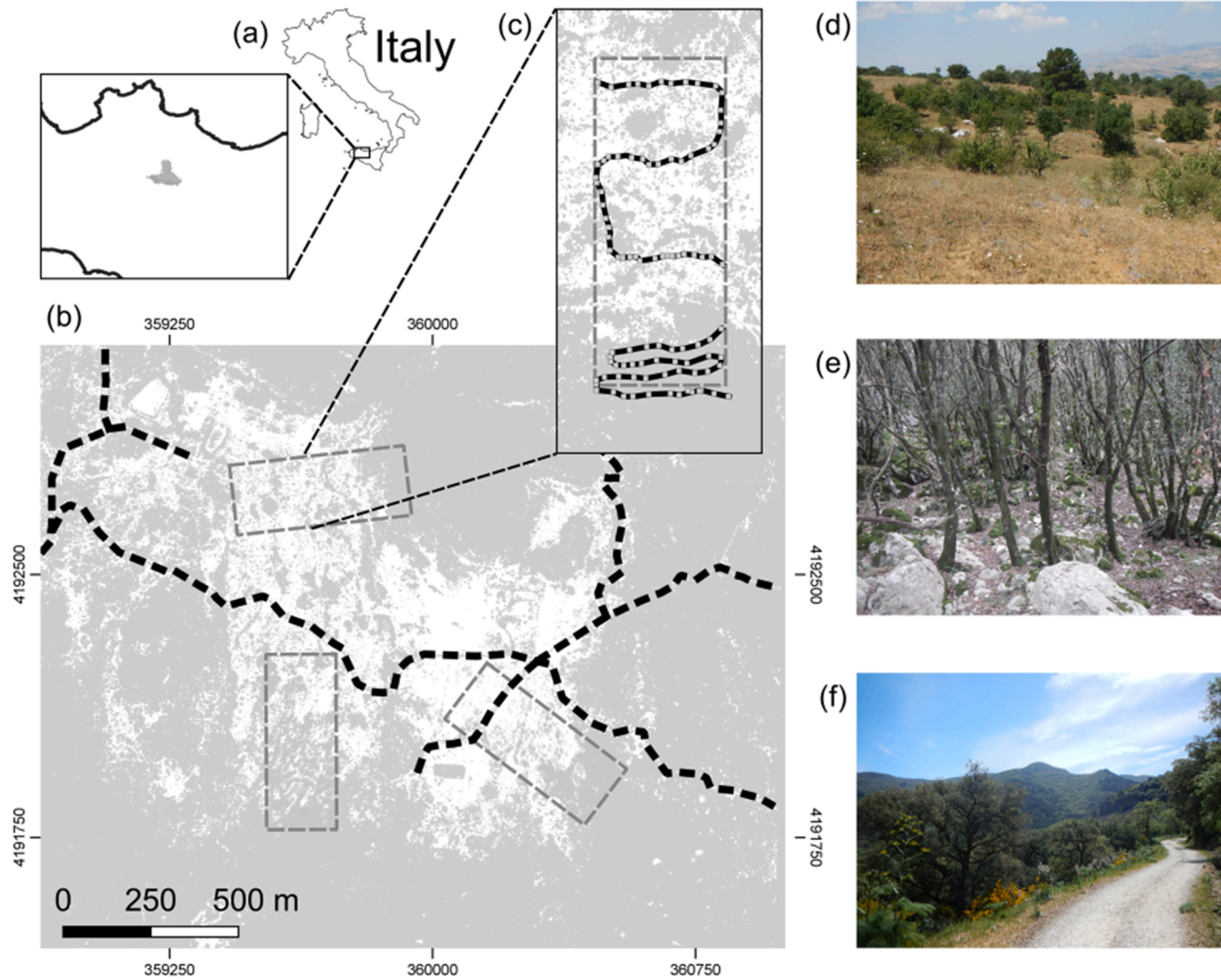


Fig. 1. Location of study site and description of sampling design. A) Location of Ficuzza Natural Reserve in Sicily. B) Woody cover (gray) and pastureland (white) in FBCD with location of the three plots where woody vegetation expansion was measured (Bueno et al., 2020a) and the soft linear developments (dashed black line). C) Example of the spatial configuration of the sampling transects (black lines) in the forest (bottom) and in the woodland pasture, with gray quadrats indicating the distribution of the bird sampling plots over the transects sampled in one survey. D) Aspect of the woodland pasture. E) Aspect of the holm oak forest. F) Soft linear development.

center of the reserve (37°52' and 13°24', Fig. 1). Classified as a “meso-Mediterranean” climate, our study site has a mean altitude of 950 m, an average rainfall of 850 mm, and mean annual temperatures of 14.3 C, with the temperatures ranging from an average of 9.4 C in the coldest months (January and February) to an average 23.5 C in the hottest months (July and August).

The woody vegetation composing the forest remnants in FBCD is dominated by thermophilous evergreen oaks (*Quercus ilex* and *Q. suber*), deciduous oaks (*Quercus pubescens*), and to a lesser extent by maple (*Acer campestre*) and manna ashes (*Fraxinus ornus*). The woodland pasture is composed of a heterogeneous vegetation structure, covered by grasslands, with isolated woody shrubs and trees and varied-sized patches of woody vegetation, composed mostly by fleshy-fruited species (wild pear *Pyrus amygdaliformis*, hawthorn *Crataegus monogyna*, blackberry *Rubus ulmifolius*, wild rose *Rosa canina*, blackthorn *Prunus spinosa*). Nineteen Sicilian mammals species are present at FBCD, and most of the Sicilian resident and migrant frugivorous birds like thrushes, warblers, robin (*Erithacus rubecula*), redstarts and pigeons are present (L'Ala, 2016; Massa and La Mantia, 2007). Cattle raising is a historical activity in FBCD, with grazing permissions dating back to at least the end of 1800 century (A.S.F.D, 1959; Bianchetto et al., 2015).

2.2. Sampling design

In FBCD, we established three plots of 500x200m covering the gradient from continuous forests to woodland pastures (Fig. 1), where vegetation expansion was previously quantified (Bueno et al., 2020b). The three plots had an average woody cover of 47.9% (plot 1 = 38.8%, plot 2 = 59.1% and plot 3 = 45.8%). Our objective was to assess the community-wide seed dispersal services delivered by mammals and birds in relation to three main habitats: forest, woodland pasture (hereafter WP), and SLDs. To reach that objective, we used different methods to measure the seed rain, that is, the cumulative seed deposition (seeds in animal feces) with an area-based sampling (see Escribano-Avila et al., 2012 for a similar procedure). Birds are smaller than mammals, generally occur in higher densities, and have shorter gut passage times. Consequently, birds deposit a higher density of feces and seeds in comparison with that of mammals (Escribano-Avila et al., 2012; Rumeu et al., 2020). To compensate for such differences, we dedicated more effort (i.e. sampling area) to sample for mammals feces. Forests are expected to have a higher occupancy of animals and consequently a higher detectability and density of feces (Escribano-Avila et al., 2012). However, in our study site, the woodland pasture presents a high density of fleshy-fruited plants, and a strong woody cover expansion is present (Bueno et al., 2020b), indicating strong seed dispersal and habitat use by frugivores. In turn, SLDs may be used only by a subset of the species, although some of them may present a disproportionate preference towards this habitat (Peredo et al., 2013; Suárez-Esteban et al., 2013b). However, there is inadequate information regarding bird (or even some mammal) preferences towards SLDs. As our main objective was to compare habitat use (i.e. number of feces) as well as birds and mammals seed dispersal services (i.e. number of seeds dispersed) between these three habitats and within disperser group and species, we established different sampling designs for each group (i.e. mammals and birds), but the same sampling effort within each habitat for each group. The exception was that for forest and WP, where we sampled three 800 m transects to have a more comprehensive sampling of the whole pastureland, while just one 2400 m transect was established in the SLDs once they are already spatially constrained (Fig. 1).

Mammal seed rain was assessed monthly along two fruiting seasons (September 2015 – February 2016 and September 2016 – February 2017) through a survey of fixed-width line transects across the three habitats. In forests and WP, we surveyed one 800 x 2 m transect located in each habitat within each of the three plots. In both WP and forest habitats, the transects began from random points at the edge of each plot and lasted until the opposite side. From there, the surveyor walked along the border towards the initial edge, in a zig-zag pattern without overlaying the paths in consecutive surveys and always with different starting points (adapted from Fedriani and Delibes, 2009). In the WP, transects covered mostly grasslands, as we avoided dense woody patches impossible to walk for searching seeds. However, in October 2016, we searched for mammals' feces in 200 3 m² sampling points inside dense, woody patches. For monitoring seed rain within SLDs, we sampled unpaved roads surroundings the plots along 2400 x 2 m transects, located at the edge of the roads. The same roadside was not surveyed in consecutive months. For each detected feces, we labeled the species, with differences between red fox and pine marten defined with a combination of size, color, shape, and odor (Lopez-Bao and Gonzalez-Varo, 2011). Transects were walked in a constant speed by the same observer, totaling 28.8 km or 5.76 ha sampled in each habitat, for a total of 84 surveys.

Bird seed rain was sampled in four months (January and September 2016, November, and January 2017). We surveyed and collected all bird feces found at 50 ground quadrats of 1 m² in each habitat (forest and WP) within each plot, as well as 150 quadrats along the SLDs, totaling 600 m² in each habitat. The quadrats were established randomly along the mammal transects, with the majority (ca 80%) falling close (< 5 m) to woody plants and the remaining in the pastureland. All collected samples were dried in the sun and analyzed in laboratory, been carefully broken and processed using a set of metal sieves up to the minimum mesh of 2 mm, where all retained seeds were identified, counted and classified as intact or mechanically predated (broken, crushed). All collected feces from birds and mammals were considered as unitary and comparable samples.

2.3. Data analysis

To answer our first and second research questions, we compared the seed dispersal services provided by birds and mammals, while taking into account the influence of habitat in the density of feces (i.e. a proxy for habitat use), density of intact seeds found per survey (i.e. effective seed dispersal), and the presence/absence and number of intact seeds found per feces. Due to differences in sampling efforts, the impossibility of identifying bird species from their feces, and to guarantee an equivalent taxonomic resolution for samples, we fitted six generalized linear mixed models (GLMM). First, we ran one model for density of feces and one model for density of intact seeds found per survey, comparing mammal species within the three habitats. Second, we ran two models comparing the two variables

between birds and mammals (all species pooled as a group), but excluding SLDs due to the lack of bird feces. To compare the presence/absence of seeds and the number of intact seeds in the feces between birds and mammals, we fitted two GLMMs using habitat, species (birds and the five mammals), and plot as fixed factors, and month (nested within fruiting season) as a random factor to control for temporal heterogeneity. In this case, we compared mammal species and birds as we considered each feces as a unitary and comparable sampling unit. We included plot as a fixed factor to control for the spatial non-independence of samples. In the comparison between birds and mammals as a group, we first run full models including the interaction between habitat and group (birds and mammals), but once none was significant ($p > 0.05$), we dropped interactions from the models. For the GLMM assessing the presence/absence of seeds, we used the binomial distribution with logit link, and for the other GLMM, we used negative binomial distribution with log link, once Poisson and quasi-Poisson models presented significant overdispersion. All analysis were carried out with R v 3.6.1 (R Core Team, 2019), with GLMM fitted with *lme4* package.

2.3.1. Plant-frugivore network

To characterize and illustrate the structure of interactions between mammals, birds, fleshy-fruited plants, and the three habitats (question 3), we used a network approach (Bascompte and Jordano, 2007). The trophic network was derived from a matrix including the density of seeds dispersed by each animal species (rows) of each plant species (columns), which was derived from the pooled number of seeds registered in all surveys transformed in densities respectively to the sampling effort. The spatial network was built to measure how animals dispersed seeds in relation to habitat heterogeneity, and consequently whether disperser behavior influences the spatial distribution of the seeds of each plant species. We built a matrix with the density of seeds dispersed by each disperser and of each plant species (columns) in the three habitats (rows), pooling the number of seeds dispersed in each habitat (see Rumeu et al., 2020 for a similar approach).

The network characterization was obtained by two metrics: specialization and modularity.

Specialization (H^2 , range 0–1) is a measure of functional redundancy or complementarity and represents the degree of occurrence of specialized pair-wise interactions, that is species that interact with other species that have few or null further interactions (trophic level) or species that have stronger links (i.e. higher number of seeds) towards a specific habitat from those available (i.e. spatial level; Blüthgen et al., 2006). Specialization was obtained with the *networklevel* function within the *bipartite* package. We used modularity index to check for the specific contribution of each species to the structure of the networks and for the presence of sub-groups of frugivores and plant species that interact more tightly between them (i.e. a trophic module) and between the three different habitats (i.e. a spatial module) (Dormann and Strauss, 2014). For that, we used the quantitative bipartite modularity algorithm (QuanBiMo), which is based on a simulated annealing-Monte Carlo approach, which is particularly developed for a quantitative bipartite networks such ours (seed rain density), obtained with the function *computeModules* in the *bipartite* package (Dormann and Strauss, 2014). To construct our random networks, we used the Patefield null model algorithm and to test the significance of the models, we compared the observed outputs against 500 simulated networks using the *nullmodel* function (Dormann et al., 2009). Finally, we plotted the network in a bipartite graph to illustrate the structure and proportions of the interactions. Network graphs (function “plotweb”) were made with the *bipartite* package on R v 3.6.1 (R Core Team, 2019).

3. Results

3.1. Quantitative and qualitative contribution of birds, wild and domestic mammal's to seed dispersal

We collected 155 bird feces, of which 76.8% contained seeds, for a total of 435 seeds from nine different wild plant species, with an average of 2.8 (± 3.37 SD) and a maximum of 21 seeds in a single feces. Just 2.6% of the feces contained 2 plant species, while all the other contained only one. No predated seeds were found. The most frequent species found in the feces was wild rose, present in 33.1% of the feces, while black bryony *Tamus communis* was the rarest species, present in just 1.6% of feces. Regarding the microhabitat of the deposition, 89.3% of the feces and 94.9% of the seeds were found close (< 5 m) or under woody individuals. Along the 86.4 km of transects, we found 606 mammal feces from 8 different species (Table S1). All feces were collected within the transects, as we found no feces at the open quadrats inside the dense woody patches. Three mammal species (fallow deer *Dama dama* $n = 91$, rabbit *Oryctolagus cuniculus* $n = 3$ and hedgehog *Erinaceus europaeus* $n = 8$) didn't have any seeds within their feces and were excluded from further analyses. From the 504 mammal's feces, 63% contained at least one seed, with an average of 36.4 (± 43.8 SD) and a maximum of 309 seeds in a single scat, for a total of 12.339 seeds from 7 different plant species. From the total number of dispersed seeds, 95.1%

Table 1

Summary of the results of the generalized linear mixed models testing the effects of habitat, seed dispersal group and plots on the density of feces and intact seeds found per survey. The missing levels mammals, forest and plot 1 are included in the intercept.

	Number of feces ha ⁻¹				Number of intact seeds ha ⁻¹			
	Estimate	SE	z	p	Estimate	SE	z	p
Intercept	2.83	0.17	16.49	<0.001	3.12	0.18	17.13	<0.001
Woodland pasture	0.39	0.13	2.93	0.003	0.64	0.28	2.28	0.023
Birds	2.63	0.17	15.17	<0.001	0.77	0.38	2.02	0.043
Plot 2	0.45	0.16	2.79	0.005	0.39	0.34	1.15	0.250
Plot 3	0.43	0.16	2.67	0.008	0.72	0.34	2.16	0.031

belonged to four wild plant species (wild pear, blackberry, wild rose and blackthorn), while the 4.9% remaining, all dispersed by red fox, were from 3 cultivated species not present in our study site (*Ficus carica* n = 511 seeds in 4 feces, *Morus sp.* n = 86 in 2 feces, and *Vitis vinifera* n = 6 in 2 feces). Wild pear was consumed by all mammal species and was present in 47% of the feces, accounting for 62% of the total number of seeds. Just 7.5% of the seeds showed mechanical damage (predation), with higher rates found in crested porcupine (34.4%) (Table S1). The proportion of cattle feces with seeds (47.7%) was significantly lower than that of wild mammals (average of 64.5%, Table 2), although, as expected due to the larger size, cattle dispersed more intact seeds per feces (Table 2). However, such differences did not reflect the seed rain density, once only crested porcupine significantly dispersed less seeds ($z = -3.73$, $p < 0.001$; Table 3).

Birds dispersed a higher density of seeds than mammals (Table 1, Figs. 2 and 3), even if the number of seeds per feces was much lower (Table 2, Fig. S1). Both plots 2 and 3 received a higher proportion of feces, although this difference reflected a more intense seed rain only in plot 3 (Table 1). WP received more feces and seeds than forest (Table 3, Figs. 2 and 3), although both mammals and birds did not present a clear pattern in the density of feces with seeds in relation to the three habitats (Table 2). Red foxes and birds were responsible for higher proportion of feces with seeds, although all mammals and especially birds dispersed lower number of seeds per feces than cattle (Table 2).

3.2. Defecation patterns and seed rain across habitats

Overall, mammal defecation patterns varied across habitats. SLD and WP received a higher density of feces than the forest, although we did not found feces of pine marten and wild boar in SLDs (Table 1, Fig. 2). In turn, wild boars accounted for 44.2% of the seeds dispersed in the forest, cattle account for 36.7% of the seeds at the WP, and red fox accounted for 48.7% of the seeds at the SLDs. No differences were found within plots, suggesting a homogeneous meso-scale habitat use by mammals not affected by plot configuration (e.g. woody cover or fruit abundance). Accordingly to our predictions, SLD was a magnet for seed rain, receiving more intact seeds than in the other two habitats. This magnet effect seems to be stronger in relation to the forest, judging by the low proportions of feces and seeds dispersed in this habitat by cattle (12.7% and 9.8% respectively) and red fox (22.1% and 14.4% respectively). Again, no differences were found between plots (Table 1, Fig. S1).

3.3. Specialization and modularity of the trophic and spatial seed dispersal networks

The bipartite network between mammals, birds and fleshy fruited plants highlight the strong complementarity between these groups as well as a non-random pattern of organization. Effectively, specialization (H^2) was higher than the estimated by null models in all networks ($p < 0.05$), although the higher coefficient was observed in the network between seed dispersers and plants ($H^2 = 0.53$), reflecting the exclusive dispersal of six species by birds and wild pear by mammals, among which cattle emerged as the most specialized species (Fig. 4a). Modularity was also significant (all z scores > 50) in all networks, indicating consistent interactions between species in different modules. However, as expected, the QuaBiMo algorithm clearly detected the two distinct modules composed by birds and mammals in the trophic network ($Q = 0.18$, Fig. S2). The animal-habitat spatial networks in turn were characterized by one mixed module ($Q = 0.16$), comprising WP, forests, birds, pine marten and wildboar and another module with SLD, cattle, red fox and crested porcupine (Fig. 4, S3). The habitat-plant network was divided in three modules ($Q = 0.12$), highlighting the interactions of WP and wild rose and blackberry and wild madder (Fig. S4).

Table 2

Summary of the results of the generalized linear mixed models testing the effects of habitat, species and plots on the presence/absence of seeds per feces and number of intact seeds found per dispersal event (feces with seeds). The missing levels cattle, forest and plot1 are included in the intercept. Only significant interactions are shown.

	Presence/absence of seeds				Number intact seeds			
	Estimate	SE	z	p	Estimate	SE	z	p
Intercept	-0.64	0.42	-1.51	0.13	4.15	0.35	11.86	<0.001
Woodland pasture	0.07	0.23	0.31	0.76	0.09	0.34	0.26	0.79
SLD	0.43	0.37	1.15	0.25	0.03	0.37	0.09	0.93
Birds	1.43	0.35	4.13	<0.001	-2.95	0.36	-8.16	<0.001
C. porcupine	0.42	0.42	0.99	0.32	-2.39	0.48	-5.00	<0.001
Pine marten	0.96	0.46	2.10	0.036	-1.35	0.38	-3.53	<0.001
Wildboar	0.78	0.33	2.33	0.020	-0.94	0.36	-2.63	0.009
Red fox	1.80	0.30	6.05	<0.001	-0.78	0.36	-2.14	0.032
Plot 2	0.43	0.26	1.65	0.099	-0.18	0.13	-1.35	0.18
Plot 3	0.61	0.27	2.23	0.026	-0.01	0.13	-0.10	0.92
SLD*C. porcupine	-	-	-	-	1.59	0.69	2.30	0.022

Table 3

Summary of the results of the generalized linear mixed models testing the effects of habitat, species and plots on the number of feces and intact seeds found per survey per hectare across mammals species. The missing levels cattle, forest and plot 1 are included in the intercept. Only levels with at least one significant interaction are shown.

	Number of feces ha ⁻¹				Number of intact seeds ha ⁻¹			
	Estimate	SE	z	p	Estimate	SE	z	p
Intercept	0.87	0.34	2.55	0.011	4.01	0.71	5.67	<0.001
Woodland pasture	1.26	0.44	2.85	0.004	0.77	0.45	1.73	0.083
SLD	1.42	0.63	2.27	0.023	2.32	0.82	2.82	0.005
Crested porcupine	-0.30	0.45	-0.67	0.50	-2.43	0.65	-3.73	<0.001
Pine marten	0.33	0.44	0.75	0.45	-1.06	0.73	-1.45	0.15
Wildboar	0.94	0.45	2.12	0.034	0.07	0.69	0.10	0.92
Red fox	0.84	0.45	1.87	0.061	0.30	0.64	0.46	0.65
Plot 2	0.39	0.25	1.57	0.12	0.46	0.51	0.91	0.36
Plot 3	0.21	0.25	0.84	0.40	0.44	0.51	0.86	0.39
WP*Pine marten	-2.22	0.63	-3.52	<0.001	-2.64	1.29	-2.05	0.040
SLD*Crested porcupine	-2.78	0.96	-2.90	0.004	-1.08	1.80	-0.60	0.55

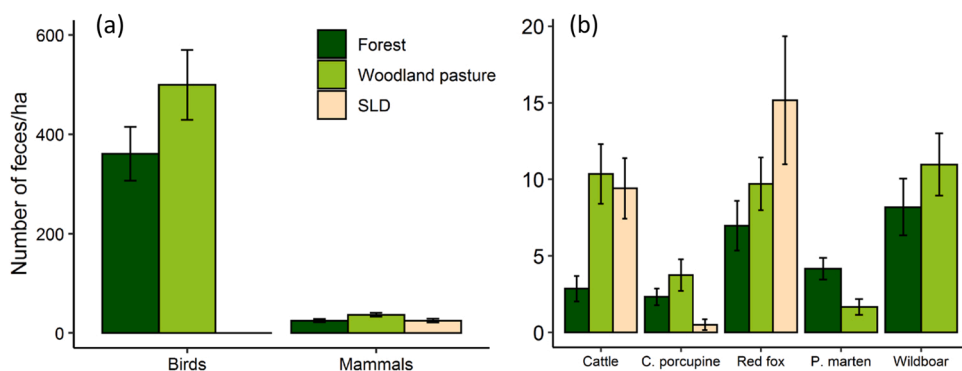


Fig. 2. Mean (\pm SE) number of feces ha⁻¹ of birds and mammals (a) and mammals species (b) found in the surveys in the three habitats in FBCD, Sicily, Italy. Note the different scales.

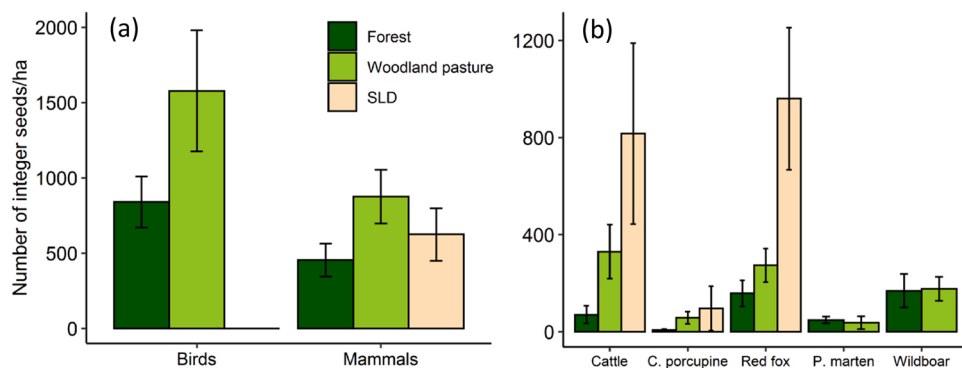


Fig. 3. Mean (\pm SE) density (number of integer seeds ha⁻¹) found in the surveys dispersed by birds and mammals (a) and across mammals species (b) in the three habitats in FBCD, Sicily, Italy. Note the different scales.

4. Discussion

4.1. Quantitative and qualitative contribution of birds, wild and domestic mammal's seed dispersal

An animal's defecation pattern is a proxy of its spatial habitat use, and habitat use is often considered a proxy of effective seed delivery patterns (Suárez-Esteban et al., 2013b). For birds, habitat use and seed dispersal services spatially matched. However, mammal defecation patterns were not always linked with the effective deposition of seeds. SLDs received a disproportionate number of seeds regardless of the lower number of defecations, and WP received more mammal feces but with the same seed densities than forests

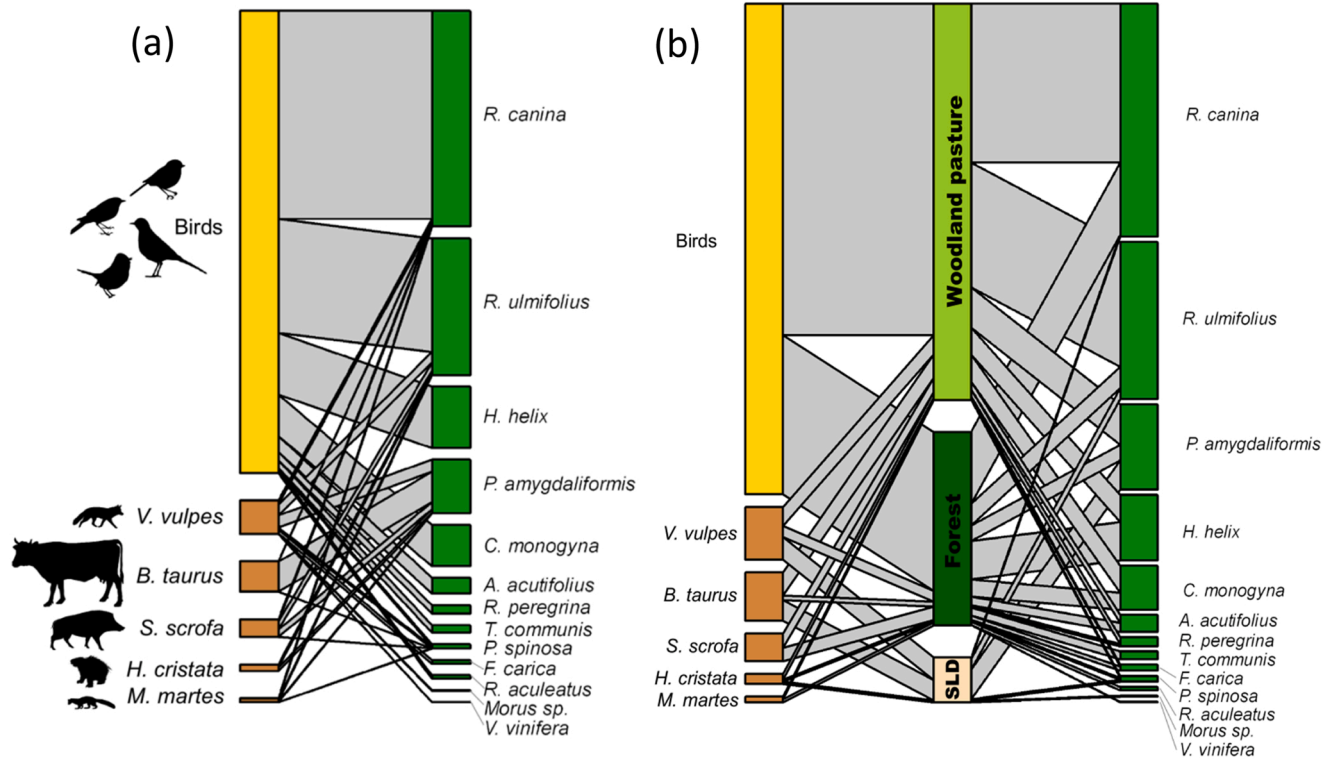


Fig. 4. a) Weighted trophic bipartite network representing proportionally the overall (columns height) and species specific (gray links width) density of seeds of all fleshy fruited plants including the three cultivated (right column) dispersed by mammals and birds (left column) in FBCD. b) Weighted spatial bipartite network representing proportionally the density of seeds (gray links) dispersed by mammals and birds (right column) and density of seed of each plant specie (left columns) dispersed in the woodland pasture (WP), forest and soft linear development (SLD - central columns) in FBCD.

(Figs. 2 and 3, Table 3). In our previous study (Bueno et al., 2020b), we detected strong woody cover expansion in all three studied plots, and such cover was composed mostly by the fleshy-fruited species detected in birds and mammals feces. Such patterns were expected because all plots share the same pool of plant species, and the fruiting landscape is known to influence the seed rain (Martínez and García, 2015; Rumeu et al., 2019). However, only plot 3 differed significantly in the seed rain density and in the proportion of feces with seeds (Tables 1 and 2), while mammal's seed rain density did not differ at all. This is interesting, as the densities of the most dispersed and abundant tree (wild pear) in plot 1 (6.7 ind/ha) is 4 and 5 times lower than in plot 2 and plot 3, respectively. Such compensation is probably caused by the abilities of mammals to easily cover even the longest distances among plots (ca 1.3 km), reducing the relative importance of the meso-scale fruiting landscape. Such compensation between plots is less expected to be dominant for birds, as most passerines rarely disperse seeds that long (Jordano et al., 2007). Future research with the use of DNA barcoding could help to verify the magnitude in which a fruit is eaten and its seeds are dispersed within the same plot or are being exchanged between plots (González-Varo et al., 2017).

4.2. Properties of the trophic seed dispersal network

Seed dispersal network theory predicts that deterministic patterns are influenced by specialized pair-wise interactions (Bascompte and Jordano, 2014). The structural and topological features of FBCD seed dispersal network corroborate such theory, with a higher level of specialization distributed in distinct modules, although the identity of the pair-wise interactions as well as their strength differed consistently. Accordingly to our hypothesis and previous comparative studies, birds dispersed more species, presented highest proportions of feces with seeds and higher seed rain density than mammals, and distributed seeds in a less clumped pattern. Therefore, bird seed dispersal dominated the topology of the trophic seed dispersal network (Acosta-Rojas et al., 2019; Escribano-Avila et al., 2012; Jordano et al., 2007; Santos et al., 1999). In contrast to these studies, however, the overall difference in seed rain density between birds and mammals were smaller and the contributing plant species varied consistently. Blackberry is usually the leading fleshy-fruited species in both birds and mammal's diet in the Mediterranean (Peredo et al., 2013; Rumeu et al., 2020), but in FBCD, wild rose, a species poorly connected on those networks, was dominant. Birds were also the unique dispersers of hawthorn, a key species in the woody vegetation expansion over the WP (Bueno et al., 2020b). Beyond eventual variations in the fruit abundance, the abundance of resident birds may be relevant, once blackberry fruiting peak overlap with southward bird migration, while wild rose have weaker interactions with migrant birds (González-Varo et al., 2021).

In mammal's trophic network, the blackberry was displaced by the strong pair-wise interactions with wild pear, greatly increasing the level of specialization of the network (Fig. 4b). Despite the wide range of occurrence of wild pear in the Mediterranean, and its great potential to compose silvopastoral systems, its seed dispersal mechanisms are poorly understood (but see Fedriani et al., 2018 and references therein). Context-dependency are relevant for such patterns, once for example, most wild pear seed dispersal studies were conducted in Donanà Natural Park (Spain), where *Pyrus bourgaeana* and their main seed dispersers (red fox and badger) occur in low densities (Fedriani and Delibes, 2009). Contrary, at FBCD, despite being very rare in the forest, wild pear is the most abundant tree in the pastureland (Bueno et al., 2020b) and the relevant seed dispersal role of badger seems to have been overtaken by cattle.

Domestic animals are usually the most abundant and biggest animals in anthropogenic mosaics, and such features are usually coupled with higher seed rain densities and higher trophic generality (Fort et al., 2016). However, seed dispersal service was not proportional to body size. Bird feces contained on average 8 times less seeds than wild mammal feces, and 18 times less seeds than cattle feces. but a medium sized frugivorous bird (e.g. *Turdus* sp.) weighed on average 15 times less than the smallest mammal (pine marten) and 5000 times less than a medium cattle. In FBCD, cattle density is officially reported as 1.5 animals/ha, but the real densities are estimated to be much higher (Bianchetto et al., 2015). However, both abundance and size seemed not so relevant in our case, as cattle dispersed only one plant species (wild pear) and despite the higher number of seeds per feces, a consequence of their larger size and capacity of ingesting more fruits, the seed rain density did not differ from red fox, pine martens and wildboars (Table 2, Fig. 4b). Cattle has been reported to act as seed disperser (Malo et al., 2000; Miguel et al., 2018), but regardless of their almost ubiquitous presence in many anthropogenic mosaics around the world, the seed dispersal role of domestic animals in general still poorly investigated, and those few studies available show contrasting results (Velamazán et al., 2020). For example, the only study we found that compared seed dispersal services by birds, domestic (sheep) and wild animals indicated a very low contribution of sheep to seed dispersal, although this study analyzed just one fleshy-fruited species (Escribano-Avila et al., 2012). Even if seed fate, including the potential effects of the clumped deposition pattern and consequent transition probabilities need to be checked to ascertain effectiveness (Hulme, 1997; Jordano and Schupp, 2000), cattle demonstrated to be a highly specialized frugivore, contrasting the neutral scenario where abundant frugivores tend to have more generalized trophic interactions (Rumeu et al., 2019). Nonetheless, we can suppose that they are actively contributing to the strong woody expansion verified in our previous study (Bueno et al., 2020b), having all the characteristics (large body size, high gut retention time and high daily movement range) to promote long distance seed dispersal events.

These findings have interesting applied outcomes. For example, pasturelands can be enriched with wild pear trees, or fruits can be given to cattle to actively disseminate its seeds at low costs to restore degraded areas (Fedriani et al., 2018). In turn, cattle promotes woody vegetation expansion over the pasturelands, that if remains uncontrolled, will reduce their own carrying capacity (Bianchetto et al., 2015). Despite the very low frequency and intensity of interactions, the appearance of seeds from the three cultivated species in red fox scats is interesting as the closest individuals of those plants are located kilometers away in the rural matrix outside the reserve, suggesting therefore long distance seed dispersal (Acosta-Rojas et al., 2019; Jordano et al., 2007). Curiously, rabbits, an important seed disperser in several Mediterranean areas (Escribano-Avila et al., 2012; Perea et al., 2013; Suárez-Esteban et al., 2013b), in our site are rare and were found to be irrelevant for seed dispersal of fleshy fruited plants. In turn, despite showing the highest rate of seed

predation among mammals (34%), crested porcupines were found to be legitimate seed dispersers, a functional role poorly described so far (Mori et al., 2017).

4.3. Properties of the spatial seed dispersal network and SLDs as seed rain magnets

The spatial distribution of the seeds over the environment is crucial to define a good dispersal service, particularly when considering the heterogeneity of habitats generated by anthropogenic land use changes (Escribano-Avila et al., 2012; Jordano et al., 2007). Even similar assemblages of seed dispersers in the same macro-region can present different temporal or spatial seed rain patterns (Escribano-Avila et al., 2014; Matías et al., 2010; Peredo et al., 2013). In our study, both trophic and spatial networks were more specialized than predicted. Both the forest and WP received seeds from all species (Fig. 4b), although the combined bird and mammals seed rain density in the forest was less than half of the one falling in the WP. In turn, SLDs presented a more deterministic pattern, receiving mostly seeds from wild pear dispersed by cattle and red fox. The lower specialization coefficient in the spatial networks is likely because just few seeds were dispersed solely in one habitat, and the seed dispersers that not delivered seeds in the SLD delivered in both forest and WP. However, the presence of the SLD separated mammals in two distinct modules (Fig. S2) and separated wild pear from the other species (Fig. S3). Cattle and red fox presented the lower proportion of feces and seed rain density in the forest. Thus, we believe that such lower rates were a consequence of their behavior towards SLDs, changing the spatial properties of the seed dispersal network. On the other side, the higher extension of SLDs inside and in the surroundings of plot 1 seems to have not been sufficient to promote significant differences in the defecation patterns and seed rain between plots (Table 3), probably due to the higher mobility of mammals.

Fruiting landscape is known to influence frugivore behavior (González-Varo et al., 2017; Martínez and García, 2015), even though fruit abundance may not always be a proxy for seed dispersal abundance (Donoso et al., 2016). In FBCD, the higher abundance and diversity of the fleshy fruited plants in the WP, and the passage of SLDs within such WP, may explain higher seed rain densities found in these habitats. Such compensation also occurred within habitats, once different species presented different proportions of defecations and defecations with seeds at the same habitat. For example, pine marten feces densities were higher in the forest, but the same amount of seeds were delivered in the WP. In turn, cattle and red fox dispersed more seeds in SLDs, even if defecation densities did not differ from forest or WP. As we predicted, SLDs received the largest fraction of mammalian seed rain. However, human management in the edges, particularly though the vegetation cleaning for fire-breaks probably reduces or erases the recruitment potential for the dispersed seeds. In turn, we cannot discard the potential of SLDs acting as highways for landscape scale seed disperser movement, potentially facilitating inter-populations long distance seed dispersal (Plissock et al., 2020). Interestingly, our results partially corroborate the hypothesis that animals might overlap in their topological role in trophic and spatial networks, as observed in the WP (Rumeu et al., 2020). However, SLDs and forests had very few fleshy fruits, but received a relevant proportion of the seeds, indicating that other factors than fruit abundance influence frugivores seed deposition. Additionally, plot 1 has more SLD surfaces over and close to it, but the GLMM involving only mammals (that are more affected by SLDs) indicated significant differences in only the presence/absence of seeds in feces between plot 1 and 3 ($p = 0.026$) with no significant differences in seed rain. Such lack of variation suggests that the magnet effect of SLDs occurs at broader scales (e.g. a fruit eaten in plot 1 might be defecated in the SLD close to plot 3), and the between plot differences in plant density and cover are compensated by high mobility mammals (Plissock et al., 2020; Suárez-Esteban et al., 2016).

A considerable part of shade-intolerant plant species characteristic of the WP (e.g. wild rose, blackthorn, blackberry, wild pear) were dispersed inside the dense oak forest both by birds and mammals (Fig. 4b). Although in the Mediterranean, the secondary succession towards mature forests is naturally followed by an overall richness decrease (Amici et al., 2013; La Mantia et al., 2008), in FBCD, the forests surrounding the pastureland were intensively managed in the past, currently being composed predominantly by two oak species (*Quercus pubescens* and coppices of *Quercus ilex*) with most of the fleshy-fruited plants occurring in very low densities (R. S. Bueno *unp. data*). Such pattern is very different from the forests reported in many Temperate and Mediterranean studies, where fleshy fruited trees and shrubs are relevant structural components (Escribano-Avila et al., 2012; García et al., 2016; Jordano and Schupp, 2000; Matías et al., 2010). Our results demonstrated that birds and mammals are keeping seed limitation under control (La Mantia et al., 2019), and that cattle herbivory is somewhat constant over the last decades. Therefore, other factors not measured here merit investigation (Chacón-Labela et al., 2016). For example, fallow deer populations are constantly increasing over the last years, potentially changing the current and future recruitment patterns in the WP (Bueno et al., 2020a; Paton et al., 2002). On the other side, an accurate management of the holm oak coppices may promote an increase in plant diversity inside the forest (Chacón-Labela et al., 2016).

5. Conclusions

By unraveling the role of mammals and birds on Mediterranean seed dispersal, we provide practical insights that can be applied in different perspectives inside human-dominated landscapes. The ecological restoration of degraded areas is urgently needed, with more than 400,000 km² in the Mediterranean are under desertification risk due to anthropogenic land-use changes (Praválie et al., 2017). As such areas are usually defaunated of wild mammals and consequently their seed dispersal services (Fedriani et al., 2018; La Mantia and Bueno, 2016), rewilding is under debate in Europe (Lundgren et al., 2020). Our results show that cattle may give some interesting predictions of the potential seed dispersal outcomes of large herbivores, although we also demonstrate that they cannot replace wild animals to fully rewire the seed dispersal network (Ceausu et al., 2015; Costa et al., 2018; Lundgren et al., 2020). Our results also encourage to not underestimate the potential positive and negative impacts of SLDs inside protected areas. In addition, our system can

be considered a high nature value silvopastoral systems, therefore representing a good template to be reproduced for a more sustainable cattle ranching, holding richer ecological networks and higher biodiversity, particularly considering the large extensions covered by such anthropogenic mosaics in the Mediterranean.

CRedit authorship contribution statement

RDSB, TLM and MG conceived the research. RDSB and DG developed the sampling design and the analytical framework. RDSB collected and analyzed the data and wrote the first manuscript. All authors revised and contributed to the final version.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Tommaso La Mantia reports financial support was provided by Ministero dell'Istruzione, dell'Università e della Ricerca.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01880](https://doi.org/10.1016/j.gecco.2021.e01880).

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