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Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds

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The positive link between biodiversity and ecosystem functioning is a current paradigm in ecological science. However, little is known of how different attributes of species assemblages condition the quality of many services in real ecosystems affected by human impact. We explore the links between the attributes of a frugivore assemblage and the quantitative and qualitative components of its derived ecosystem service, seed dispersal, along a landscape-scale gradient of anthropogenic forest loss. Both the number and the richness of seeds being dispersed were positively related to frugivore abundance and richness. Seed dispersal quality, determined by the fine-scale spatial patterns of seed deposition, mostly depended on frugivore richness. In fact, richness was the only attribute of the frugivore assemblage affecting the probability of seed dispersal into deforested areas of the landscape. The positive relationships between frugivore richness *per se* (i.e. independent of frugivore abundance and composition) and all components of seed dispersal suggest the existence of functional complementarity and/or facilitation between frugivores. These links also point to the whole assemblage of frugivores as a conservation target, if we aim to preserve a complete seed dispersal service and, hence, the potential for vegetation regeneration and recovery, in human-impacted landscapes.

Keywords: biodiversity–ecosystem function; functional complementarity; habitat loss; seed rain; species richness; *Turdus* spp.

1. INTRODUCTION

Biodiversity matters for the provision of ecosystem functions and services [1]. This now axiomatic concept emerges from the positive relationships between the attributes of biological assemblages, in terms of the number and types of organisms, and the magnitude and/or the stability of different ecosystem processes [2,3]. Rich biota increase and maintain both ecosystem stocks (e.g. plant biomass) and ecological rates (e.g. nutrient cycling) better than do impoverished communities [4,5]. This biodiversity–ecosystem function link has been widely demonstrated in small-scale experimental communities submitted to random species extinction [6,7]. However, the actual relevance of biodiversity for many ecological functions, such as trophic processes, in real-world ecosystems (i.e. those suffering deterministic species decays and extinctions due to different drivers of global change) is still poorly understood [8–10]. This knowledge gap is especially relevant if we are aiming to develop conservation tools based on the role of biodiversity as insurance for ecosystem services provision [11,12].

Equally important to discerning whether biodiversity matters for real-world ecosystem functioning is to address *how* it matters [3,9]. In this sense, most studies have evaluated the relationship between species richness and single quantitative components (average magnitude or spatio-temporal variation of stocks and rates) of ecosystem functions, with scant coverage of multiple and qualitative components [3,13]. In the case of plant pollination by animals, for example, it is known that pollinator richness may increase the magnitude of pollination (e.g. seed set) and its stability in space and time ([14,15]; but see [16,17]). However, little is known of how pollinator diversity affects the qualitative outcomes of pollination (e.g. the vigour of seed embryos) that, in some cases, may be more relevant than quantity from a functional perspective (e.g. germination ability of plant offspring; [16,18]). Thus, ascertaining the actual relevance of biodiversity in ecosystem functioning requires integrating the role of different components of biodiversity (e.g. species abundance, composition and richness) on the quantitative and qualitative components that make up ecosystem functions.

Seed dispersal by frugivorous animals is a pivotal service in many temperate and tropical ecosystems, as animals that move seeds from source plants are driving plant gene flow and population dynamics in undisturbed habitats, as well as vegetation recovery in deforested lands [19]. Frugivore assemblages and seed dispersal comprise an optimal system for testing the prevalence of the biodiversity–ecosystem services link in the real world for several reasons. First, frugivore assemblages are composed of species that usually differ strongly in their relative abundance and functionality [20,21]. Second, different drivers of global change, e.g. habitat loss, are known to affect these assemblages, leading to decays of seed dispersal function along the gradients of anthropogenic change [22,23]. And third, the relevance of seed dispersal as an ecosystem

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service depends not only on how many seeds are dispersed but also on how and where they are dispersed (e.g. the recovery of deforested land depends largely on the arrival of seeds triggering recruitment; [22,24]). In fact, qualitative components of seed dispersal, such as the spatial patterns of seed deposition, are expected to be highly responsive to the anthropogenic alterations of the frugivore assemblage, as frugivores frequently differ strongly among themselves in terms of spatial behaviour and response to disturbance [23,25].

In this paper, we explore the relationship between the attributes of a frugivore assemblage and the quantitative and qualitative components of seed dispersal in a real-world ecosystem. As an alternative to biodiversity experimental manipulation, we study the observational gradients of frugivore abundance, composition and richness found in a landscape affected by anthropogenic land use (see also [26,27]). Working with a small assemblage of frugivorous birds and fleshy fruited trees in highly fragmented temperate forests of north Spain, we show the positive role of frugivore richness on seed dispersal, independent of frugivore abundance and composition. More importantly, we show that richness effects are proportionally more important for the qualitative components of seed dispersal than for the net quantity of seeds and seed species being dispersed.

2. METHODS

(a) *Study system*

Our study focuses on the temperate secondary forest of the Cantabrian Range (north Spain), a common, but low-cover (less than 30%) and highly fragmented forest type in mid-elevation areas [28]. Secondary forest occurs as fringe patches, adjacent to mature stands, and as variable-sized fragments (from isolated remnant trees to patches of several hectares) embedded in a historically deforested matrix of stony pastures and heathland (*Erica* spp., *Ulex europaeus*).

The system under study is composed of fleshy fruited trees and frugivorous birds. Fleshy fruited trees, namely holly (*Ilex aquifolium*), hawthorn (*Crataegus monogyna*), and yew (*Taxus baccata*), account for more than 70 per cent of tree cover in the studied forest [29]. Their fruits are 10–15 mm diameter, sugar-rich red berries (arillated seed in yew) that ripen in autumn (September to November) and contain one to four seeds (5–9 mm [29]). Their main frugivores are thrushes, encompassing the whole richness of the *Turdus* spp. in west Europe: blackbird *Turdus merula*, fieldfare *Turdus pilaris*, mistle thrush *Turdus viscivorus*, redwing *Turdus iliacus*, song thrush *Turdus philomelos*, and ring-ouzel *Turdus torquatus*. Some of these (*T. pilaris*, *T. iliacus* and *T. torquatus*) are overwintering species in northern Spain, whereas others (*T. merula*, *T. viscivorus* and *T. philomelos*) are resident species which are joined by overwintering migrant individuals [30]. All thrushes swallow the entire fruits, defecating the intact seeds in their faeces (i.e. they are legitimate seed dispersers; [31]). Other vertebrates able to disperse fleshy fruited plants in the Cantabrian Range are robin *Erithacus rubecula*, blackcap *Sylvia atricapilla*, common wood-pigeon *Columba palumbus* and carnivorous mammals (fox *Vulpes vulpes*, badger *Meles meles*, martens *Martes* spp.), but all feed scarcely on tree fruits [30]. In sum, by focusing on the dispersal of seeds of fleshy fruited trees by thrushes, we are accounting for a major part of the service of mobility and deposition of seeds of the woody plant community provided by frugivorous animals in Cantabrian secondary forest. Despite the strong taxonomic affinity, the species of thrushes under consideration differ markedly in functional terms (relative abundances, fruit consumption patterns, response to habitat features; [30]). Therefore, we consider that even a six-species gradient of richness will be enough to detect any effect of diversity on the quantitative and qualitative components of seed dispersal.

(b) *Study site and spatial framework*

The study site was located in the Sierra de Peña Mayor (43°17′ N, 5°30′ W, 900 m a.s.l., Asturias region, Spain), where secondary forest is intermingled with meadows, heathland and limestone rocky outcrops. We set up a 400×440 m rectangular plot in which the amount of forest cover varied from densely covered sectors to areas of scant cover and isolated remnant trees (figure 1*a*), thus representing a gradient of forest loss [32]. The plot was subdivided into 440, 20×20 m sampling cells. We developed a Geographical Information System (GIS, ArcGIS v. 9.0) based on a 1 : 5000-scale ortophotomap image of the study plot. The GIS platform incorporated a grid of 440, 20×20 m cells and a layer of digitized forest cover from which we estimated the amount of forest cover (in square metre) per cell.

(c) *Bird counts*

Direct observations of thrushes were made from five different vantage positions in elevated outcrops, located along the central axis of the plot (figure 1*a*; for a detailed methodology, see electronic supplementary material, text S1 and figure S1). Observations were made between October 2009 and February 2010, with 105 h of cumulative observation time allocated throughout the season and between stations in a balanced number of 1 h observation periods. In each observation period, one observer counted and identified at the species level all thrushes seen (or heard) in different sectors of the surveyed area. Thrush sightings were assigned to the different geo-referenced sampling cells covered from each vantage position. A high level of visual and acoustic detectability of birds was achieved across almost the entire plot. However, owing to the denser tree canopy and topography, detectability was lower in some easternmost highly forested cells of the plot (figure 1*a*; electronic supplementary material, figure S1) and therefore, complementary bird observation was accomplished from positions within the forest in these areas. Twelve forest point-count positions were established, each one corresponding to the centre of a group of four cells. Observations were made in 10 min periods, recording any thrush heard or seen within the four surrounding cells. Observation time from each point count was 110 min. We calculated the abundance of thrushes per cell as the cumulative number of birds heard or seen in each cell through the season, for both each individual species and all species together. We divided the cumulative number of thrushes by total observation time, calculating the number of thrushes per 10 h of observation. We estimated the total number and the identity of the species of thrushes observed in each cell through the whole season.

(d) *Counts of dispersed seeds*

We assessed the occurrence of seeds dispersed by thrushes in sampling stations across the whole plot. Ten sampling stations, separated from each other by 2 m, were placed along the central longitudinal axis of 220 sampling cells following a chess-board design (figure 1*b*). In each station,

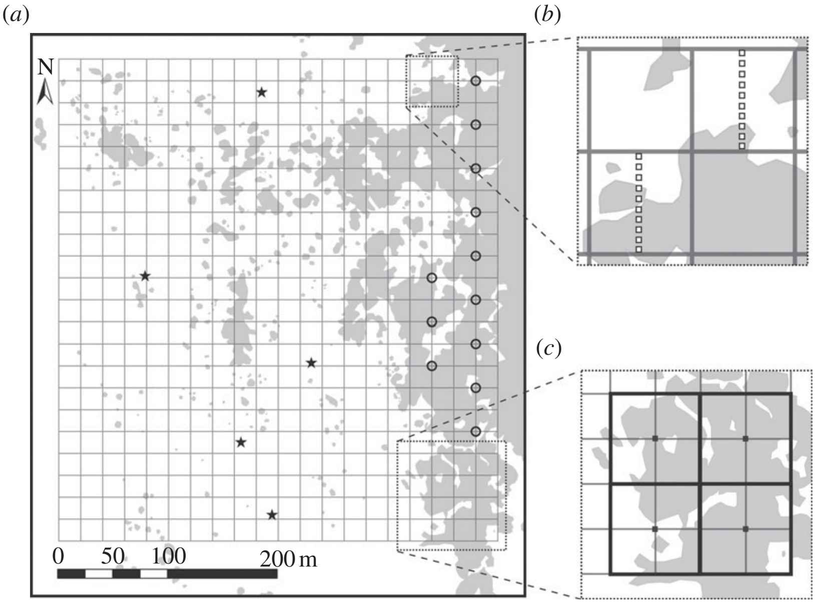

Figure 1. Scheme of the study plot representing: (*a*) the configuration of the forest cover (grey area), the plot subdivision into 20 × 20 m sampling cells, and the vantage (black stars) and point-count (circles) positions for bird observation, (*b*) a detail of the position of the stations for sampling seed deposition by frugivores (white squares) along the central longitudinal axis of cells following a chess-board design, and (*c*) a detail of four of the 40 × 40 m blocks (squares outlined in black and showing a black-dotted centroid) used to combine, for analytical purposes, the data corresponding to each group of four adjacent sampling cells.

we set up a permanently labelled, open-ground 50 × 50 cm quadrat where all tree seeds dispersed by birds were collected and counted. Bird-dispersed tree seeds are unequivocally identifiable: they are clean of pulp remains, unlike seeds on fruits fallen beneath trees, and occur in small clusters easily distinguishable from those occurring in mammal faeces, and they can be almost exclusively attributable to thrushes [30]. We estimated the total number of dispersed seeds per sampling station as the sum of seeds found in two consecutive surveys (late November and early January). From these collections, we also estimated the richness of species of the dispersed seeds in each sampling station. A previous study in the same site demonstrated that this methodology provides estimates of seed abundance and richness reliable enough for the evaluation of the large-scale patterns of seed dispersal [22]. Depending on the structural features of the cover where the quadrats were located, each sampling station was assigned to either covered (under woody canopy) or open (uncovered by woody canopy) microhabitat.

(e) *Data analysis*

Despite our sampling scheme being based on 20 × 20 m plot cells (i.e. sampling cells, see above), we combined the data corresponding to each four adjacent sampling cells, resulting in 110, 40 × 40 m blocks (figure 1*c*). This procedure was necessary to avoid species-area constraints in the estimation of frugivore richness, as we considered the original cell size (40 m^2) a too small extent (in terms of sampling scale) for detecting the highest possible frugivore richness. We estimated, on a per-block basis, the structure of the landscape, the components of biodiversity of the frugivore assemblage, and the quantitative and qualitative components of seed dispersal.

Landscape structure was represented by *forest cover*, estimated as the proportion of area occupied by forest canopy with respect to total block area. As biodiversity-related attributes of the frugivore assemblage, we considered the total abundance of frugivorous thrushes, thrush species richness and the composition of frugivore assemblage. *Abundance of thrushes* was estimated as the average abundance of birds sighted in the four cells of each block (i.e. considering a cell-based observation grain). *Richness of thrushes* was estimated as the total number of different species observed in the four cells of each block (i.e. considering a block-based observation grain). *Composition of the frugivore assemblage* was estimated by means of a non-metric multi-dimensional scaling analysis (NMDS) on the matrix of the Bray–Curtis distances of the average abundances of the different species of thrushes in each block (electronic supplementary material, text S2; [33]). NMDS analyses were carried out with two axes (NMDS1 and NMDS2) that provided scores for each sampled block. These NMDS score vectors were considered to represent gradients in the composition of the assemblage of frugivorous thrushes across the whole studied landscape, with similar score values representing similar compositions in the assemblage (electronic supplementary material, figure S2).

As the quantitative components of seed dispersal service, we considered *abundance of seeds*, calculated as the average number of dispersed seeds from the 20 quadrats included in each block (as each block covered two non-adjacent cells containing seed sampling stations; figure 1*b*), and *richness of seeds*, estimated as the average number of species of dispersed seeds from the same quadrats. As qualitative components, first we estimated *arrival rate*; the proportion of quadrats per block receiving at least one dispersed seed. This provides a measure of the spatial distribution of seed dispersal, with near-to-one values indicating a widespread process but near-to-zero values indicating a process highly restricted in space. Second, we calculated *colonization rate*; the per-block proportion of quadrats in open microhabitats that received at least one dispersed seed: a measurement which represents seed deposition as the process that triggers the recovery of tree populations in deforested areas. Owing to the regular structure of the sampling design, there was a risk of misestimation of colonization rate in those blocks with high forest cover and very few quadrats in open microhabitats; therefore, it was only calculated for those blocks ($n = 86$) containing at least nine open quadrats.

Our analytical goal was to evaluate the relative effect the different components of biodiversity of the frugivore assemblage had on the various components of seed dispersal. Thus, we built multiple regression models considering abundance of thrushes (log-transformed), NMDS axes, and richness of thrushes as independent variables, and each component of seed dispersal, i.e. abundance of seeds (log-transformed), richness of seeds, arrival and colonization rates (both arcsin-root transformed), as response variables. Given that biodiversity parameters (species abundance, richness and assemblage composition) are frequently correlated between themselves [34], we used a Type-III sum-of-squares procedure in multiple regression models. This method ensures that all shared variance is not attributed to collinear predictors, thereby providing effect estimates which are independent of any potential co-variation between predictors. Owing to the spatial structure of sampling along a marked gradient of forest cover, the data from both the above predictors and response variables could be highly auto-correlated in space. We therefore used simultaneous autoregressive models (SAR; [35]) in order to take into account the potential effect of spatial non-independence in multiple regression models. SAR models provide standardized regression coefficients that represent the direct effect(s) of the predictor(s), free of spatial analytical constraints.

Prior to the SAR models, we verified the degree of correlation among the attributes of frugivore biodiversity, and between each biodiversity attribute and each seed dispersal component, by means of Pearson's coefficients. Similarly, we tested correlation between forest cover and, respectively, frugivore assemblage attributes and seed dispersal components. In order to account for the potential effects of spatial autocorrelation in the degree of significance of correlation tests, we used Dutilleul's method which corrects the number of degrees of freedom in order to re-calculate the degree of significance of the original correlation coefficients (electronic supplementary material, text S3). All spatially explicit tests were performed with SAM v. 4.0 software [36].

3. RESULTS

Within our study site, forest cover per block averaged 25.9 per cent (±3.0 s.e.). Thrushes were observed in 84.5 per cent of sampling blocks, and the maximum richness of frugivores (six species) was detected in at least two blocks. A mean value of 3.7 (±0.8 s.e.) thrush individuals per 10 h of observation per block was estimated, with an average of 2.5 (±0.2 s.e.) species per block. Frugivore richness was positively correlated with the total abundance of thrushes, whereas NMDS1 was negatively correlated to both frugivore abundance and richness (electronic supplementary material, table S3). The relative occurrence of the different species varied markedly, with *T. iliacus* accounting for 49.0 per cent of observations, *T. merula* for 20.7 per cent, *T. viscivorus* for 17.2 per cent, *T. philomelos* for 10.1 per cent, and *T. pilaris* and *T. torquatus* for less than 2 per cent each. An average number of 15.6 (±3.1 s.e.) dispersed seeds were found per quadrat per block, with an average richness of dispersed seeds of 0.54 (±0.04 s.e.). *Ilex aquifolium* seeds dominated the seed rain generated by frugivores (93.5% of the 34 363 collected seeds), with *C. monogyna* and *T. baccata* accounting for 2.5 per cent and 4.0 per cent, respectively. Dispersed seeds occurred in 88.8 per cent of sampling stations under tree canopies ($n = 538$), but only in 23.2 per cent of stations in open microhabitats ($n = 1662$). Average arrival rate per block was 0.39 (±0.03 s.e.), whereas average colonization rate was 0.28 (±0.02 s.e.).

The abundance and the richness of thrushes, as well as all components of seed dispersal, were positively related to forest cover (electronic supplementary material, table S3). The distributions of these parameters across the plot (figure 2) also reflected a negative response of frugivore and seed dispersal variables to forest loss gradient. Nevertheless, the spatial distribution of abundance was somehow different to that of richness of thrushes. Namely, the abundance of thrushes decreased sharply from northeast to southwest, whereas the richness was not only higher along the eastern side of the plot but also along an east-to-west axis that mirrored the distribution of scattered patches of forest. Moreover, more seeds and more seed species occurred in those parts of the landscape visited by a larger number, but also by more species, of thrushes (figure 2; electronic supplementary material, table S3). Similarly, as judged by the distribution of arrival rate, seed dispersal was also more widespread in these areas. However, seed colonization rate mostly encompassed the spatial variability of richness of thrushes across the plot, suggesting that the probability of deposition in open microhabitats was higher in frugivore-rich—but not necessarily frugivore-abundant—patches (figure 2; electronic supplementary material, table S3).

SAR models evidenced the effects of different attributes of the frugivore assemblage on the components of seed dispersal, irrespective of the degree of collinearity among these attributes (table 1). Large proportions of the variability in the abundance and the richness of seeds were accounted for by the positive and, as judged by the standardized regression coefficients, equivalent effects of the abundance and richness of thrushes. With regard to the qualitative components of seed dispersal, arrival rate was also explained by the abundance of thrushes and, to a greater extent, by the richness of thrushes. The SAR model applied to seed colonization rate had a lower predictive power, but evidenced that richness was the only component of frugivore biodiversity with a significant effect on this response variable. The lower predictability of the colonization rate model was not derived from its smaller sample size, given that similar results were found when the models corresponding to the other seed dispersal components were run with a similarly reduced sample size (electronic supplementary material, table S4). No independent effects of the NMDS axes, representing the composition of the frugivore assemblage, were found in any component of seed dispersal, providing evidence that the raw effects of the NMDS axes on seed dispersal were driven by the correlations of these vectors with frugivore abundance and richness (electronic supplementary material, table S3).

4. DISCUSSION

Our results show that the provision of seed dispersal service along a gradient of habitat loss was closely related to the attributes of the frugivore assemblage. Both the

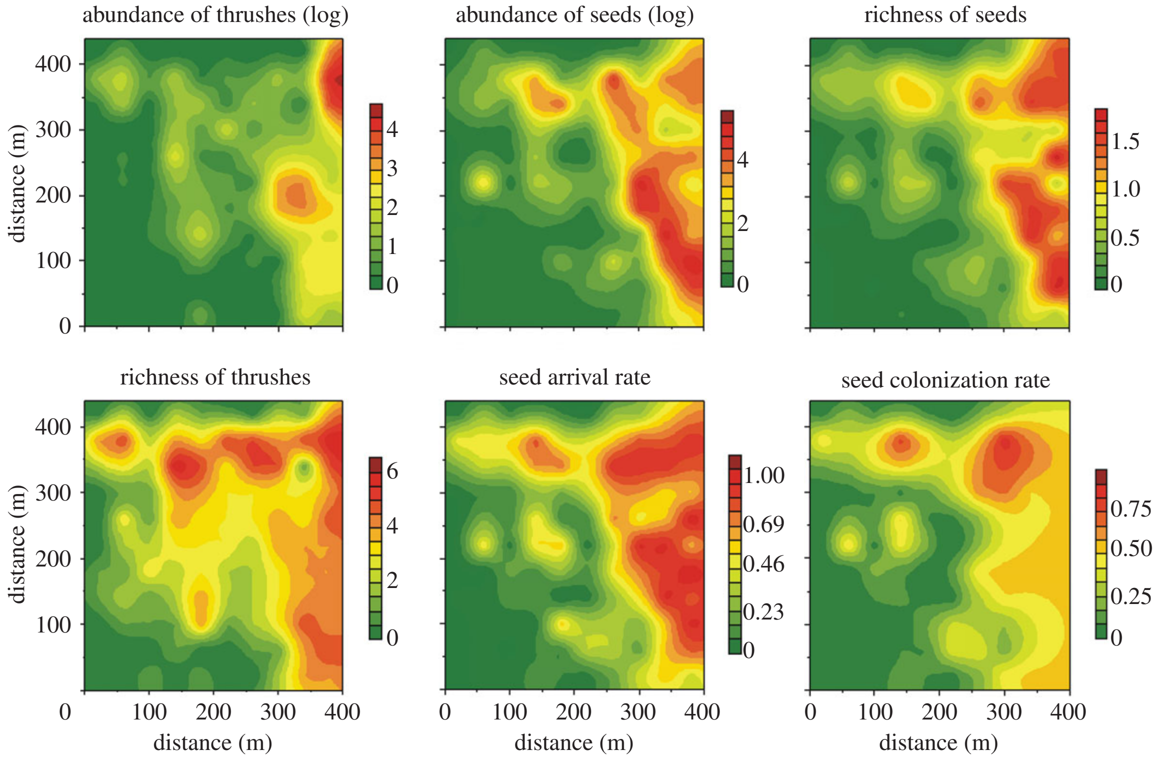

Figure 2. Distribution of the abundance (log) and the richness of frugivorous thrushes, the abundance (log) and the richness of dispersed seeds, and the rates of seed arrival (proportion sampling units receiving at least one seed) and of seed colonization (proportion sampling units in open microhabitats receiving at least one seed) across the study plot. Coloured contours are interpolated from the values of the corresponding variable in the centroid of each 40 × 40 m block ($n = 110$ for all parameters except colonization rate, in which interpolation from 86 blocks has been expanded to cover the whole plot for representation purposes). The colour scales are shown.

Table 1. Summary of the spatial simultaneous autoregressive models (SAR) considering, as predictor variables, the components of the frugivore assemblage (total abundance of thrushes; frugivore composition represented by axes of a non-metric multi-dimensional scaling analysis; richness of thrushes), and, as response variables, the quantitative and qualitative components of seed dispersal. The total variance explained by the predictors (r^2), the degree of significance of the whole model (F-value based), the value of the unstandardized (± s.e.) and standardized regression coefficient of each predictor, and their degree of significance (t-value based), are also shown (in bold $p < 0.05$).

	SAR coefficient (±s.e.)	standardized coefficient	t-value	p-value
abundance of seeds (log)				
model	$r^2 = 0.64$	$n = 110$	$F = 45.89$	$p < 0.001$
abundance of thrushes (log)	0.62 ± 0.16	0.39	**4.01**	**<0.001**
NMDS1	0.08 ± 0.22	0.03	0.36	0.72
NMDS2	−0.27 ± 0.19	−0.09	−1.36	0.18
richness of thrushes	0.36 ± 0.09	0.39	**3.89**	**<0.001**
richness of seeds (log)				
model	$r^2 = 0.63$	$n = 110$	$F = 43.78$	$p < 0.001$
abundance of thrushes (log)	0.11 ± 0.03	0.34	**3.54**	**<0.001**
NMDS1	−0.05 ± 0.05	−0.07	−1.04	0.30
NMDS2	−0.03 ± 0.04	−0.05	−0.80	0.42
richness of thrushes	0.06 ± 0.01	0.34	**3.48**	**<0.001**
seed arrival rate (arcsin square root)				
model	$r^2 = 0.57$	$n = 110$	$F = 37.19$	$p < 0.001$
abundance of thrushes (log)	0.11 ± 0.04	0.27	**2.68**	**0.008**
NMDS1	−0.05 ± 0.06	−0.06	−0.75	0.46
NMDS2	−0.01 ± 0.05	−0.01	−0.19	0.85
richness of thrushes	0.09 ± 0.02	0.38	**3.63**	**<0.001**
seed colonization rate (arcsin square root)				
model	$r^2 = 0.35$	$n = 86$	$F = 11.11$	$p < 0.001$
abundance of thrushes (log)	0.07 ± 0.05	0.16	1.22	0.23
NMDS1	−0.01 ± 0.056	−0.01	−0.06	0.95
NMDS2	0.02 ± 0.05	0.03	0.36	0.72
richness of thrushes	0.08 ± 0.03	0.40	**2.76**	**0.007**

abundance and the richness of frugivorous thrushes had positive effects on seed dispersal. Nevertheless, the relative effect of abundance and richness differed between components of seed dispersal, with quantitative components being equally affected by frugivore abundance and richness, but the quality of seed dispersal being mostly, or even exclusively, dependent on frugivore richness.

Concerning the effects of frugivore abundance, we found more dispersed seeds in areas visited by larger numbers of thrushes. This quantitative link has been previously demonstrated in the same system over a different landscape context, as well as in other ecosystems dominated by bird-dispersed, fleshy fruited woody plants [22,37]. Although our study covered a narrow gradient of seed species richness, somewhat limiting its generalization to more diverse systems, it does though indicate that a richer seed rain occurred in frugivore-abundant areas. Thus, provider abundance proved to be a good surrogate of the magnitude of seed dispersal, as evidenced in other ecosystem services derived from the trophic activity of highly mobile animals (e.g. dung burial and pollination by insects [19,38]). More importantly, our study suggests a positive effect of frugivore richness in all components of seed dispersal. These richness effects emerged even after accounting for the role of habitat loss on the attributes of frugivore assemblage (as demonstrated by *a posteriori* models, including forest cover as additional predictor; electronic supplementary material, table S5), indicating the resilience of the effect of biodiversity on ecosystem services even under the impact of global change drivers [9]. These results are similar to those found in other animal-derived services across disturbed landscapes (e.g. pollination; [14]), but contrast with previous research which has failed to detect frugivore richness effects on frugivory or seed dispersal magnitude [37,39,40]. Moreover, as far as we know, our study is the first to suggest a positive effect of frugivore diversity in the probability of tree colonization outside forest boundaries, as the degree of seed deposition in open microsites, although less predictable than the other dispersal components, was exclusively driven by frugivore richness. We expect these seed arrival events to be further translated into effective recruitment, as previous work in this plant-disperser system has highlighted the significant role of seed dispersal on driving the spatial template of seedling establishment [29].

Our field study was not explicitly designed to identify the mechanisms underpinning the link between biodiversity and ecosystem functioning (i.e. sampling effects, complementarity and facilitation [1,41]). Nonetheless, the analytical segregation between the abundance, composition and richness of frugivores enables the exploration of why different biodiversity components affected seed dispersal. Namely, the existence of effects of frugivore richness *per se* (i.e. independent of frugivore abundance and composition) suggests that a richer assemblage would provide a better seed dispersal service due to complementarity and/or facilitation between frugivores (see also [8,38]). At least two sources of complementarity—diet and spatial behaviour—may operate among thrushes in the Cantabrian Range. With respect to diet, a previous work [30] suggests that different thrushes feed on different parts of the community fruiting template, and hence a richer coterie of thrushes could provide a better coverage of all fleshy fruited species to be deposited in the seed rain. Concerning spatial behaviour, thrushes are also known to differ markedly in their response to habitat spatial heterogeneity in our study site (e.g. in the relative use of open versus covered microhabitats; [30]). Such behavioural differences would increase the correlation between frugivore functional diversity and species richness, making seed arrival and colonization rates especially sensitive to richness changes. Finally, some facilitation effects may also come into play, such as higher richness being derived from some species of thrushes tracking the presence of others across the foraging landscape [42], and thereby providing an additive local dispersal service. These sort of facilitative interactions do probably occur in our system, given that observations of different species feeding simultaneously at the same group of neighbour fruiting trees, or flying together in multi-specific flocks, are frequent (D.G. & D.M. 2009–2012, unpublished data).

Further to complementarity and facilitation, our study also provides some clues about sampling effects, whereby a richer frugivore assemblage should have an increased probability of containing dominant species, monopolizing seed dispersal function and hence increasing greatly the magnitude of service [1]. The lack of net composition effects (i.e. independent of frugivore abundance and species richness) in our results suggests that the studied frugivore pool does not include functionally dominant species, that is, those able to generate sampling effects by monopolizing seed dispersal function even at low abundances (see also [8]). However, the positive effects of frugivore abundance on the quantitative components of seed dispersal may be indicative of sampling effects related to the inclusion of numerically dominant species in the frugivore pool. As such, *T. iliacus* accounted for almost 50 per cent of observations and its specific abundance was strongly correlated to seed dispersal magnitude (electronic supplementary material, table S6). Moreover, the abundances of all remaining species (excepting the rarest *T. pilaris*) were positively correlated with seed dispersal (electronic supplementary material, table S6), and all pairwise correlations between species abundances were positive (data not shown), suggesting a lack of density compensation [43] among the six thrushes. Thus, although *T. iliacus* seems to be the numerically dominant seed disperser, the greatest magnitude of dispersal service would only be achieved through the aggregate abundance of frugivore species [38,43]. In sum, complementarity, facilitation and sampling effects are probably co-occurring mechanisms explaining the role of frugivore biodiversity on seed dispersal.

5. CONCLUDING REMARKS

By dissecting the role of frugivore assemblage attributes on seed dispersal in a real-world ecosystem, this study goes beyond previous research on the positive link between biodiversity and ecosystem services. Namely, our results suggest that species richness matters for all the components of a given ecosystem service but, compared with other biodiversity components, matters more for the quality than for the magnitude of the service. We would argue that the dominant role of richness on qualitative components derives from a strong dependence of these components on the functional diversity and complementarity within the frugivore assemblage. We surmise these findings to be generalized to many trophic-derived services whose quality is expected to be driven by the degree of functional heterogeneity among animal species (e.g. pollination, biological control and detritivory [40,44]).

Our results provide a first step towards a mechanistic understanding of how frugivore richness affects seed dispersal at a scale relevant in conservation terms [11]. Thus, we urge that it should be taken into account in the management of ecosystem processes and economic activities derived from tree regeneration in standing forests (e.g. forest carbon storage, sustainable exploitation of forest species and ecotourism) but also those related to the recovery of vegetation in deforested lands (e.g. ecosystem resilience, ecological restoration). All these processes could be altered by frugivore decays and extinctions derived from anthropogenic processes (e.g. local overhunting, climate warming [23]). We encourage, therefore, the consideration of the whole assemblage of legitimate dispersers as a conservation target in the fragmented Cantabrian forests, with the aim of preserving as wide as possible a set of services derived from seed dispersal. This rationale may be applied to other temperate and tropical systems whose plant-frugivore assemblages are now suffering a similar impact of global change processes [23].

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