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Austria and Switzerland

Basic and Applied Ecology 14 (2013) 378–386

Basic and Applied Ecology

www.elsevier.com/locate/baae

Mammalian seed dispersal in Cantabrian woodland pastures: Network structure and response to forest loss

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Received 15 January 2013; accepted 13 May 2013
Available online 7 June 2013

Abstract

We evaluated the role of wild large mammals as dispersers of fleshy-fruited woody plants in woodland pastures of the Cantabrian range (N Spain). By searching for seeds in mammal scats across four localities, we addressed how extensive seed dispersal was in relation to the fleshy-fruited plant community, and applied a network approach to identify the relative role of mammal species in the seed dispersal process. We also tested the response of mammalian dispersers to forest availability at increasing spatial scales. Five carnivores and three ungulates dispersed seeds of eight fleshy-fruited trees and shrubs. Mammalian seed dispersal did not mirror community-wide fruit availability, as abundant fruiting trees were scarce whereas thorny shrubs were over-represented among dispersed species. The dispersal network was dominated by bramble (*Rubus ulmifolius/fruticosus*), the remaining plants being rarer and showing more restricted disperser coteries. Fox (*Vulpes vulpes*), badger (*Meles meles*), and wild boar (*Sus scrofa*) dispersed mostly bramble, whereas martens (*Martes* sp.) dispersed mostly wild rose (*Rosa* sp.). Ungulates occasionally dispersed holly (*Ilex aquifolium*) and hawthorn (*Crataegus monogyna*). The empirical network reflected a skewed distribution of interactions and some functional complementarity (as judged from the low levels of connectance and nestedness), but also some degree of specialization. Mammals overused uncovered microsites for seed deposition, and increased their disperser activity in those landscape sectors devoid of forest. Combined with previous findings on avian seed dispersal, this study suggest a strong functional complementarity coming from the low overlap in the main plant types that mammals and birds disperse – thorny shrubs and trees, respectively – and the differential patterns of seed deposition, with mammals mostly dispersing into deforested areas, and birds into forest-rich landscapes.

Zusammenfassung

Wir untersuchten die Rolle wilder Großsäuger als Samenausbreiter von Gehölzen mit fleischigen Früchten in Waldweiden des Kantabrischen Gebirges (Nordspanien). Indem wir nach Samen in der Losung von Säugern an vier Standorten suchten, wollten wir herausfinden, wie erheblich die Samenausbreitung in Bezug auf die Gemeinschaft der Pflanzen mit fleischigen Früchten ist, und wir wandten einen Netzwerkansatz an, um die relative Bedeutung der Säugerarten für den Prozess der Samenausbreitung zu bestimmen. Wir testeten auch die Reaktion der ausbreitenden Säuger auf die Verfügbarkeit von Wald bei zunehmenden räumlichen Skalen. Fünf Karnivore und drei Ungulaten waren an der Ausbreitung der Samen von acht Gehölzarten mit fleischigen Früchten beteiligt. Die Samenausbreitung durch Säuger spiegelte nicht die Verfügbarkeit von Früchten in der Gemeinschaft wider, denn häufige Fruchtbäume waren selten unter den ausgebreiteten Arten, während Dornbüsche überrepräsentiert waren. Das Ausbreitungsnetzwerk wurde dominiert von der Brombeere (*Rubus ulmifolius/fruticosus*). Die übrigen Gehölze waren seltener und mit kleineren Ausbreitercliquen verknüpft. Fuchs (*Vulpes vulpes*), Dachs (*Meles meles*) und Wildschwein (*Sus scrofa*) Das

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1439-1791/$ – see front matter
http://dx.doi.org/10.1016/j.baae.2013.05.003

breiteten hauptsächlich Brombeere aus, während Marder (*Martes* sp.) hauptsächlich Wildrosen (*Rosa* sp.) ausbreiteten. Von Huftieren wurden gelegentlich Stechpalme (*Ilex aquifolium*) und Weißdorn (*Crataegus monogyna*) ausgebreitet. empirische Netzwerk zeigte eine schiefsymmetrische Verteilung der Interaktionen sowie eine gewisse funktionale Komplementarität (kenntlich an den geringen Werten für Konnektanz und 'nestedness'). Die Säuger nutzten offene Habitate überproportional für die Samendeposition und steigerten ihre Ausbreitungsaktivität in den Landschaftssektoren ohne Wald. Kombiniert mit früheren Befunden zur Samenausbreitung durch Vögel legt diese Untersuchung nahe, dass es eine deutliche funktionale Komplementarität gibt, die aus der geringen Überlappung der hauptsächlich von Säugern bzw. Vögeln ausgebreiteten Pflanzentypen -namentlich Dornbüsche bzw. Bäume- und den unterschiedlichen Mustern der Samendeposition resultiert, wobei die Säuger meist in entwaldete Gebiete ausbreiten und die Vögel in waldreiche Landschaften.

Keywords: Ecosystem service; Fleshy-fruited plants; Functional complementarity, Mutualistic networks, Northern Spain; Plant–animal interactions

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Introduction

Seed dispersal by animals shapes both plant population dynamics in undisturbed habitats and vegetation recovery in disturbed areas (Howe & Miriti 2004). Due to its repercussions on human well-being, it is currently recognized as an ecosystem service dependent on mobile agents (Kremen et al. 2007). In fact, the magnitude and the quality of seed dispersal depend on both the abundance and the richness of frugivorous animals (García, Zamora, & Amico 2010; García & Martínez 2012). More importantly, the resilience of seed dispersal has been found to be affected by the heterogeneity among frugivores in their ability to withstand anthropogenic disturbances (i.e. response diversity; Elmqvist et al. 2003; García, Martínez, Herrera, & Morales 2013). Thus, comprehensive studies on the structural and functional diversity within whole plant–frugivore assemblages are essential to manage seed dispersal service in real-world landscapes (McConkey et al. 2012).

Fleshy-fruited woody plants are the main components of many temperate forest ecosystems, and their primary seed dispersers are small-to-medium sized birds (Jordano 2000). Temperate plant–bird assemblages sustain high numbers of species (e.g. Mello et al. 2012), but their seed dispersal service seems highly constrained by the landscape-scale availability of woody habitats and/or fleshy fruits (García et al. 2010). In addition to birds, large wild mammals may provide additional dispersal service to temperate woody plants (e.g. Grünewald, Breitbach, & Böhning-Gaese 2010; López-Bao & González-Varo 2011). Local guilds of mammalian seed dispersers may contain multiple functional types (from carnivores to ungulates, e.g. Grünewald et al. 2010; Matías, Zamora, Mendoza, & Hódar 2010) with the ability to range over heterogeneous habitats (López-Bao & González-Varo 2011; Matías et al. 2010). In fact, seed dispersal by wild mammals may reach even deeply degraded habitats (e.g. Rost, Pons, & Bas 2012). Thus, to ascertain the functional relevance of mammals as seed dispersers, and their degree of complementarity with other frugivore groups, it is necessary to simultaneously address the relative contribution of mammals to the dispersal of different woody plants, as well as the relationship between human-induced habitat heterogeneity and seed deposition (Schupp, Jordano, & Gómez 2010).

In this paper, we evaluate the role of wild large mammals as seed dispersers of fleshy-fruited woody plants in woodland pastures of the Cantabrian range (N Spain). Specifically, we first evaluate how extensive mammalian seed dispersal is in relation to plants with fleshy-fruits, by comparing the occurrence of seeds in mammal scats with that in fruiting crops. Second, we apply a network approach to identify the relative role that mammal species play in specific, but also community-wide, seed dispersal process. Third, we assess the response of mammalian dispersers to woodland loss, by relating seed deposition with forest availability at different spatial scales. We finally interpret the complementarity between mammals and birds as seed dispersers, taking into account that tree species are mostly dispersed by frugivorous thrushes whose function is strongly affected by woodland loss (Martínez, García, & Obeso 2008; García et al. 2013).

Methods

Study system and environmental framework

This study was conducted in mid-elevation woodland pastures of the Cantabrian range (Asturias region). This is a variegated habitat resulting from the historical loss and fragmentation of Atlantic temperate forests for extensive cattle raising (García et al. 2013). Woodlands contain variable-sized fragments of primary (beech *Fagus sylvatica* and oak *Quercus pyrenaica*) and, more frequently, secondary forest embedded in an extensive (>70% cover), human-promoted matrix of stony pastures and heathland. Secondary forest is dominated by fleshy-fruited plants, including trees (e.g. holly *Ilex aquifolium*, hawthorn *Crataegus monogyna*, yew *Taxus baccata*), treelets (e.g. elder *Sambucus nigra*), and thorny shrubs (e.g. bramble *Rubus ulmifolius/fruticosus*, wild rose *Rosa* sp.) which also occur occasionally in the deforested matrix. Fruits of these species are sugar-rich, 10–16 mm in diameter, and include berries (e.g. holly), aggregated drupelets (e.g. bramble), and arilate seeds (yew), and all ripen in autumn (Martínez et al. 2008).

Sampling was carried out in four localities where woodland, surrounded by pastures and heathland, covered <40% of the area (Sierra del Aramo, Puertos de Marabio, Sierra de Peña Mayor, Puerto de San Lorenzo; Fig. 1A; Appendix A: Table 1). In September 2010, we established three 500-m long linear transects arbitrarily placed to represent the complete variability in habitat structure of each locality (Fig. 1B). Transects were located at least 250 m from each other, covering altitudinal gradients less than 250 m, and were subdivided into twenty five 20-m long sections (Fig. 1C).

We sampled fruit abundance along transects in order to assess the availability of fleshy fruits and seeds produced by the woody community (i.e. standing fruit and seed crops). We estimated the number of fleshy fruits of each individual of all species present in a 10-m wide band on either side of each transect. We visually assigned crop values by means of a Fruit Abundance Index (FAI) considering six intervals: 0 = no fruits; 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10,000; 5 ≥ 10,001. Then, crops were extrapolated from FAI ranks following an allometric equation fitted to the actual crop size of a sub-sample of trees ($crop\ size = 1.77 \times e^{1.92FAI}$, $r^2 = 0.80$; $n = 130$ trees; Herrera, Morales & García 2011). According to the specific ripening phenologies, fruits were counted in September for most species, and in October for *I. aquifolium* and *C. monogyna*.

We developed a Geographical Information System (GIS) based on 1:5000-scale ortophotographs which included a layer of digitized forest cover from which we estimated the amount of forest cover (in m^2) on each transect section, considering 10-m and 20-m wide bands on either side of each transect (Fig. 1C). We calculated the forest proportion for each section, transect and locality.

Sampling of mammal scats

Transects were walked fortnightly from September 2010 to February 2011, searching for mammal scats on a 1.5-m wide band on each side of the transect axes. Every scat was collected and identified to species level (genus in *Martes* spp. and *Mustela* spp.) by criteria combining size, shape and scent. For herbivores, all pellet clumps separated by at least 2 m were considered as different scats. We also recorded the transect section and the microhabitat (below forest canopy or in open microhabitats like pasture, heath or rocky ground) where the scat had been dropped. Defecation by carnivores is typically biased toward human-made paths or roads (López-Bao & González-Varo 2011). Hence in order to compensate for a low scat collection derived from sampling in arbitrarily chosen transects, we also searched for scats over additional surfaces (ca. 1000 m × 3 m) along walking paths or dirt roads in each locality on the same survey dates. Scats were oven-dried at 60 °C for 1 week and, prior to analysis, they were washed in a 0.5 mm × 0.5 mm fine-meshed sieve. All undamaged seeds from fleshy-fruited plants were counted and identified to species level with the help of a seed reference collection from the study area.

Seed dispersal network

We used a quantitative network approach to evaluate the structure of interactions between fleshy-fruited plants and mammalian seed dispersers (Bascompte & Jordano 2007). The interaction network was based on a matrix of seed occurrence, with plant species as rows, mammal species as columns, and the number of dispersed seeds as cell counts. We pooled the number of seeds of each plant–mammal pair from all scats (those from sampling transects and the additional ones from paths) across localities through the whole season (Table S2).

Network structure was depicted with a bipartite graph, and evaluated with basic metrics chosen to represent complementary aspects of the structure of a mutualistic network, and, when possible, to be robust to constraints derived from small sample size (Blütghen, Fründ, Vázquez, & Menzel 2008; Dormann, Fründ, Blütghen, & Gruber 2009). We estimated *connectance* (*C*; the proportion of realized interactions from all potential interactions in the network), *nestedness* (*WNODF*; the degree to which the interactions of little connected species are a subset of those of highly connected species), *complementary specialization* (H'_2; a measure of niche complementarity between species), *generality* (*G*; weighted average number of dispersed plants per frugivore), and *vulnerability* (*V*; weighted average number of frugivores per plant). To test whether the metrics estimated for the empirical network differed significantly from networks with randomly interacting species, we compared the observed values with those of 1000 random networks based upon a Patefield null model (Dormann et al. 2009). All network analyses were carried out with the ‘bipartite’ library (Dormann et al. 2009) in R 2.9.1 (R Development Core Team 2011).

Habitat-seed dispersal relationships at multiple spatial scales

We tested the effect of forest availability (as an inverse gradient of forest loss) on the probability of mammalian seed dispersal at increasing spatial scales. First, at a fine, microhabitat scale, we checked if the probability of seed deposition below forest canopy agreed with that expected from microhabitat availability. We compared, by means of a χ^2-test, the proportion of dispersal events (i.e. scats containing at least one seed) occurring under forest canopy in the pool of scats found in sampling transects, with the proportion expected from the availability of forest canopy across all transects and localities. Second, at a local, landscape scale, we tested if the frequency of seed dispersal within each transect was affected by its amount of forest. For this, we built a Nominal

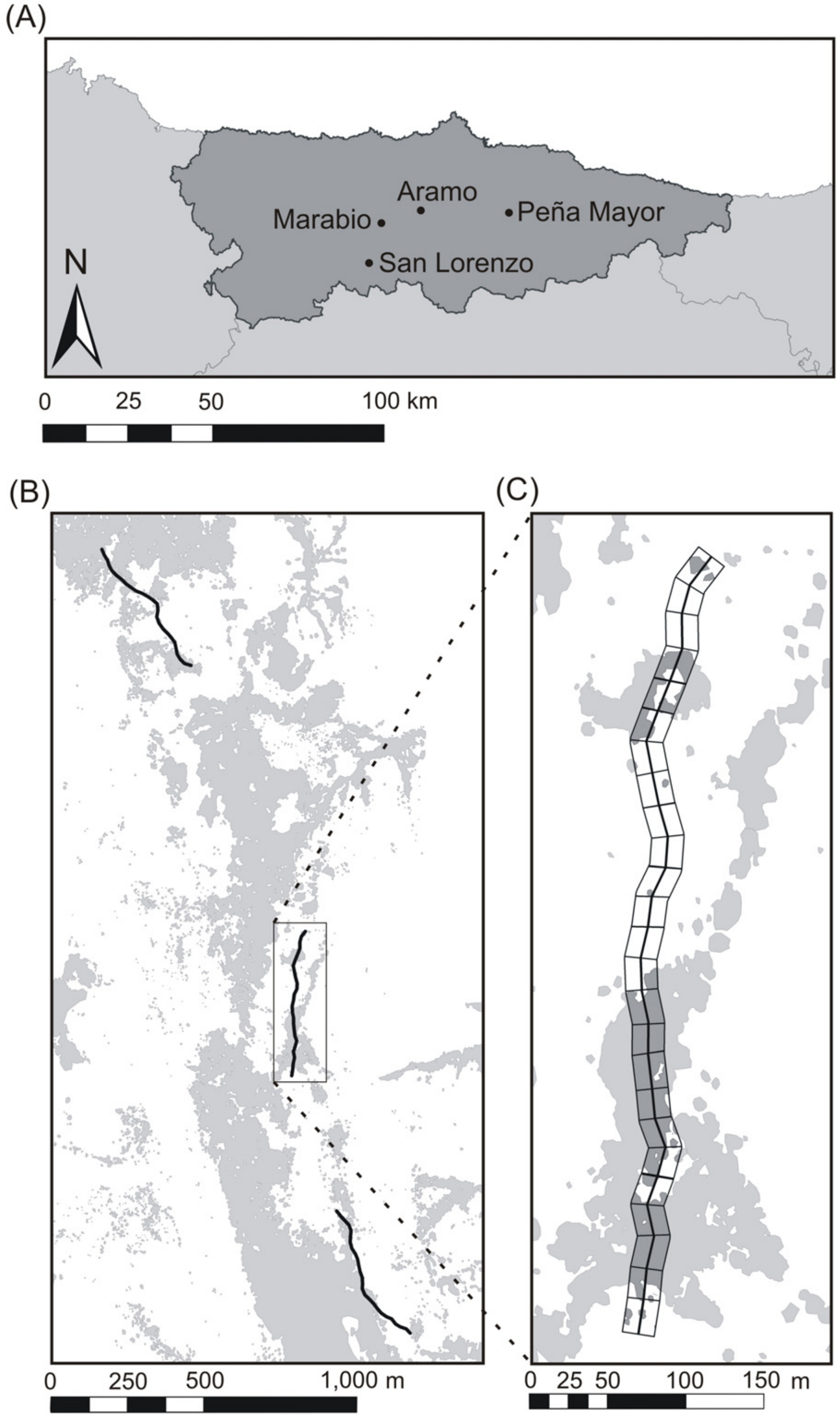

Fig. 1. Study framework showing: (A) the four sampling localities in the Asturias region (N Spain); (B) a map of the Sierra de Peña Mayor depicting forest cover (gray) within the pasture-heathland matrix (white), and sampling transects; and (C) a sampling transect highlighting 20-m long sections and 10-m wide bands where forest cover (dark gray) and fruit abundance were measured.

Logistic Model (NLM) including the occurrence of seed dispersal within each transect section as response variable, the proportion of forest cover in a 10-m wide band as main predictor, and both locality and transect (nested within locality) identities as blocking factors. Third, at a large, regional scale, we tested whether seed dispersal frequency was affected by forest cover over large spatial extents (the whole transects). To do so, we used a General Linear Model (GLM) considering individual transects as replicates, the frequency of seed dispersal within each transect as response variable, the

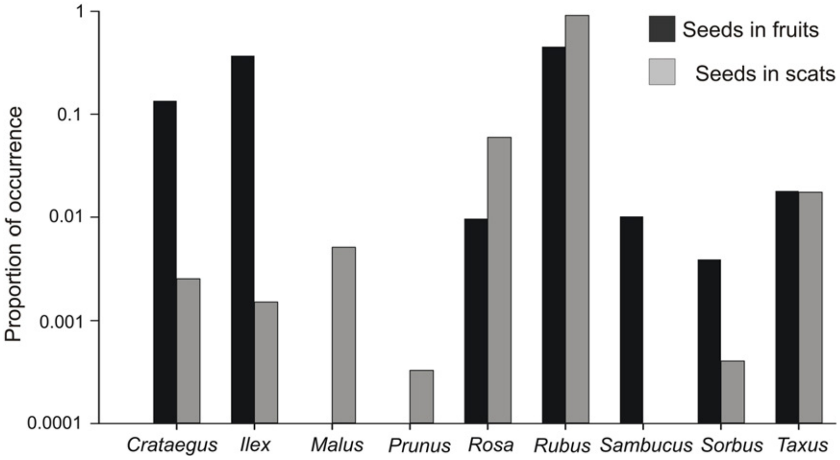

Fig. 2. Frequency of occurrence of seeds of fleshy-fruited plants, in standing fruit crops of plants (black), and in mammal scats (gray). Data were pooled across four localities.

proportion of forest cover in a 20-m wide band per transect as main predictor, and the locality as blocking factor.

Results

Field surveys provided 206 mammal scats (145 within transects) belonging mostly to four carnivores (56.7% of scats, in decreasing frequency of occurrence: red fox *Vulpes vulpes*, stone/pine martens *Martes* spp., badger *Meles meles*, stoat/weasel *Mustela* spp.) and three ungulates (41.4% of scats: wild boar *Sus scrofa*, roedeer *Capreolus capreolus*, red deer *Cervus elaphus*; Appendix A: Table 2). Intact seeds of fleshy-fruited woody species appeared in scats of all these frugivores. The frequency of occurrence of dispersed seeds was higher in carnivores (75.8% of scats) than in ungulates (30.6%; $\chi^2 = 42.7$, $p < 0.0001$). The quantity of seeds per dispersal event (i.e. scats containing at least one seed) varied strongly between plants and mammals (Appendix A: Table 3), although carnivores and ungulates did not differ in the average number of seeds per dispersal event (respectively 292 ± 73 SE and 501 ± 137 SE; $t = -0.92$, $p = 0.36$).

Seed availability and seed dispersal

The fleshy-fruits of seven woody species occurred along transects, with hawthorn *C. monogyna*, holly *I. aquifolium*, and bramble *R. ulmifolius/fruticosus*, proportionally bearing the largest fruit and seed crops (Appendix A: Table 1; Fig. 2). However, the pool of seeds of fleshy-fruits found in mammal scats differed from that found in standing crops ($\chi^2 = 872.9$, $p < 0.0001$) in that it was strongly dominated by bramble but

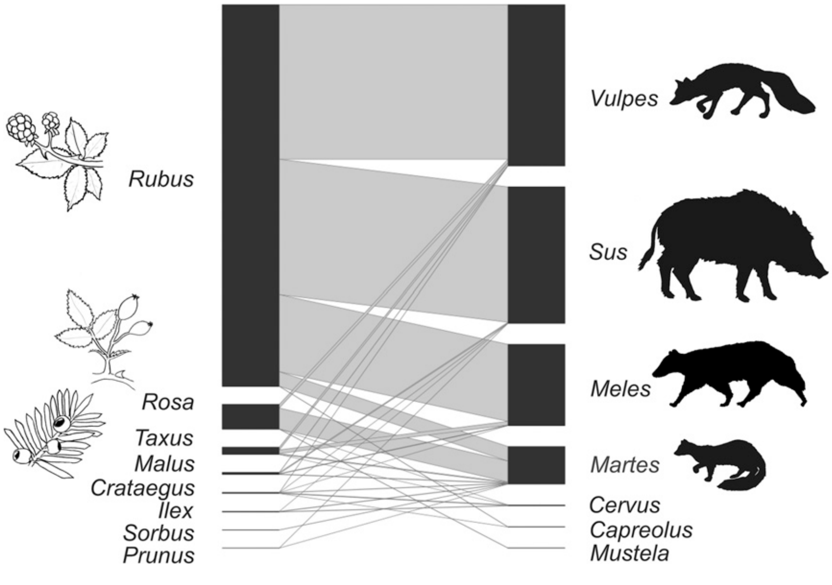

Fig. 3. Bipartite network graph representing the proportion of dispersed seeds of fleshy-fruited species (left black column), those dispersed by mammals (right black column), and, the proportion of dispersed seeds per plant and mammal (gray links; artwork by Daniel Martínez).

scarcely contained hawthorn and holly. Wild rose (*Rosa* sp.) seeds appeared in bigger proportions in scats than in standing crops, whereas yew (*T. baccata*) occurrence was proportional to their abundance in fruiting trees. Three species absent from the transects (apple *Malus* sp., wild cherry *Prunus avium* and blackthorn *Prunus spinosa*) did occur in scats.

Seed dispersal network

The bipartite network between fleshy-fruited plants and frugivore mammals showed strong biases in the distribution of interactions (Fig. 3; Appendix A: Table 2). The interactions of bramble with fox, wild boar, badger, and martens accounted for the majority of interactions in the seed dispersal network (91.2% of links). Most wild rose seeds were dispersed by martens, whereas yew seeds mostly occurred in badger scats. From the perspective of mammals, most species dispersed several plants, but the deposition of foxes, wild boars and badgers was strongly dominated by bramble. Martens showed a more diverse and balanced composition of defecated seeds, including many rare species (Fig. 3). Roedeer, red deer and stoat/weasel were occasional dispersers, mostly of the rarest plant species in the network (e.g. holly, hawthorn).

The seed dispersal network showed lower connectance (*C*) than expected by a null model (Table 1) as almost half of all potential plant–frugivore links were not realized (Fig. 3). Nestedness (*WNODF*) was also lower than expected (Table 1), derived from the fact that the interactions of little connected species (like holly or red deer) were poorly nested within those of highly connected species (like bramble or fox; Fig. 3). The degree of specialization within the network (H'_2) was higher than that from the null model, likely because rarer plant species were almost exclusively dispersed by occasional frugivores (i.e. complementarity within the network). Each frugivore dispersed, on average, four plant species, a raw value contrasting with a low level of generality (*G*, Table 1). Vulnerability (*V*) was higher than generality (but both metrics were lower than the null model), given that the occurrence of the different mammals within each plant was more evenly distributed than that of plants within each mammal (Table 1).

Habitat-seed dispersal relationships at multiple spatial scales

Most of the scats containing seeds occurred in open microhabitats in a frequency higher than expected from the availability of non-forest area within transects (91.6% vs. 71.0%, $\chi^2 = 10.7, p < 0.001$). However, the probability of dispersal was unaffected by the proportion of forest cover in transect sections (NLM: $\chi^2 = 0.62, p = 0.43; df = 1$), although it varied between transects (NLM: $\chi^2 = 29.21,\ p < 0.001; df = 8$) and localities (NLM: $\chi^2 = 20.28, p < 0.001; df = 3$). At a regional scale, the higher the proportion of forest cover per transect, the lower the frequency of dispersal events (Fig. 4; GLM: forest cover, $F_{1,7} = 11.95, p = 0.010$; locality, $F_{3,7} = 1.89, p = 0.22$).

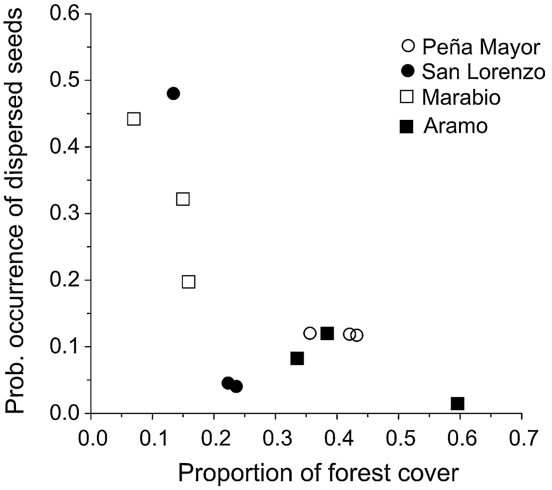

Fig. 4. Frequency of seed dispersal (i.e. proportion of transect units containing scats with dispersed seeds) as a function of forest cover. Values for each sampling transect and locality (as combinations of symbols and black/white fillings) are shown.

Discussion

Mammals as legitimate seed dispersers

Our study evidences the role of wild mammals as consumers of fleshy fruits in the temperate woodland pastures of the Cantabrian range (see also Martínez et al. 2008; López-Bao & González-Varo 2011). By covering a wide assemblage of fleshy-fruited woody plants and large mammals, we confirm carnivores as a major group of frugivores, but widen this trophic role to ungulates (as is found in other Mediterranean systems, Matías et al. 2010; Perea, Delibes, Polko, Suárez-Esteban, & Fedriani 2013). We consider all these mammals to be *legitimate* seed dispersers (*sensu* Jordano 2000), given that damaged seeds were only occasionally found in sampled scats (see also Perea et al. 2013), and high viability after gut passage is expected for most seed species (Matías et al. 2010; Rost et al. 2012).

As judged by the comparison of seed occurrence in fruiting crops and scats, mammal seed dispersal did not mirror community fruit availability (but see López-Bao & González-Varo 2011), given that seeds from abundant fruiting trees were scarce in scats whereas those from thorny shrubs were over-represented. The fact that fruits on high tree branches might actually be inaccessible to mammals cannot entirely account for this discordance, given that some species (martens) are good climbers, and many fallen fruits may be taken from the ground (e.g. Guitián & Munilla 2010). Feeding preferences, probably related to fruit size or composition (e.g. holly fruits are rich in toxic saponins; Barnea, Harborne, & Pannell 1993), might well underpin the skewed dispersal

Table 1. Metrics of the seed dispersal network between fleshy-fruited plants and mammals in the Cantabrian woodland pastures, together with mean values and lower and upper confidence intervals from 1000 networks calculated by a Patefield null model. Results of *t*-tests comparing observed and null-model values are also shown.

Metric	Estimate	Null model		t	p
		Mean	CI		
Connectance (C)	0.52	0.68	0.67–0.70	25.59	<0.0001
Nestedness ($WNODF$)	49.82	74.48	70.88–78.07	14.34	<0.0001
Specialization (H'_2)	0.52	0.0010	0.0008–0.0012	−6983.12	<0.0001
Generality (G)	1.30	1.4618	1.4617–1.4619	5557.98	<0.0001
Vulnerability (V)	3.16	3.6186	3.6184–3.6188	6222.69	<0.0001

patterns. Moreover, mammals brought into the study areas seed species absent in the sampled fruiting community. Some wild species (e.g. *Prunus* sp.) could have been present in the surroundings of transects, the cultivated apple seeds were most probably carried from distant orchards (Matías et al. 2010; Rost et al. 2012).

Dispersal network composition and structure

The network approach enabled the untangling of our plant–mammal assemblage, showing the composition of interactions to be strongly unbalanced. From the perspective of plants, the network was dominated by bramble, the remaining plants being rarer and showing more restricted disperser coteries. From the mammals' perspective, carnivores like fox and badger almost exclusively dispersed bramble, whereas martens mostly dispersed wild rose (see also Matías et al. 2010; López-Bao & González-Varo 2011). Our results also indicate wild boar to be a major disperser of bramble (Perea et al. 2013; but see Matías et al. 2010), and highlight that the occasional dispersal of trees (holly, hawthorn) was mostly accomplished by ungulates.

Concerning its global structure, the present dispersal network was similar to other mutualistic networks in terms of low connectance (Jordano 1987). Such a low connectance may be the result of a restricted number of observations in the network (Blütghen et al. 2008). Nevertheless, we consider that the absence of potential links derives here from mammal feeding preferences, rather than from spatio-temporal or trait mismatches between species (Bascompte & Jordano 2007). Moreover, the studied network showed a nestedness value lower than expected (see also Menke, Böhning-Gaese, & Schleuning 2012), and a specialization higher than expected from null models. Both metrics indicate some degree of niche differentiation and functional complementarity (Mello et al. 2012; Menke et al. 2012). In our case, the complementarity seems to emerge from frugivore diet segregation, leading the thorny shrubs to depend mostly on fox, badger and wild boar, whereas trees depend mostly on marten and ungulates. Finally, generality and vulnerability suggested that mammals were a more heterogeneous mutualistic resource for the plants than the plants for the mammals. It must though be recognized that the present dispersal network depicts only a partial view of the whole assemblage of fleshy-fruited plants and frugivorous vertebrates, which would also include birds (thrushes, Martínez et al. 2008). It is expected that, due to dietary differences (thrushes mostly feed on holly, hawthorn and yew; Martínez et al. 2008), a network explicitly incorporating birds would show lower connectance and nestedness, but a higher modularity than those described here (e.g. Mello et al. 2012).

Seed deposition by mammals and forest loss

The present work further demonstrates that seed dispersal by mammals depended on forest availability at different spatial scales. At the fine scale, mammals overused uncovered microsites for seed delivery (see also Jordano, García, Godoy, & García-Castaño 2007; Martínez et al. 2008). This spatial bias scaled-up to the regional extent, as wild mammals increased their activity as dispersers in those sectors devoid of forest (see also Escribano-Ávila et al. 2012). The spatial pattern cannot be attributed to the feeding preference of mammals for thorny shrub fruits given that these fruits were actually more abundant in forest-rich areas (data not shown). Alternatively, the scent marking behavior of carnivores, with selective defecation in open and conspicuous sites such as on stones and at path edges, and the extensive use of anthropic landscape mosaics by mammals (Grünewald et al. 2010; López-Bao & González-Varo 2011; Escribano-Ávila et al. 2012) could explain this multi-scaled spatial bias.

Concluding remarks

Combining the present results of seed dispersal by mammals with those previously reported for frugivorous birds in the same ecosystem (Martínez et al. 2008; García et al. 2013), we may conclude that a strong functional complementarity exists between mammals and birds as suppliers of seed dispersal service (Jordano et al. 2007; Escribano-Ávila et al. 2012). Complementarity would emerge, first, from a restricted overlap in the main plant types that mammals and birds disperse: shrubs and trees, respectively, and second, from the differential seed dispersal patterns, with mammals mostly dispersing into deforested areas, and birds into forest-rich sites. Differences in seed dispersal effectiveness (*sensu* Schupp et al. 2010), derived from seed clumpiness (as mammals seem to defecate more seeds per scat than birds; Martínez et al. 2008), could somehow offset complementarity between birds and mammals in demographic terms. Nonetheless, by increasing the species diversity in the community seed pool, as well as the diversity in the response of seed dispersal to forest habitat loss, mammals appear to enhance the resilience of this ecosystem service in the human-modified landscapes of the Cantabrian range.

Authors' contributions

Designed the study: DG, DM; Collected the data: AP, DM; Analyzed the data: DG, JRP, DM; Wrote the manuscript: DG; Revised the manuscript: AP, DM, JRP.

Acknowledgements

Funding was provided by the Spanish Government and the European Social Fund (MEC Collaboration Grant to AP, FPI grant to DM, CGL2011-28430 grant to DG) and by the Government of Asturias (PCTI IB08-039 grant to DG). V. Lendrum revised the English.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2013.05.003.

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