



Changes in the fruiting landscape relax restrictions on endozoochorous tree dispersal into deforested lands

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Keywords

Frugivorous birds; Landscape structure; Mobile links; Montane pastures; Recolonization; Rewilding; Seed dispersal; Temperate forest

Nomenclature

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Abstract

Question: Passive forest restoration is based on the natural recovery of degraded habitats. However, tree recruitment is frequently hampered in deforested lands. Tree seed dispersal is scarce and spatially constrained, confining the potential of forest regeneration to a narrow band surrounding forest remnants. Understanding how landscape configuration can favour endozoochorous seed dispersal into deforested lands is thus crucial to recover forest extent and the concomitant ecosystem services. Can distance restrictions on seed dispersal be modified as a result of temporal variability of fruit–frugivore systems?

Location: Deforested montane pastures surrounding fragments of secondary temperate forest, Cantabrian Range, Spain.

Methods: For 2 yr, we evaluated the patterns of fruit production, frugivorous bird movement and tree seed dispersal through the landscape. Seed dispersal in deforested sampling stations was related to their distance to forest cover and the amount of forest cover in their surroundings.

Results: The large-scale spatial distribution of fruits varied strongly between years, with relatively higher fruit production in isolated trees within pastures in the second year, when birds were more frequently observed perching on isolated trees. In both years, few seeds were dispersed into deforested areas, and those dispersed occurred close to forest cover. Nevertheless, seed arrival at longer distances increased during the second year. When more fruits were produced within the pastures, birds more often overcame their reluctance to leave the forest, and this change in frugivore foraging patterns cascaded into the spatial patterns of seed dispersal.

Conclusions: By influencing frugivore activity, temporal dynamism in fruiting landscapes can relax the restriction on tree seed dispersal into deforested areas. Landscape biological dynamism should be taken into account in order to manage rewilding in European temperate forests.

Introduction

The extent of European natural forests has been severely reduced due to historical exploitation for timber and firewood, clearing for pastures and arable lands and their replacement with timber plantations (Darby 1956; Behre 1988; Kaplan et al. 2009). However, the current abandonment of montane rural areas throughout Europe (MacDonald et al. 2000; FAO 2011), and the concomitant release of fertile ground once devoted to extensive traditional practices, is opening up opportunities for natural forest recovery (Navarro & Pereira 2012). Understanding and

favouring this rewilding process is crucial to recover the ecosystem services provided by forests (ranging from climate modulation or soil stabilization to CO₂ storage; Myers 1997; Chazdon 2008), especially in the context of global change mitigation (Bonan 2008).

Passive restoration is based on the natural, unassisted recovery of forests affected by disturbance, once the disturbance agent disappears (Rey Benayas et al. 2008; Holl & Aide 2010). Allowing natural succession in abandoned lands can be the simplest way to recover forest, but this process is often spatially restricted, slow in time, deflected or may even be arrested (Martínez-Garza & Howe 2003;

Cramer et al. 2008). Therefore, understanding the ecological factors limiting seed dispersal and deposition is crucial for managing forest recolonization.

Both the rate and the composition of forest recovery depend on the different environmental filters affecting the initial stages of the tree regeneration cycle in the disturbed environment (e.g. factors driving dispersal, predation and germination of seeds, and survival of seedling and saplings; Holl et al. 2000). As the first step in tree regeneration, effective seed dispersal from remnant forests to abandoned lands has been described as one of the main limiting processes in forest recovery in both tropical and temperate regions (e.g. Debussche & Lepart 1992; Holl et al. 2000; Duncan & Chapman 2002; Bustamante-Sánchez & Armesto 2012). Seed arrival in deforested lands depends mostly on two landscape features, namely, the distance from seed sources to recovering sites and the quantity of surrounding seed sources, usually represented by the amount and spatial configuration of cover of remnant forest (Kunstler et al. 2007; Rey Benayas et al. 2008; García et al. 2010; Holl & Aide 2010). As a generalized spatial pattern, seed input typically declines sharply with distance from forest patches (Willson & Crome 1989; Aide & Cavelier 1994; Cubiña & Aide 2001) and, consequently, dispersal limitation restricts further forest regeneration to a narrow band surrounding the remnant forest cover (Günter et al. 2007). Such a distance constraint occurs even in those plants dispersed by animal vectors, as frugivorous animals frequently show behavioral barriers to forage in open areas, far from forest cover (Cardoso da Silva et al. 1996; Duncan & Chapman 2002; García et al. 2010). The presence of isolated trees standing in pastures, offering fruits or perching sites, can encourage frugivores to leave the forest (McDonnell & Stiles 1983; Cardoso da Silva et al. 1996; Duncan & Chapman 2002) and disperse seeds into the deforested matrix more often (Herrera & García 2009; Carlo et al. 2013). However, even in these cases, seed deposition is restricted to the area beneath the canopy of remnant trees, resulting in a pattern of cover-nucleated seed rain similar to that found in forest areas (Duncan & Chapman 1999; Carrière et al. 2002; Bustamante-Sánchez & Armesto 2012).

When studying the potential of animal-generated seed dispersal for passive restoration, we have to consider that plant–frugivore interactions are inherently variable in space and time (Levey & Benkman 1999; Jordano 2000). Inter-annual variation typically occurs both in quantity of fruits and their large-scale spatial distributions (i.e. the fruiting landscape), which should have a strong influence on foraging patterns of frugivores. As such, this source of landscape-scale dynamism often leads to important variations in the magnitude of seed dispersal in fragmented landscapes (Hampe et al. 2008; García et al. 2013; Perea

et al. 2013). For example, seed dispersal is strongly biased to large forest patches when fruits mostly occur in dense forests, but it is enhanced under isolated trees when they mast, which contribute to widening the distribution of fruits across the whole landscape (Herrera & García 2009). Previous studies have shown that inter-annual changes in fruiting landscape may increase the probability of seed dispersal from forest into pastures (García et al. 2013). Nevertheless, no study has yet explicitly evaluated how the temporal dynamism of fruit–frugivore systems modulates the distance constraint of seed dispersal into deforested land. We hypothesize that distance constraints on seed dispersal should weaken when fruiting landscapes widen the foraging ranges of frugivores.

In this paper, we evaluated the spatio-temporal variability in tree fruit availability, frugivorous bird abundance and activity, and tree seed dispersal by birds from forest patches to the surrounding matrix of deforested pastures, in a fragmented landscape of the Cantabrian Range. Specifically we sought to answer the following questions: (i) does the landscape context, in terms of forest cover extent and isolation, affect seed arrival at pastures; (ii) do these landscape–context effects change between years; and if so, (iii) can inter-annual changes in seed dispersal be interpreted as a result of the different responses of birds to the fruiting landscape?

Methods

Study system

Our study system is the temperate secondary forest of the Cantabrian mountain range (northern Spain). This is a common but low-cover habitat (García et al. 2005a) occurring as fringe patches adjacent to mature stands (mainly composed of *Fagus sylvatica*) and as variable-sized fragments or isolated remnant trees embedded in a dominant (>70% cover) matrix of stony pastures and heathlands (*Erica* spp., *Ulex europaeus*; pastures hereafter) used for extensive livestock grazing (mainly cattle and horses).

Secondary forest is dominated by the fleshy-fruited tree species hawthorn (*Crataegus monogyna*), holly (*Ilex aquifolium*), yew (*Taxus baccata*), rowan (*Sorbus aucuparia*) and whitebeam (*Sorbus aria*), accounting for more than 70% of tree cover (García et al. 2013), as well as hazel (*Corylus avellana*). Fleshy-fruited tree species show an overlapping ripening period in early autumn, with their fruits (arilated seeds on *T. baccata*) staying on trees until mid-winter. The regeneration of these tree species depends primarily on the availability of dispersed seeds (i.e. demographic dispersal limitation) in the study system (García et al. 2005b). Their main frugivores are thrushes (*Turdus* spp.; Martínez et al. 2008), which swallow the entire fruits, expel the intact seeds in their faeces, and hence act as legitimate seed

dispersers (Jordano 2000). Seed dispersal by frugivorous birds is considered a major demographic driver for fleshy-fruited trees in the Cantabrian Range (García et al. 2005b). The activity of these birds is highly influenced by forest cover, such that there is a much lower probability of seed arrival in non-forested habitats than under forest cover (García et al. 2013). Mammals like badger (*Meles meles*), fox (*Vulpes vulpes*) and marten (*Martes* spp.) contribute to tree seed dispersal, although with much lower quantitative relevance than thrushes (Martínez et al. 2008; Peredo et al. 2013).

Study site

The study site was located in the Sierra de Peña Mayor (1000 m a.s.l.; 43°17'59" N, 5°20'29" W Asturias, north-west Spain). At this site, secondary forest is intermingled with mature forest within a dominant non-forested matrix. The study was conducted within a 400 m × 440 m rectangular plot (Fig. 1a) mainly covered (ca. 70%) by pastures, heathlands and limestone rocky outcrops, where secondary forest cover varies from dense stands to scattered trees isolated within the non-forested matrix (García & Martínez 2012). Thus, from the perspective of pastures as sites of seed deposition, the plot represents a wide range of contexts that differ in their quantity of, and their distance to, surrounding forest cover. Previous studies have proven the suitability of the spatial extent of the study plot to represent landscape-scale patterns of habitat cover, fruit production, bird activity and seed dispersal (Herrera et al. 2011b; García & Martínez 2012; Carlo et al. 2013; García et al. 2013). For better management of spatial information, the plot was subdivided into 440 20 m × 20 m cells. The study was carried out over two consecutive years: autumn–winter season 2009–2010 and 2010–2011 (hereafter, 2009 and 2010, respectively).

Forest cover and fruit counts

We developed a geographic information system (GIS, ArcGIS9.3; ESRI, Redland, CA, US) of the study plot based on a recent (2009) 1:5000-scale orthophotograph. We generated a layer with precise geo-referenced information related to the plot, including the grid of 440 20 m × 20 m cells (Fig. 1a). Another GIS layer was generated representing the extent and location of forest cover by carefully digitizing it from the orthophotograph and verifying it afterwards in the field. The forest cover layer included the canopy projection of all trees (DBH > 10 cm, height > 1.5 m), including that of isolated individuals within pastures.

In October of both sampling seasons, we surveyed the entire plot, mapping all trees and identifying them to

species level. For each fruiting individual, we visually estimated the number of standing fruits by using a semi-logarithmic scale (*Fruit Abundance Index* FAI: 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10000; 5 > 10000). In the system and site studied, fruiting of all individuals of the different study species is synchronous and ripening occurs within 1–2 mo (although fruits remain attached to trees for a further 1–3 mo). Thus, we considered that a single sampling of fruit abundance at the beginning of the season provided an appropriate estimate of the spatial arrangement of fruit resources (García et al. 2013).

Then, using the GIS, we calculated the area of forest cover and fruit abundance in each of the 440 cells. Fruit abundance was obtained as the sum of the crop sizes of all the fruiting trees in a cell. The crop sizes of the fruiting trees were extrapolated from FAI ranks, taking into account the fit between the actual crop size of a subsample of trees and FAI, by following an allometric equation ($actual\ crop\ size = 1.765^{(1.924 \cdot FAI)}$; $R^2 = 0.80$; $N = 136$; Herrera et al. 2011a).

Bird censuses

We performed bird observations in the study plot to estimate the abundance and the spatial distribution of frugivorous birds (*Turdus* spp.) in the different cells of the study plot during the fruiting season each year. Observations of thrushes were made from vantage positions covering large high-visibility areas, and from positions within the forest for more reduced areas, where bird detectability was lower. Observations were made with the time being balanced between the various positions throughout each season. We assigned each bird sighting to the cell of the study plot where it happened, and to one of the following microhabitats (Fig. 1d–f): forest (when the bird occurred perching in a tree within the main forest cover), remnant tree (when it perched in isolated trees within the pastures) and open ground (when it landed on the pasture, with no tree cover at all). The abundance of birds per cell was calculated as the cumulative number of birds detected in each cell during the season divided by the total observation time for each cell, calculating the number of birds per 10 hr of observation. Similarly, after classifying all bird observations by the three different perching microhabitats, the same procedure was employed to calculate the number of birds per cell in different microhabitats. For detailed information on the methodology of bird censuses see Appendix S1 (see also García & Martínez 2012; García et al. 2013).

Sampling of dispersed seeds

We assessed seed deposition by birds in sampling stations across the whole plot in 2009 and 2010. Ten sampling

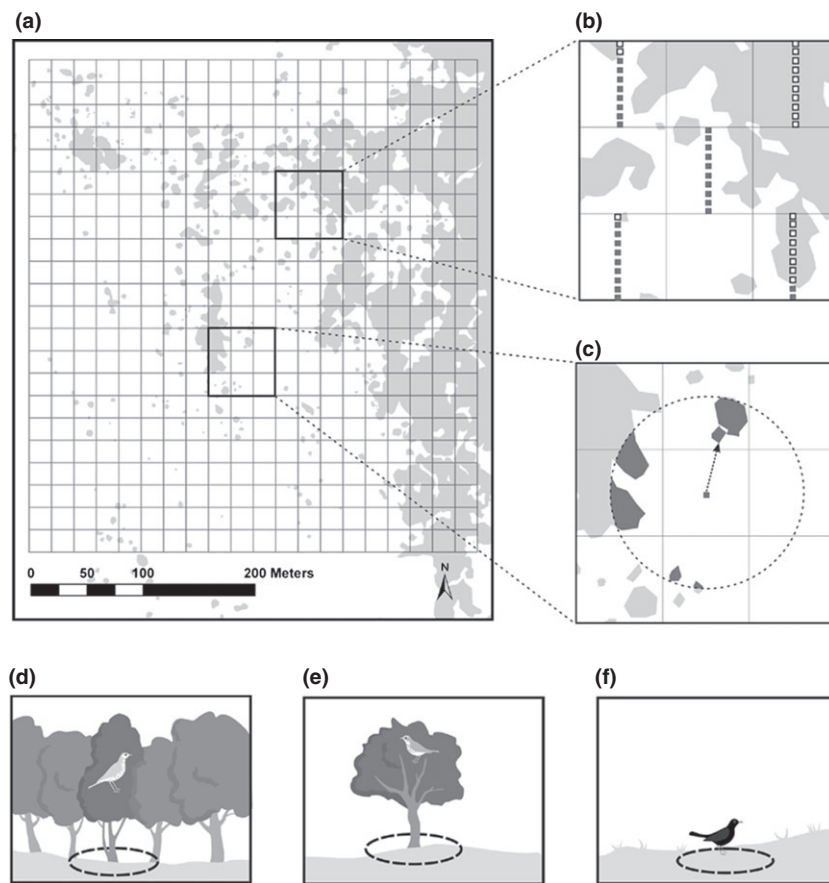


Fig. 1. (a) Map of the study plot, subdivided into 20 m × 20 m cells, showing the extent of forest cover (light grey area). (b) Detail showing the checkerboard design for seed dispersal sampling. Sampling stations located in open microhabitats are represented as dark grey quadrats, while those under forest cover are in white. (c) Detail representing the forest context metrics for an open sampling station (dark grey quadrat): minimum distance to forest cover (dashed arrow) and forest cover extent (dark grey) in a surrounding 25-m radius circumference. (d–f) Different microhabitats considered for bird observations.

stations, separated from each other by 2 m, were placed along the central north–south axis of half (220) the cells of the plot, selected following a checkerboard design (i.e. every second cell; Fig. 1b). In each station, we set a permanently labelled 50 cm × 50 cm quadrat on the ground, and all fleshy-fruited tree seeds deposited by birds found within it were collected and counted. Bird-dispersed seeds are unequivocally identifiable: they are clean of pulp remains, unlike seeds in fruits fallen beneath trees, and occur in small clusters easily distinguishable from those occurring in mammal feces, and they can be almost exclusively attributable to thrushes (Martínez et al. 2008). 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), and further expressed this density as number of seeds per m². According to the structural characteristic of the cover where each quadrat was located, we determined the microhabitat of the sampling station, assigning it to the category of either

covered (under woody canopy) or open (uncovered by woody canopy) (Fig. 1b). This design resulted in 541 sampling stations in covered and 1659 in open microhabitat. Previous work has demonstrated that the removal of dispersed seeds by predators like rodents from quadrats is low, especially in open microhabitats (García et al. 2005b). No secondary dispersal agents are known for these seed species in the study system.

Characterization of forest context around sampling stations

The position of all sampling stations was geo-referenced and introduced as a layer in the GIS. For each open microhabitat sampling station we estimated (from the GIS) *distance to forest* (m) as the linear distance to the nearest forest cover, and *forest cover* (m²) as the area covered by forest in a 25-m radius extent around each station (Fig. 1c). Previous studies have proven this radius to be an appropriate scale

to simultaneously represent variability in habitat cover and seed dispersal across a local landscape (García & Chacoff 2007; Carlo et al. 2013).

Statistical analysis

Fruit abundances in the study plot were compared between years (2009–2010) using generalized linear models (GLMs) with a quasi-Poisson distribution of errors and *log* link function. To describe the distribution of fruits along a gradient of forest cover, we grouped the cells into exclusive categories according to the extent of forest cover on them, considering four consecutive 100-m² span intervals (i.e. 0–100, ..., 301–400 m²), and summed the fruit abundance from all cells within each category. We compared the distributions of fruits between years using a χ^2 test.

Between year differences in bird abundance at the whole plot scale were checked using GLMs (quasi-Poisson distribution, *log* link). Similar models were applied to each of the cell subsamples corresponding to the different perching microhabitats.

Two descriptors of seed dispersal were considered: *seed arrival* (presence/absence of seeds in a given sampling station) and the *number of dispersed seeds* per sampling station. Between year variations in seed dispersal at the whole plot scale were analysed using GLMs (binomial distribution and *probit* link for seed arrival; quasi-Poisson distribution and *log* link for number of dispersed seeds). The model for number of dispersed seeds considered only those sampling stations containing any dispersed seeds.

We sought to examine the effect of forest context on seed dispersal into open habitats across years. Due to the correlation between distance to forest and forest cover (Pearson correlation: $r = -0.85$, $P < 0.0001$, $N = 1659$), we constructed independent GLMs for these two variables. These models only included sampling stations in open microhabitats. We first assessed how seed arrival was affected by the distance to forest, the year and the interaction *distance* \times *year* (binomial distribution, *probit* link function). A second model considered as predictors forest cover, year and the interaction *forest cover* \times *year*. Then, two equivalent GLMs (quasi-Poisson distribution, *log* link) were applied to the number of dispersed seeds as a response variable. Predictor variables were standardized in all models. The present sampling design may suffer from spatial non-independence in the estimation of landscape effects on seed dispersal, given that the study plot represented a gradient of forest cover (Fig. 1a), and that sampling stations were clustered on a per cell basis (Fig. 1b). Thus, in order to obtain estimates of main effects in GLMs that were free of spatial autocorrelation bias, we applied a spatial eigenvector mapping approach (SEVM; Griffith & Peres-Neto 2006; Dormann et al.

2007). This methodology explicitly accounts for the influence of space in the dependent variable by including these spatial effects as additional independent variables in GLMs. For a given original GLM, uncorrelated explicative eigenvectors are obtained from the decomposition of the spatial autocorrelation (SAC) found in model residuals, using the eigen function decomposition of spatial connectivity matrices (Griffith & Peres-Neto 2006). Once obtained, eigenvectors are sequentially added to the GLM model until no significant SAC is found in the residuals (measured as Moran's *I* statistic). A final GLM model is then recalculated, including the matrix of selected eigenvectors as additional predictors.

When significant interaction terms (*distance* \times *year*, *forest cover* \times *year*) occurred in the GLMs above, *a posteriori* analyses were performed to compare seed dispersal between years, at different sections of the gradients of distance or forest cover. To do that, we sub-divided the distributions of *distance to forest* and *forest cover* into three different categories (short, medium and long for distance; low, medium and high for cover). We considered short/low values as those ranging from 0 to the respective medians of the distribution of distance and cover. Medium values were grouped from above the median to the 90th percentile. Those values above 90% of the distribution were considered long/high (Fig. 3; Appendix S2, Fig. S2.1). Inter-annual differences in seed arrival and in the number of dispersed seeds were checked using Fischer tests for each section of the respective distance and forest cover gradients. All analyses were performed using R 2.15 (R Foundation for Statistical Computing, Vienna, AT), with *spdep* package for SEVM.

Results

Fleshy-fruited trees in the plot were mainly *I. aquifolium* and *C. monogyna* (1663 and 662 trees, respectively), accompanied by a low number of *T. baccata* individuals (103 trees). The extent of forest cover in the plot remained constant during the study. Total fruit abundance was similar between years in the study plot (Table 1; GLM: $t = 0.65$, $P = 0.52$; $df = 879$), but the relative contribution of the different tree species varied between years (GLM: $t = -6.31$ for *I. aquifolium*, and $t = 9.68$ for *C. monogyna*; $P < 0.0001$; $df = 879$). *I. aquifolium* accounted for 81.2% of total fruit abundance in 2009, but only 25.5% in 2010, when *C. monogyna* was numerically dominant (Fig. 2). *T. baccata* fruits accounted for <10% of total fruit abundance, with no differences between years (GLM: $t = 0.82$, $P = 0.41$, $df = 879$). Associated with the variation in the fruit availability of different plant species, the distribution of fruits along the gradient of forest cover also changed from year to year ($\chi^2 = 3.12 \cdot 10^6$, $P < 0.0001$, $df = 3$).

Table 1. Summary of abundance of fruits and frugivorous birds, rate of seed arrival and the abundance of dispersed seeds for different study years; average values are shown \pm SE. Fruits: number of fruits m^{-2} cell $^{-1}$. Birds: abundance of frugivorous birds cell $^{-1}$ 10 hr $^{-1}$, and abundance in different microhabitats. Seeds: Seed arrival rate as the percentage of sampling stations showing dispersed seeds (from a total of 2200 stations), and their arrival in forest (541 stations) and open (1659 stations) microhabitats. Number of dispersed seeds per m^2 for all sampling stations, and distinguishing between stations in covered and open microhabitats.

Year	2009	2010
Fruits		
No. Fruits m^{-2}	17.4 \pm 1.5	18.8 \pm 1.5
Birds		
No. Birds 10 hr $^{-1}$	3.79 \pm 0.46	2.25 \pm 0.39
Forest	3.34 \pm 0.46	1.87 \pm 0.39
Isolated Tree	0.33 \pm 0.06	0.31 \pm 0.05
Open	0.12 \pm 0.03	0.07 \pm 0.01
Seeds		
Seed Arrival	39.4%	34.6%
Covered	72.4%	64.3%
Open	24.7%	21.5%
No. Dispersed Seeds m^{-2}	62.5 \pm 5.4	27.0 \pm 2.7
Covered	205.5 \pm 20.5	88.4 \pm 10.3
Open	3.2 \pm 0.3	2.8 \pm 0.3

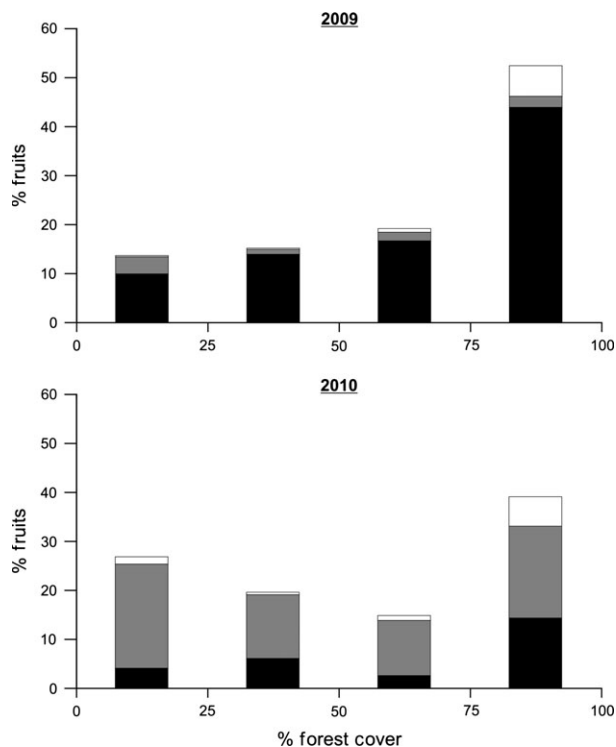


Fig. 2. Percentage of each fruit, as a proportion of total fruit production, produced in cells of different categories of forest cover in the study plot, for both study years. Each bar is subdivided into the proportion of fruits produced by *T. baccata* (white), *C. monogyna* (grey) and *I. aquifolium* (black).

Namely, fruit abundance was mostly concentrated in areas with high forest cover in 2009, whereas it was more widely distributed in 2010, with fruits appearing in areas with both high and low forest cover (Fig. 2).

The abundance of frugivorous birds was significantly lower in 2010 than in 2009, at the whole plot scale (GLM: $t = -2.48$, $P = 0.01$, $df = 879$; Table 1). When considering bird abundance in the different microhabitats, a lower number of birds was found in forest in 2010 relative to 2009 (GLM: $t = -2.48$, $P = 0.01$, $df = 351$; Table 1), but abundances were similar between years in remnant trees and in open ground (GLM: $t = -0.26$, $P = 0.8$, $df = 283$ for remnant trees; $t = -1.55$, $P = 0.12$, $df = 653$ for open ground; Table 1). While bird sightings in forest accounted for 88.3% of the total abundance in 2009, this decreased to 83.2% in 2010. Conversely, the proportion of birds observed in remnant trees increased from 8.7% in 2009 to 13.6% in 2010.

We found a total of 34,375 dispersed seeds in sampling stations during 2009 and 14,850 during 2010. The arrival of dispersed seeds decreased from 2009 to 2010 (GLM with SEVM approach: $z = -3.76$, $P < 0.001$, $df = 4399$; Tables 1, 2). The pattern for the number of dispersed seeds was similar (GLM: $t = -5.63$, $P < 0.0001$, $df = 1623$; Tables 1 and 2). Both decreasing trends were stronger under forest cover than in open microhabitats (Table 1).

Seed arrival in open microhabitats was negatively affected by distance to forest, drastically declining with distance from the forest, but it was similar between years (Table 2). A significant interaction between distance and year also occurred (Table 2). *A posteriori* analyses showed that this interaction resulted from a decrease in seed arrival at short distances but an increase at long distances in 2010, when compared to 2009 (Fisher tests: short distances: odds ratio = 0.73, $P = 0.004$; medium distances: odds ratio = 0.78, $P = 0.07$; long distances: odds ratio = 2.64, $P = 0.03$; Fig. 3a). The pattern for forest cover was similar (Table 2; Fisher test: low cover: odds ratio = 2.36, $P = 0.03$, medium cover: odds ratio = 1.04, $P = 0.86$, high cover: odds ratio = 0.63, $P < 0.0001$; Fig. 3b).

As shown for seed arrival, the number of seeds dispersed into open microhabitats decreased sharply with distance to forest edge, and was also significantly higher when the sampling stations were surrounded by high forest cover (Table 2). No effects of year or interaction between forest context descriptors and year were found (Table 2).

Discussion

In this study, we evaluated the patterns of bird-generated, community-wide seed dispersal into deforested habitats

Table 2. Effects of distance to forest and forest cover (evaluated by independent analyses) on (A) seed arrival and (B) number of seeds dispersed into open microhabitats. Year was included as a predictor variable for both seed dispersal descriptors. Spatial eigenvectors (obtained by SEVM) describing the spatial autocorrelation of the response variable were included as predictors only for seed arrival. Maximum likelihood estimates, their SE, values of the z and t statistics and P-values are shown. R^2 is shown for every model.

(A) Seed Arrival				
	Estimate	SE	z	P
Distance to Forest $R^2 = 0.13$				
Intercept	-1.592	0.080	-19.9	<0.001
Distance to Forest	-1.043	0.107	-9.7	<0.001
Year	-0.122	0.109	-1.1	0.262
VecC1	-0.343	0.060	-5.7	<0.001
VecC2	-0.238	0.049	-4.8	<0.001
VecC3	-0.197	0.052	-3.8	<0.001
Distance × Year	0.331	0.142	2.3	<0.001
Forest Cover $R^2 = 0.14$				
Intercept	-1.587	0.078	-20.2	<0.001
Forest Cover	1.154	0.091	12.6	<0.001
Year	-0.047	0.106	-0.4	0.658
VecD1	-0.292	0.052	-5.6	<0.001
VecD2	-0.188	0.051	-3.7	<0.001
Cover × Year	-0.506	0.117	-4.3	<0.001
(B) Number of Seeds Dispersed				
	Estimate	SE	t	P
Distance to Forest $R^2 = 0.12$				
Intercept	1.062	0.058	18.2	<0.001
Distance to Forest	-0.247	0.073	-3.4	<0.001
Year	-0.119	0.088	-1.3	0.180
Distance × Year	0.102	0.100	1	0.311
Forest Cover $R^2 = 0.16$				
Intercept	1.033	0.059	17.5	<0.001
Forest Cover	0.293	0.069	4.2	<0.001
Year	-0.082	0.088	-0.9	0.353
Cover × Year	-0.107	0.095	-1.1	0.262

(i.e. pastures) in a temperate, montane locality of the Cantabrian Range. The characteristics of the forest context surrounding pastures highly influenced seed dispersal. This main result accords with those from tropical forest ecosystems, where animals dispersed low proportions of tree seeds into pastures, and deposited most seeds in areas surrounded by high levels of forest cover, and, in addition, close to the cover (Willson & Crome 1989; Aide & Cavaler 1994; Cubiña & Aide 2001). Nevertheless, we found that this restriction was relaxed in one of the study years, resulting in a higher proportion of seeds being delivered into pastures and at further distances from forest cover. We argue that this variation in the effects of forest context resulted from the temporal dynamism of the plant–frugivore system, with frugivore foraging varying in response to inter-annual changes in the fruiting landscape.

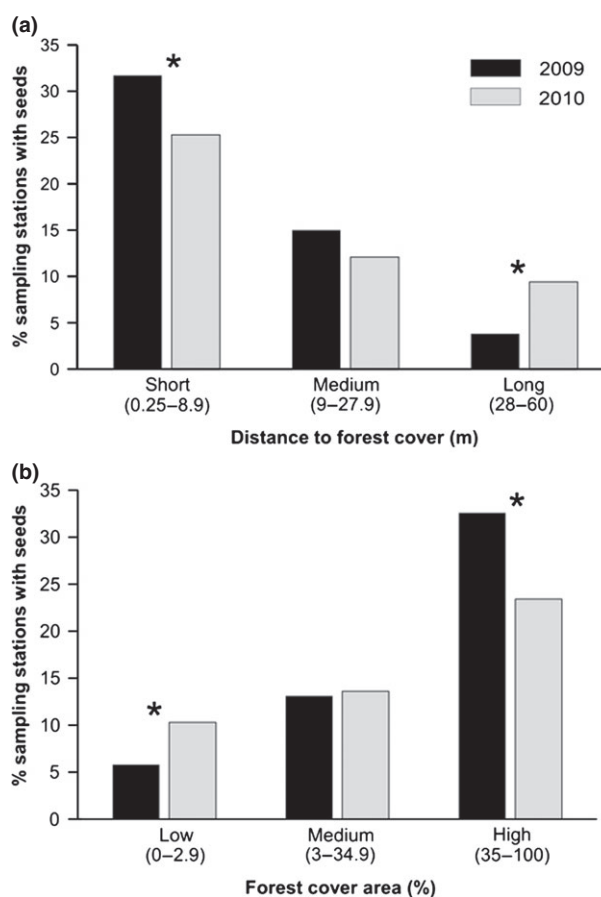


Fig. 3. Seed arrival (percentage of sampling stations receiving dispersed seeds) in different categories of distance to forest (a) and forest cover (b) for different years. Between year differences in a given category after a Fisher test are highlighted (* $P < 0.05$; n.s.: $P > 0.05$).

Patterns of seed dispersal into pastures

In this study, frugivorous birds carried seeds into less than 25% of the sampling stations in pastures, but to more than 65% of stations under forest cover (Table 1). Similar to previous findings (e.g. Kollmann & Pirl 1995; Holl et al. 2000; Duncan & Chapman 2002), we found that seeds not only arrived at fewer sites in pastures, but were also deposited there in considerably lower numbers. In fact, the quantity of seeds arriving in open areas was two orders of magnitude lower than under forest cover (Table 1; see also García et al. 2013). The early recruitment of the tree species studied here is supposed to be more limited by seed density than by the availability of suitable microsites for seedling establishment (García et al. 2005b), and, thus, we consider that the potential for forest regeneration in these open areas is quite poor. Nevertheless, even though we observed a strong difference in seed deposition between open and forested areas in both years, we also found some

temporal variability in the magnitude of this difference. That is to say, a significant decrease in both presence and abundance of seeds took place in forested areas from 2009 to 2010. Despite this, we found that the magnitude of seed dispersal remained constant in the open areas (Table 1). This actually meant an increase in the relative importance of seed dispersal into deforested habitats, as seeds in open microhabitats accounted for 4.5% of the total seed rain in 2009 but this increased to 8.0% in 2010 (Table 1). Previous works in this study system have also suggested inter-annual variations in the magnitude of seed deposition (Herrera & García 2009; García et al. 2013), enlarging the temporal scope of the present data.

A negative effect of distance from forest edge in shaping the spatial pattern of seed dispersal into pastures has been reported previously in tropical ecosystems (Willson & Crome 1989; Aide & Cavelier 1994; Cubiña & Aide 2001). Here, we show that this pattern can be extended to our temperate system, as the number of dispersed seeds decreased sharply with increasing distance to forest cover. Although some seeds arrived as far as 50 m from the forest cover, more than the 75% of dispersed seeds did not proceed further than 11 m in either year. Thus, the potential for tree regeneration in these Cantabrian pastures is not only low but also spatially restricted to a narrow spillover band surrounding the remnant forest (see also Günter et al. 2007). In 2010, however, we detected a relaxation of this forest cover effect, as suggested by the increased probability of seed arrival at long distances from forest as well as in landscape sectors with low forest cover (Fig. 3). We also found a lower proportion of the dispersed seeds deposited in highly covered areas, close to the forest edge.

Mechanisms behind variable seed dispersal patterns

Changes in the influence of forest context on seed dispersal into deforested habitats have been explained as a result of the local variability in the presence of isolated trees or other structures acting as perches (with pastures having more isolated trees receiving more seeds; McDonnell & Stiles 1983; Holl et al. 2000), or as a consequence of the differences in the structure of the forest context itself (with pastures in areas with higher or more complex forest cover receiving more seeds; Kollmann & Pirl 1995; Cole et al. 2010). Our study was carried out in a study plot with no inter-annual variation in the extent or the spatial configuration of forest cover. Thus, the abovementioned cover-related factors do not seem to determine the variations in forest context effects observed here. We suggest that this variability in fact results from the important dynamism of the

plant–frugivore system, namely that concerning the abundance and the spatial distribution of fruits and frugivores (García et al. 2013). Our study did not find variations in total fruit abundance, but the spatial pattern of fruit abundance markedly changed from one year to the next (Fig. 2). While in 2009 the distribution of fruits in the study plot was strongly skewed towards areas with high forest cover, in 2010 it was more evenly shared between these areas and those devoid of forest, dominated by pastures with few isolated remnant trees (Fig. 2). This shift in the large-scale spatial template of fruits reflects a change in the identity of the dominant fruiting species (Fig. 2), since *I. aquifolium* was mainly restricted to densely forested areas whereas *C. monogyna* appeared both in the forest and in the pastures as isolated trees. The pattern of activity of birds across different habitats within the landscape changed from 1 year to the next, mirroring the change in fruiting spatial templates. In 2010 a lower proportion of birds was observed in the forest, while visits to isolated trees increased (Table 1). The present study only covered 2 yr, but previous work in the same system evidenced similar inter-annual changes in the fruiting landscape, with concomitant changes in frugivory and seed dispersal (Herrera & García 2009; García et al. 2013). Taken together, our present as well as previous results suggest that, over a longer time period, frugivorous birds perceived the large-scale landscape context and optimized their foraging activity according to the fruiting scenario they found in each year (see also Tellería et al. 2008; García et al. 2013). In other words, when fruit production was low in the forest but comparatively high in small stands and isolated trees within the pastures, frugivorous birds would need to leave the forest to forage in open areas more often. This change in habitat use would consequently lead to variations in the seed rain that frugivores generate (Nathan & Muller-Landau 2000; Culot et al. 2010), and a higher proportion of seeds would likely be dispersed at longer distances into pastures, as, in fact, we demonstrate in the present study.

Integrating landscape dynamic structure and seed dispersal into deforested lands

Frugivorous animals acting as mobile links (moving seeds between different landscape patches, from forest into pastures; Lundberg & Moberg 2003) have frequently been considered as important agents in vegetation passive restoration plans (Wunderle 1997; Holl et al. 2000; Cavallero et al. 2013). An equivalent role may be attributed to frugivorous birds in our study system, in which seed availability has been suggested to strongly limit tree

recruitment (García et al. 2005b). Furthermore, bird reluctance to use open habitats constrains the initial potential for tree regeneration in pastures to a narrow halo surrounding the remaining forest. Fruiting landscape dynamics, like those observed here, confer variability to the behavior of frugivorous birds and, subsequently, to seed dispersal patterns (Cardoso da Silva et al. 1996; García et al. 2013). In certain years, responding to landscape-scale widespread fruit distributions, birds forage outside the forest more frequently, carrying more seeds, and carrying them over further distances, into pastures. We suggest that a relaxing of distance constraints on seed arrival, similar to that we evidence here, would also take place during other events of within-forest fruit shortage. If this is true, the spatial pattern of forest regeneration in pastures that can be expected in the long term will be shaped by the summed templates of different spillover bands, in the form of tides of seeds within the pastures (Fig. 4). While in most years seed arrival will occur quite close to the forest edge (Fig. 4a), in other years spring tides of seeds will take place, extending the initial potential for forest recolonization further into the pastures (Fig. 4b). Indeed, between 2009 and 2010 we observed an increment of 2 m in the average distance at which seeds arrived. This widening of the spillover band will also contribute to an enlargement of the scale at which forest regeneration potentially operates as, translated into surface terms, it represents an increase of 10% in the unfor-ested surface of the study plot affected by seed dispersal.

The present study has some limitations that must be considered in relation to the interpretation of results. First, we focused on the raw, community-wide potential for

forest recolonization, without considering potential differences between tree species. We found that, in 2009, the different tree species occurred in the same relative frequencies in open and in covered stations, but, in 2010, the proportion of seeds of *I. aquifolium* decreased, while that of *C. monogyna* increased, in open with respect to covered stations (data not shown). These species-specific patterns may also affect recolonization dynamics through effects on vegetation composition. Second, even though seed dispersal spatially constrains the potential for forest recovery, final recolonization templates may differ from those initially determined by seed rain. Environmental filtering which affects subsequent plant regeneration stages may blur the seed dispersal footprint (Holl et al. 2000). Third, this study is based on a single locality, restricting the extrapolation of our results over larger extents. That said, we consider that the local conditions of our study system are frequently replicated throughout the region, as both the plant–frugivore assemblage (e.g. Guitián et al. 2000) and the patterns of forest loss and fragmentation – due to regional processes of exploitation (e.g. García et al. 2005a) – are highly predictable across the Cantabrian Range. Indeed, high degrees of habitat loss and fragmentation are encountered in many mature and secondary forests of other mid-mountain areas in Europe (Darby 1956; Behre 1988; Kaplan et al. 2009).

Conclusions

As proposed by Holl & Aide (2010), some important factors should be taken into account for the effectiveness of natural recolonization as a strategy for restoring woody

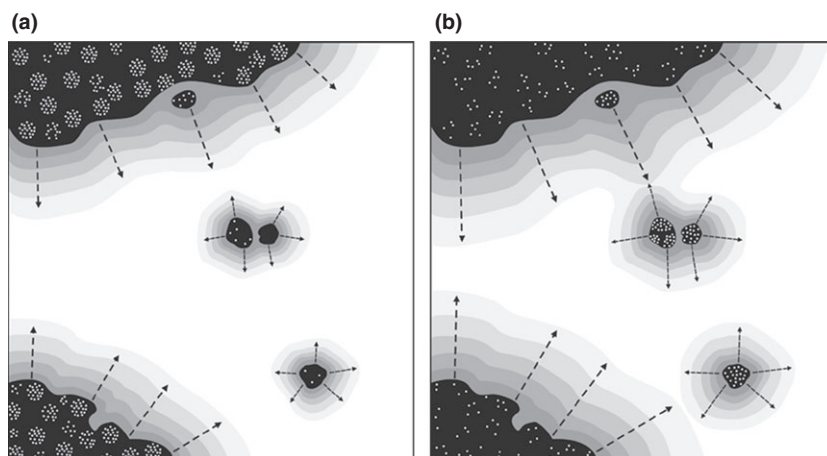


Fig. 4. Representation of inter-annual variation in seed dispersal from forest cover into pastures. Forest is represented in black and pasture in white (with isolated remnant trees as small black polygons). Fruits are represented as white spots within forest cover. Seed arrival in pastures is represented as a decreasing gradient from forest edge (grey tones). (a) When fruits are concentrated in large forest patches, seed dispersal is constrained to a narrow spillover band surrounding forest cover. (b) When fruits are widespread across the whole landscape, and even more abundant in isolated remnant trees than in large forest patches, birds visit deforested land more frequently, widening and spreading the spillover band of seed dispersal.

vegetation in degraded areas. The success of passive restoration plans will rely on the intrinsic recovery capacity (resilience) of the ecosystem, on the level of degradation suffered and also on the characteristics of the landscape context surrounding the area. Our study system seems to be a perfect candidate for achieving significant forest recovery, as it retains the potential for natural tree regeneration. Areas available to recover are extensive livestock grazing pastures with low levels of soil perturbation and moderate-to-high fertility and, thus, they are potentially suitable sites for seedling establishment once seeds have arrived. Even when the matrix is mainly open, some forest patches and isolated trees still remain, acting also as seed sources for regeneration. Moreover, the main forest tree species are all dispersed via mobile animal vectors that contribute to their spread. Here, in addition, we show that the spatio-temporal variability inherent to this system is an important source of forest resilience (see also García et al. 2013). Variable fruiting patterns at the landscape scale, as found here, can contribute to relaxing the restrictions that limit forest recovery in degraded areas. Planting fruiting trees within the deforested matrix can help to increase that dynamism, leading to more widespread tree recruitment within these areas. We thus encourage the consideration of this type of landscape biological dynamism when aiming to manage rewilding in European temperate forests (Navarro & Pereira 2012).

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References

- Aide, T.M. & Cavelier, J. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2: 219–229.
- Behre, K.E. 1988. The role of man in European vegetation history. In: Huntley, B. & Webb, T. (eds.) *Vegetation history*. pp. 633–672. Kluwer Academic, Dordrecht, NL.
- Bonan, G.B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.
- Bustamante-Sánchez, M.A. & Armesto, J.J. 2012. Seed limitations during early forest succession in a rural landscape on Chiloé Island, Chile: implications for temperate forest restoration. *Journal of Applied Ecology* 49: 1103–1112.
- Cardoso da Silva, J.M.C., Uhl, C. & Murray, G. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology* 10: 491–503.
- Carlo, T.A., García, D., Martínez, D., Geditsch, J.M. & Morales, J.M. 2013. Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. *Ecology* 94: 301–307.
- Carrière, S.M., André, M., Letormy, P., Olivier, I. & McKey, D.B. 2002. Seed rain beneath remnant trees in a slash-and-burn agricultural system in southern Cameroon. *Journal of Tropical Ecology* 18: 353–374.
- Castroviejo, S. (gen. coord.). 1986–2012. *Flora iberica* 1–8, 10–15, 17–18, 21. Real Jardín Botánico, CSIC, Madrid, ES.
- Cavallero, L., Raffaele, E. & Aizen, M.A. 2013. Birds as mediators of passive restoration during early post-fire recovery. *Biological Conservation* 158: 342–350.
- Chazdon, R.L. 2008. Beyond deforestation: restoring forest and ecosystem services on degraded lands. *Science* 320: 1458–1460.
- Cole, R.J., Holl, K.D. & Zahawi, R.A. 2010. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. *Ecological Applications* 20: 1255–1269.
- Cramer, V.A., Hobbs, R.J. & Standish, R.J. 2008. What's new about all fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution* 23: 104–112.
- Cubiña, A. & Aide, T.M. 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* 33: 260–267.
- Culot, L., Muñoz Lazo, F.J.J., Huynen, M.C., Pocin, P. & Heymann, E.W. 2010. Seasonal variation in seed dispersal by tamarins alters seed rain in secondary rain forest. *International Journal of Primatology* 31: 533–569.
- Darby, H.C. 1956. The clearing of the woodland in Europe. In: Thomas, W.L. Jr (ed.) *Man's role in changing the face of the Earth*, pp. 183–216. University of Chicago Press, Chicago, IL, US.
- Debussche, M. & Lepart, J. 1992. Establishment of woody plants in mediterranean old fields: opportunity in space and time. *Landscape Ecology* 6: 133–145.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bollinger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., (...) & Willson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609–628.
- Duncan, R.S. & Chapman, C.A. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* 9: 998–1008.
- Duncan, R.S. & Chapman, C.A. 2002. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In: Levey, D.J., Silva, W.R. & Galetti, M. (eds) *Seed Dispersal and Frugivory. Ecology, Evolution and Conservation*, pp 437–450. CAB International, Wallingford, UK.

- FAO 2011. *State of world's forests*. FAO, Rome, IT.
- García, D. & Chacoff, N.P. 2007. Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory and seed predation. *Conservation Biology* 21: 400–411.
- García, D. & Martínez, D. 2012. Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. *Proceeding of the Royal Society of London, series B* 279: 3106–3113.
- García, D., Quevedo, M., Obeso, J.R. & Abajo, A. 2005a. Fragmentation patterns and protection of montane forests in the Cantabrian range (NW Spain). *Forest Ecology and Management* 208: 29–43.
- García, D., Obeso, J.R. & Martínez, I. 2005b. Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does the scale matter? *Journal of Ecology* 93: 693–704.
- García, D., Zamora, R. & Amico, G.C. 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. *Conservation Biology* 24: 1070–1079.
- García, D., Martínez, D., Herrera, J.M. & Morales, J.M. 2013. Functional heterogeneity in a plant–frugivore assemblage enhances seed dispersal resilience to habitat loss. *Ecography* 36: 197–208.
- Griffith, D.A. & Peres-Neto, P.R. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87: 2603–2613.
- Gutián, J., Gutián, P., Munilla, I., Gutián, J., Beremejo, T., Larinaga, A.R., Navarro, L. & Lopez, B. 2000. Zorzales, espinos y serbales. Un estudio sobre el consumo de frutos silvestres de las aves migratorias en la costa occidental europea. Universidad de Santiago de Compostela, Santiago de Compostela, ES.
- Günter, S., Weber, M., Erreis, R. & Aguirre, N. 2007. Influence of distance to forest edges on natural regeneration of abandoned pastures: a case study in the tropical mountain rain forest in Southern Ecuador. *European Journal of Forest Research* 126: 67–75.
- Hampe, A., García-Castaño, J.L., Schupp, E.W. & Jordano, P. 2008. Spatio-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. *Journal of Ecology* 96: 668–678.
- Herrera, J.M. & García, D. 2009. The role of remnant trees in seed dispersal through the matrix: being alone is not always so bad. *Biological Conservation* 142: 149–158.
- Herrera, J.M., Morales, J.M. & García, D. 2011a. Differential effects of fruit availability and habitat cover for frugivore-mediated seed dispersal in a heterogeneous landscape. *Journal of Ecology* 99: 1100–1107.
- Herrera, J.M., García, D., Martínez, D. & Valdés, A. 2011b. Regional vs. local effects of habitat loss and fragmentation on two plant–animal interactions. *Ecography* 34: 606–615.
- Holl, K.D. & Aide, T.M. 2010. When and where to actively restore ecosystems? *Forest Ecology and Management* 261: 1558–1563.
- Holl, K.D., Loik, M.E., Lin, E.H.V. & Samuels, I.A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* 8: 339–349.
- Jordano, P. 2000. Fruits and frugivory. In: Fener, M. (ed.) *Seeds: the ecology of regeneration in plant communities*, pp. 125–166. CAB International, Wallingford, UK.
- Kaplan, J.O., Krumhardt, K.M. & Zimmermann, N. 2009. The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* 28: 3016–3034.
- Kollmann, J. & Pirl, M. 1995. Spatial pattern of seed rain of fleshy-fruited plants in a scrubland–grassland transition. *Acta Oecologica* 16: 313–329.
- Kunstler, G., Thuiller, W., Curt, T., Bouchaud, M., Jouvie, R., Deruelle, F. & Lepart, J. 2007. *Fagus sylvatica* L. recruitment across a fragmented Mediterranean landscape: importance of long-distance effective dispersal, abiotic conditions and biotic interactions. *Diversity and Distributions* 13: 799–807.
- Levey, J.L. & Benkman, C.W. 1999. Fruit–seed disperser interactions: timely insights from a long-term perspective. *Trends in Ecology & Evolution* 14: 41–42.
- Lundberg, J. & Moberg, F. 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6: 87–98.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J. & Gibon, A. 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management* 59: 47–69.
- Martínez, I., García, D. & Obeso, J.R. 2008. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. *Ecoscience* 15: 189–199.
- Martínez-Garza, C. & Howe, H.F. 2003. Restoring tropical diversity: beating the time tax on species loss. *Journal of Applied Ecology* 40: 420–439.
- McDonnell, M.J. & Stiles, E.W. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56: 109–116.
- Myers, N. 1997. The world's forests and their ecosystem services. In: Daily, G.C. (ed.) *Nature's services. Societal dependence on natural ecosystems*, pp. 215–235. Island Press, Washington, DC, US.
- Nathan, R. & Muller-Landau, H. 2000. Spatial patterns of seed rain, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278–285.
- Navarro, L.M. & Pereira, H.M. 2012. Rewilding abandoned landscapes in Europe. *Ecosystems* 15: 900–912.
- Perea, R., Delibes, M., Polko, M., Suárez-Esteban, A. & Fedriani, J.M. 2013. Context-dependent fruit–frugivore interactions: partner identities and spatio-temporal variations. *Oikos* 122: 943–951.
- Peredo, A., Martínez, D., Rodríguez-Pérez, J. & García, D. 2013. Mammalian seed dispersal in Cantabrian woodland pastures:

- network structure and response to forest loss. *Basic and Applied Ecology* 14: 378–386.
- Rey Benayas, J.M., Bullock, J.M. & Newton, A.C. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment* 6: 329–336.
- Tellería, J.L., Ramírez, A. & Pérez-Tris, J. 2008. Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography* 31: 381–388.
- Willson, M.F. & Crome, F.H.J. 1989. Patterns of seed rain at the edge of tropical Queensland rain forest. *Journal of Tropical Ecology* 5: 301–308.
- Wunderle, J.M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99: 223–235.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methodology for bird censuses.

Appendix S2. Distributions of frequencies of sampling stations with respect to forest cover descriptors.