



Functional heterogeneity in a plant–frugivore assemblage enhances seed dispersal resilience to habitat loss

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The ability of ecosystems to maintain their functions after disturbance (ecological resilience) depends on heterogeneity in the functional capabilities among species within assemblages. Functional heterogeneity may affect resilience by determining multiplicity between species in the provision of functions (redundancy) and complementarity between species in their ability to respond to disturbances (response diversity), but also by promoting the maintenance of biological information that enables ecosystems to reorganize themselves (ecological memory). Here, we assess the role of the components of the functional heterogeneity of a plant–frugivore assemblage on the resilience of seed dispersal to habitat loss. For three years, we quantified the distributions of fruits, frugivorous thrushes (*Turdus* spp.) and dispersed seeds, as well as frugivore diet and movement, along a gradient of forest cover in N Spain. The abundances and the spatial distributions of fruits and birds varied between years. The different thrushes showed similar diets but differed in spatial behavior and response to habitat loss, suggesting the occurrence of both functional redundancy and response diversity. Forest cover and fruit availability affected the spatial distribution of the whole frugivore assemblage. Fruit tracking was stronger in years when fruits were scarcer but more widespread across the whole fragmented landscape, entailing larger proportions of seeds dispersed to areas of low forest cover and open microhabitats. Rather than depending on redundancy and/or response diversity, seed dispersal resilience mostly emerged from the ecological memory conferred by the inter-annual variability in fruit production and the ability of thrushes to track fruit resources across the fragmented landscape. Ecological memory also derived from the interaction of plants and frugivores as source organisms (trees in undisturbed forest), mobile links (birds able to disperse seeds into the disturbed habitat), and biological legacies (remnant trees and small forest patches offering scattered fruit resources across the landscape).

The causal link between biodiversity and ecosystem functioning is now a recognized paradigm in ecological and environmental sciences (Loreau 2010). Richer and more diverse biota are known to accumulate more biomass, use resources more efficiently, and thus provide ecosystem services better than communities impoverished by species decays and extinctions (Hooper et al. 2005, Naeem et al. 2009). Moreover, biodiversity is predicted to affect ecological resilience, i.e. the ability of ecosystems to maintain their functions in order to resist, or recover from severe disturbances (Peterson et al. 1998, Hooper et al. 2005). In this sense, understanding how and why resilience depends on biodiversity is critical, if we aim to alleviate the decay of ecosystem services under the impact of different drivers of anthropogenic change (Griffin et al. 2009, Mooney 2010). A first step towards this goal is to take into account functional heterogeneity, i.e. the degree of variability in functional capabilities among species (Hooper et al. 2005, Petchey and Gaston 2006), because its effect on the provision and the stability of ecosystem functions may be greater than that of taxonomic variety.

At least three components of functional heterogeneity can be considered to drive ecological resilience. The first component is functional redundancy (Walker 1995, Hooper et al. 2005), as species that contribute equally in the provision of a given function may functionally compensate the loss of each other. A second aspect is complementarity in the response to disturbances (response diversity, Elmqvist et al. 2003, Nyström 2006), as species that contribute to the same ecosystem function but respond differently to disturbance may replace each other along disturbance gradients. Both the redundancy and the response diversity concept highlight that the singularities of species within functional groups promote ecological insurance, by assuring functions in the face of species extinction or environmental change (Elmqvist et al. 2003, Winfree and Kremen 2009). Besides singularities within functional groups, resilience may depend on a third component of functional heterogeneity, termed ecological memory (Nyström and Folke 2001, Folke et al. 2004). Ecological memory depends on the role of those species which, thanks to their long-term experience

with environmental fluctuations, are able to preserve the biological information that enables ecosystems to reorganize themselves. Moreover, it depends on the functioning of species as three major interacting groups (see Nyström and Folke 2001, for a seminal example with coral reefs): biological legacies (i.e. organisms – or their derived features – persisting within an area hit by disturbance, which have anchoring effects for reorganization; e.g. dead coral framework); mobile links (i.e. mobile species that transfer biological information between areas affected by different degrees of disturbance; e.g. coral larvae); and support organisms (i.e. organisms remaining in undisturbed ecosystems, acting as sources in the recovery of disturbed areas; e.g. undisturbed reefs in the seascape matrix).

Fruiting plants and the animals that eat their fruits may be optimal assemblages for evaluating the link between functional heterogeneity and ecological resilience. Plants and frugivores are a relevant component of tropical and temperate biodiversity (Jordano 2000, Bascompte and Jordano 2007) and, by providing seed dispersal, frugivores are responsible for a pivotal ecosystem service (Kremen et al. 2007, García et al. 2010). Seed dispersal patterns depend largely on frugivore attributes such as diet (Moran et al. 2004, Schleuning et al. 2011) and movement (Spiegel and Nathan 2007, Lehouck et al. 2009a), both of which are characteristics suggested to be sources of functional redundancy (Zamora 2000, Lehouck et al. 2009a). Moreover, different frugivore species are known to respond differently to the same disturbance gradients (e.g. habitat loss; Santos et al. 1999, Breitbart et al. 2010). Finally, although highly variable in space and time (Levey and Benkman 1999), plant–frugivore assemblages are considered to be a part of the ecological memory of forest ecosystems, as their species preserve the biological information needed to recover deforested lands (Elmqvist et al. 2001).

Despite the above findings, and as with many other ecological functions (Winfree and Kremen 2009, Laliberté et al. 2010), little is known about the differential effects of functional redundancy, response diversity, and ecological memory on the resilience of seed dispersal to anthropogenic disturbances. To fill this gap, we explore the spatio-temporal variability in the components of an assemblage of fleshy-fruited trees and frugivorous birds, and also in its derived seed dispersal service, along a gradient of forest loss in the Cantabrian range (N Spain). Given that forest loss entails a decay of seed dispersal function with, ultimately, effects on tree recruitment (Herrera and García 2010) we interpret resilience as being any buffering of the negative effects of forest loss on the provision of seed dispersal. Specifically, we address the following questions: 1) how much do the distributions of fruits, birds and dispersed seeds vary along the gradient of habitat loss? 2) Do frugivore species differ in functional characteristics like diet, movement and habitat use? 3) Does the frugivore assemblage respond as a whole to the major environmental features modified by forest loss (i.e. forest cover and community-wide fruit availability)? We expect seed dispersal to be less responsive to forest loss in some years (Herrera and García 2009) due to the increased role of those frugivorous species less affected by forest loss (i.e. due to redundancy and response diversity) or,

alternatively, due to a global response to the whole assemblage of frugivorous birds to the landscape-scale changes in fruit distribution, irrespective of forest loss (i.e. due to ecological memory).

Methods

Study system

The ecosystem under study is the temperate secondary forest of Cantabrian range (N Spain). This is a common, but low-cover (<30%) and highly fragmented forest type in mid-elevation areas (García et al. 2005a). Secondary forest stands occur as fringe patches, adjacent to beech *Fagus sylvatica* 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*).

Our study system – fleshy-fruited trees and frugivorous thrushes – is a major component of the plant–frugivore assemblage of this Cantabrian secondary forest. Fleshy-fruited trees, namely holly *Ilex aquifolium*, hawthorn *Crataegus monogyna*, and yew *Taxus baccata*, account for >70% of tree cover in the studied ecosystem (García et al. 2005b). Fruits are 10–15 mm diameter, sugar-rich red berries (arillated seed in yew), and contain 1–4 seeds (5–9 mm). All species ripen in autumn (September to November) and inter-annual differences in fruit abundance, both within and between species, are strong (García et al. 2005b). Their main frugivores are thrushes: blackbird *Turdus merula*, fieldfare *T. pilaris*, mistle thrush *T. viscivorus*, redwing *T. iliacus*, song thrush *T. philomelos*, and ring-ouzel *T. torquatus*. Some of these (*T. pilaris*, *T. iliacus* and *T. torquatus*) are over-wintering species in northern Spain, whereas others (*T. merula*, *T. viscivorus* and *T. philomelos*) are resident species which are joined by overwintering migrant individuals (Guitián et al. 2000). All thrushes swallow the entire fruits, defecating the intact seeds in their feces (Guitián et al. 2000). Despite the strong taxonomic affinity, the species of thrushes under consideration have been found to differ in fruit consumption patterns and response to habitat features (Martínez et al. 2008).

Study site and spatio-temporal framework

The study site was located in the Sierra de Peña Mayor (43°18'00"N, 5°30'29"W, 1000 m a.s.l., Asturias Province, Spain) where secondary forest is intermingled with meadows, heathland and limestone rocky outcrops. In September 2006, 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 (Fig. 1). Thus, the plot was chosen to represent a gradient of forest loss and increasing forest subdivision and forest edge (Herrera and García 2010). The plot was subdivided into 440, 20 × 20 m sampling cells. Previous studies carried out over larger spatial extents in the same site (Herrera and García 2009, García et al. 2011) proved that such plot and cell dimensions were appropriate to represent the scale

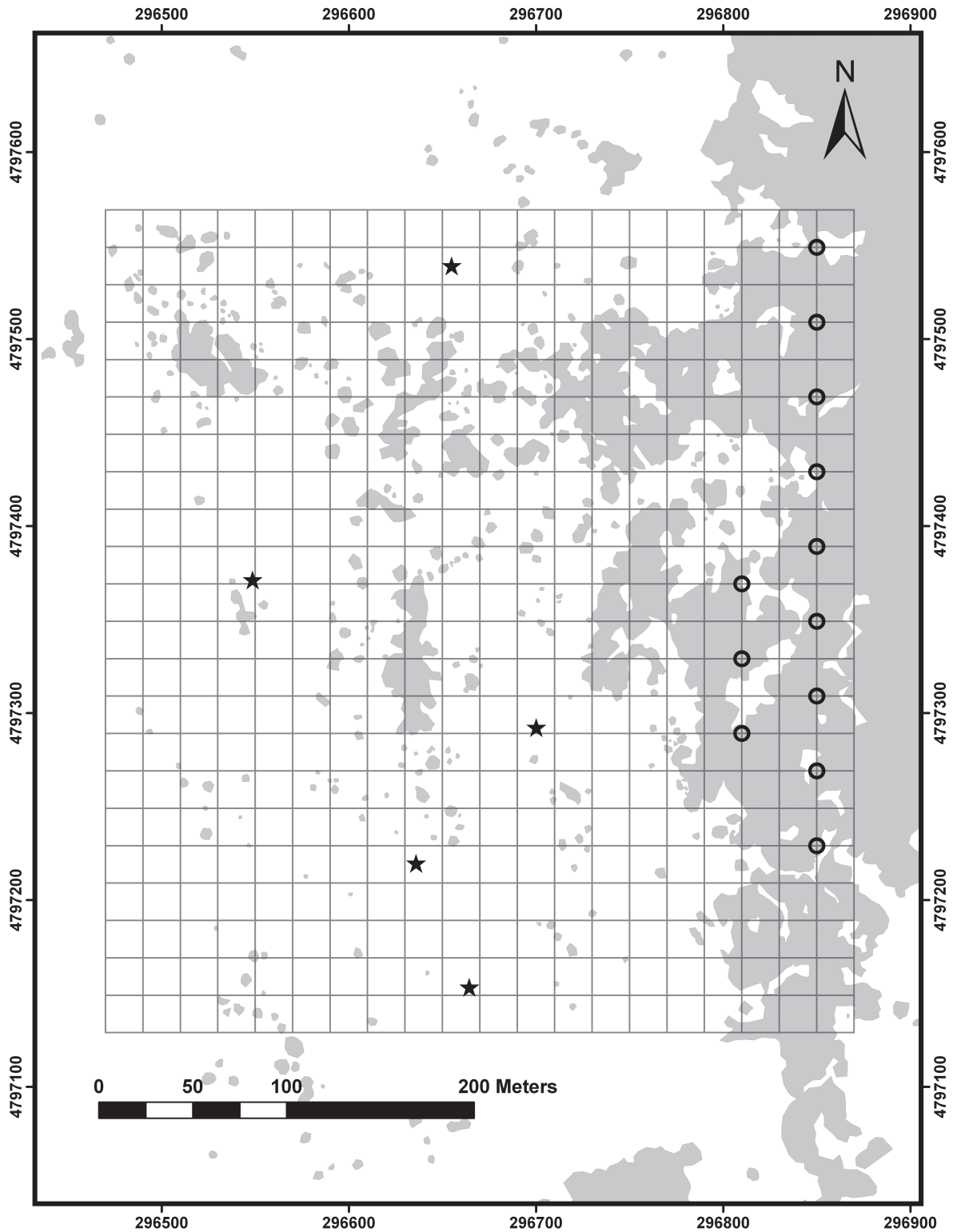


Figure 1. Scheme of the study plot representing the configuration of the forest cover (grey area), the plot subdivision into 20×20 m cells, and the vantage (black stars) and point-count (circles) positions for bird observation.

at which habitat fragmentation, frugivory and seed dispersal operate in the Cantabrian Range. Sampling was carried out from September to February over three consecutive periods: 2007–2008, 2008–2009 and 2009–2010 (hereafter 2007, 2008 and 2009 respectively).

Forest cover and fruit counts

In September 2007, we developed a Geographical Information System (GIS, ArcGIS 9.0) based on a 1:5000-scale, current orthophotomap image of the study plot. The

GIS 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 m²) per cell. In 2008 and 2009, we used the per-cell values of forest cover as estimated in 2007, as we assumed that inter-annual variability in forest cover was negligible.

In autumn of each sampling year, we walked the study plot to map all individual trees (> 1.5 m tall and/or > 4 cm trunk basal diameter) of all species. We visually assigned a standing fruiting crop value to each individual of any fleshy-fruited species, by means of a semi-quantitative fruit abundance index (FAI; considering six intervals: 0 = without fruits; 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10 000; 5 > 10 000; Saracco et al. 2005). Fruiting in the Cantabrian forest is synchronous among individuals and species, with almost all fruit ripening delimited to 1–2 months (although fruits may remain attached to trees for 1–3 additional months). We thus considered that one survey of fruit abundance at the beginning of the season provided an appropriate estimate of the yearly spatial template of fruit resources for frugivores. Since *T. baccata* shows an earlier fruiting peak than other species, we first walked the plot in late September to survey *T. baccata* fruits, and then walked the plot again in late October, recording the fruit crops of all remaining species. All data on location, species and FAI of each individual tree, for every sampling year, were incorporated into the GIS. We calculated the abundance of fruits per cell as the sum of the crops of all fruiting trees present each year, for both each tree species and all species together. Crops were extrapolated from FAI ranks following an allometric equation fitted to the actual crop size of a sub-sample of trees (crop size = $1.77 \times e^{1.92FAI}$, $r^2 = 0.80$; $n = 136$).

Bird counts

Direct observations of thrushes entering different sampling cells were made from five different vantage positions in elevated outcrops, located along the central axis of the plot (Fig. 1). Observations were made from October to February of each year, with a cumulative observation time of 62, 103 and 105 h for 2007, 2008 and 2009, respectively. Observation time was allocated in a balanced number of 1-h observation periods among stations across each season. In each observation period, the observer, with the help of 8 × 30 binoculars, counted and identified at the species level all thrushes seen (or heard) in different sectors of the surveyed area. Bird sightings were assigned to the different geo-referenced sampling cells covered from each vantage position, with the help of printed maps. In some cases, the consecutive sightings of a given species could have corresponded to the same individuals remaining within, or successively entering a given cell. In these doubtful cases, we considered as independent those sightings separated by at least five minutes. Also, the sightings potentially corresponding to a given individual bird in different cells – or in the same cell on different days – were considered to be as valid as those from different individuals.

Due to the elevated location of vantage positions (ca 70 m of elevation gradient) and the patchy and sparse structure of forest cover, a high visual and/or acoustic detectability

of thrushes was achieved across almost the entire plot, even in those cells at a considerable distance away. However, due to the denser forest canopy and topographical features, bird detectability was lower in some easternmost cells of the plot (Fig. 1) 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 center of a group of four cells. Observations were made on 10 min periods, recording any thrush heard or seen within the four surrounding cells. Observation time from each point count was 80, 160 and 110 min for 2007, 2008 and 2009, respectively.

Rather than assessing the actual size of bird populations, our goal was to provide a measure of bird abundance in functional terms, i.e. an estimation of the total activity of frugivorous thrushes across the season in the study plot. For this, we calculated the abundance of birds per cell as the cumulative number of birds heard or seen in each cell through the season, for both each bird species and all species together. We divided the cumulative number of birds by the total observation time for each cell, calculating the number of birds per 10-h of observation. Weighting by total observation time per cell enabled the comparison of abundance between cells, correcting for overestimation in those cells observed from different positions and thus accounting for longer observation times, and also between years with different observation efforts.

Bird foraging and movement

Foraging patterns of thrushes were sampled over observation sequences made from the vantage positions. Observation time was 78, 90 and 79 h for 2007, 2008 and 2009, respectively. In each sequence, a movement bout of a given individual bird was tracked with the help of 8 × 30 binoculars and printed maps of plot cells. Once a given bird was located, it was followed until lost (because it left the plot or disappeared into the canopy) recording, for all sequential steps in the movement bout (i.e. consecutive rests separated by intervening flights), the microhabitat where the bird was resting (distinguishing covered, i.e. tree canopy, vs open, i.e. tree-uncovered pasture or rock), the location of the resting site (i.e. the cell within the plot), and the species and number of fleshy fruits eaten. We calculated the proportions of fruits from different tree species consumed by each bird species, from all observations of fruit consumption for each thrush species and year. Flight distance was calculated for each flight between rests located in different cells as the euclidean distance between the centroids of the starting point and endpoint cells. Due to the unbalanced nature of sampling in observation sequences (which provided widely differing number of records of the various species in the different years), we pooled the data from different years for each species to calculate the average flight distance, and also the proportion of resting observations corresponding to covered and open microhabitats.

Counts of seeds dispersed by thrushes

We assessed seed deposition by thrushes in sampling stations across the whole plot in 2007 and 2009. Each sampling

station consisted of a permanently labelled, open-ground 50 × 50 cm quadrat where all bird-dispersed seeds were collected and counted. Seeds regurgitated or defecated by birds are very conspicuous, and easily distinguishable from the soil background. We estimated the total number of dispersed seeds (for each tree species and for all species together) per sampling station as the sum of seeds found in two consecutive surveys, in late November and early January. Each sampling station was spatially geo-positioned and assigned to covered (tree canopy) or open (pasture, rock) microhabitats, corresponding to the structural features of the area covered by (or above) the quadrat.

A total of 480 and 500 sampling stations were used in 2007 and 2009 respectively. Stations were distributed in 125 cells through the whole plot, each cell containing 3–5 sampling stations per cell separated from each other by at least 2 m. Different sampling schemes were used in 2007 and 2009. Nevertheless, both schemes represented similar spatial extents and distributions, as well as similar gradients of forest loss (Supplementary material Appendix 1). As a measure of the magnitude of seed dispersal per cell, we calculated the average number of dispersed seeds per station. Also, for each year, we estimated the frequency of occurrence of dispersed seeds as the proportion of sampling stations receiving at least one seed, both for all sampling stations and for stations in covered and in open microhabitats.

Statistical analysis

To search for major trends of variability in frugivore diet composition, we conducted a principal component analysis of the proportions of fruits of *C. monogyna*, *I. aquifolium* and *T. baccata* consumed by the different bird species in different years, which extracted two components (Supplementary material Appendix 2). The first component (PC1) accounted for 65.6% of total variance and represented a gradient of increasing proportion of *C. monogyna* and decreasing proportion of *I. aquifolium* in the diet, whereas the second component (PC2) accounted for 33.1% of variance and was related to increasing proportion of *T. baccata*. The factor scores of each component were compared between bird species and years by means of two-ways ANOVA models.

We analyzed the degree of concordance between the spatial structures of forest cover and the abundances of fruits, birds and dispersed seeds, for the different study years. The spatial structure (i.e. the degree of spatial aggregation) of these variables was quantified by means of spatial analysis by distance indices (SADIE, Perry et al. 2002; Supplementary material Appendix 3). SADIE provides two complementary measures of the spatial structure of count-data variables. First, the aggregation index (I_a) is a global measure of the degree of aggregation of a variable, with $I_a = 1$ representing random, $I_a < 1$ regular, and $I_a > 1$ aggregated distribution patterns. Second, the clustering index (ν) is a parameter calculated for each point in the data base which quantifies the degree to which the count at a given point in space contributes to the global clumpiness of a variable. Points with high positive ν values contain big counts which would contribute greatly to high-density clusters

(‘patches’), whereas points with negative ν values contain small counts which would contribute to low-density clusters (‘gaps’). Practically, the vectors of clustering indexes may be considered weighted continuous variables that depict the spatial distribution of the raw count data. Hence, vectors from different variables sampled in the same points may be correlated to verify the existence of significant spatial match between variables. Both aggregation and clustering indexes were calculated with the software Sadie Shell ver. 1.22 (Conrad 2001).

Clustering index vectors are usually highly auto-correlated in space. Thus, in order to verify the relationships between indexes from different parameters taking into account the potential effect of spatial non-independence, we used simultaneous autoregressive models (SAR; Keitt et al. 2002). SAR models provide regression coefficients that represent the direct effect(s) of the predictor(s) free of spatial constraints. They also enabled the analytical limitations derived from the fact that sampling units were different cells belonging to a single plot to be overcome. SAR models were applied to check the following questions: 1) whether the distribution of the different species of fruits and birds matched that of forest cover (the regression coefficients between the bird abundances and forest cover were considered as a measure of specific responses to forest loss); 2) whether the distribution of total bird abundance resulted from the response of birds to forest cover (i.e. overall response to forest loss) and/or to community-wide fruit availability (i.e. fruit resource tracking); and 3) whether the distribution of dispersed seeds matched that of forest cover.

We evaluated the inter-annual change in the probability of seed dispersal to covered and open sampling stations by means of a spatial logistic regression considering, as response variable, the presence/absence of dispersed seeds, and, as predictor variables, the year, the microhabitat type, and the year × microhabitat interaction, and an autoregressive term which controlled for the potential effects of spatial autocorrelation.

All spatially-explicit models were performed with SAM ver. 4.0 software (Rangel et al. 2010). Average values are accompanied by standard errors (\pm SE) throughout the results.

Results

Patterns of fruit abundance

The abundance of fleshy fruits increased across years in the study plot (fruits per square meter per cell: 2007: 9.03 ± 0.91 ; 2008: 10.25 ± 1.14 ; 2009: 17.43 ± 1.55 ; GLM, Poisson distribution, log link: L-R $\chi^2 = 25.6$, $p < 0.0001$, $DF = 2$). This trend was mostly accounted for by the increase in the absolute and relative abundances of *I. aquifolium*, given that *C. monogyna* abundance decreased across years (Fig. 2A; Supplementary material Appendix 4, Table A4). *Taxus baccata* represented a small fraction of community-wide fruit production in all study years (Fig. 2A).

The spatial patterns of fruit crops changed across years (Fig. 3). Namely, fruit distribution was more and more

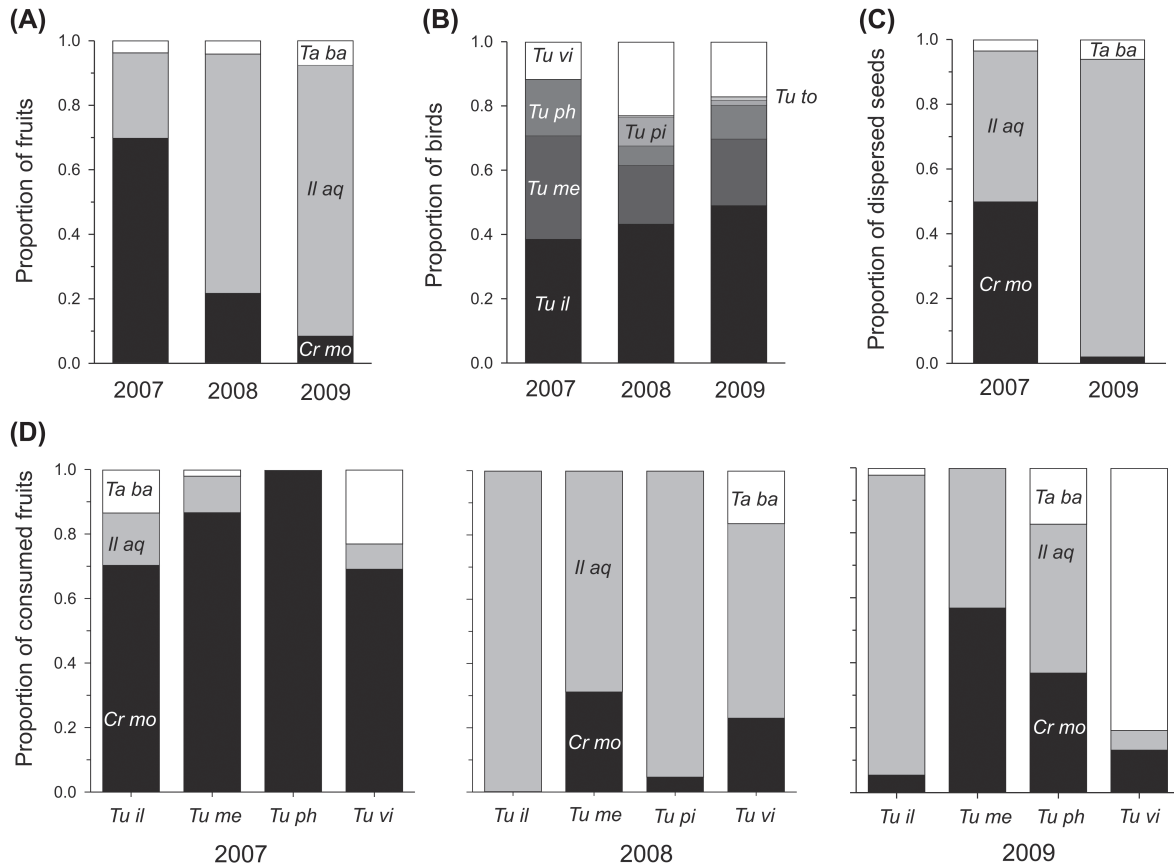


Figure 2. (A) Proportions of fruits of *Crataegus monogyna* (*Cr mo*), *Ilex aquifolium* (*Il aq*) and *Taxus baccata* (*Ta ba*) with respect to total fruit crop in different years; (B) proportions of different bird species (*Tu il*: *Turdus iliacus*; *Tu me*: *T. merula*; *Tu ph*: *T. philomelos*; *Tu pi*: *T. pilaris*; *Tu to*: *T. torquatus*; *Tu vi*: *T. viscivorus*) with respect to total bird abundance in different years; (C) proportion of seeds of different tree species with respect to the total seed rain collected in different years; (D) proportion of fruits of different tree species consumed by different bird species in different years (only cases with >25 observations are represented).

clumped, the indexes of aggregation (I_a) being 1.76, 2.64 and 3.78 for 2007, 2008 and 2009, respectively (all indexes $p < 0.001$). The strength of the relationship between the clustering indexes of forest cover and total fruit abundance increased from 2007 to 2009 (SAR coefficients: 0.14 ± 0.02 , 0.31 ± 0.03 , 0.52 ± 0.03 ; $t > 7$; $p < 0.0001$; $n = 440$). Nevertheless, tree species differed in their spatial patterns of fruiting, with *C. monogyna* distribution being less aggregated, more scattered across the study plot and unrelated to the gradient of forest cover, whereas *I. aquifolium* distribution was always strongly aggregated and significantly matched forest cover (Table 1, Fig. 3). In sum, the larger the relative production of *I. aquifolium* (as in 2008 and 2009), the more aggregated and associated to forest cover was fruit total availability; the larger the contribution of *C. monogyna* (as in 2007), the more widespread was fruit availability.

Patterns of bird abundance, diet and spatial behavior

The abundance of thrushes increased from 2007 to 2009 (number of birds per 10 h per cell; 2007: 2.53 ± 0.28 ; 2008: 2.67 ± 0.34 ; 2009: 3.96 ± 0.47 ; GLM, Poisson distribution, log link: L-R $\chi^2 = 64.1$, $p < 0.0001$, DF = 2). This increase was mostly due to *T. iliacus*, whose relative

abundance also increased across years (Fig. 2B; Supplementary material Appendix 1, Table A4). *Turdus iliacus* and *T. merula* always accounted for >50% of observed birds (Fig. 2B). *Turdus pilaris* and *T. torquatus* were observed in 2008 and 2009, and always in small proportions (Fig. 2B).

The proportion of different fruit species consumed by thrushes varied more between years than between bird species. While in 2007, the diet of all bird species was dominated by *C. monogyna* fruits, in 2008 and 2009, *I. aquifolium* was, in most cases, the major food item (Fig. 2D). The PC1 scores (representing inverse gradients of *C. monogyna* and *I. aquifolium* proportions) were similar between bird species (two-way ANOVA: $F_{5,8} = 0.84$, $p = 0.55$; Supplementary material Appendix 2, Fig. A2) but differed between years ($F_{2,8} = 5.42$, $p = 0.03$). The scores of PC2 (representing a gradient of *T. baccata* proportion) differed marginally between species (two-way ANOVA: $F_{5,8} = 3.57$, $p = 0.06$) and were similar between years ($F_{2,8} = 1.39$, $p = 0.30$).

Birds showed differences between species in post-foraging movements across the fragmented landscape. The distance of post-foraging flights was significantly larger in *T. viscivorus* and *T. philomelos* than in *T. iliacus* and *T. merula* (average \pm SE distance in m: 46.4 ± 2.4 , 41.9 ± 5.2 , 32.3 ± 2.8 , and 25.9 ± 2.0 , respectively; GLM,

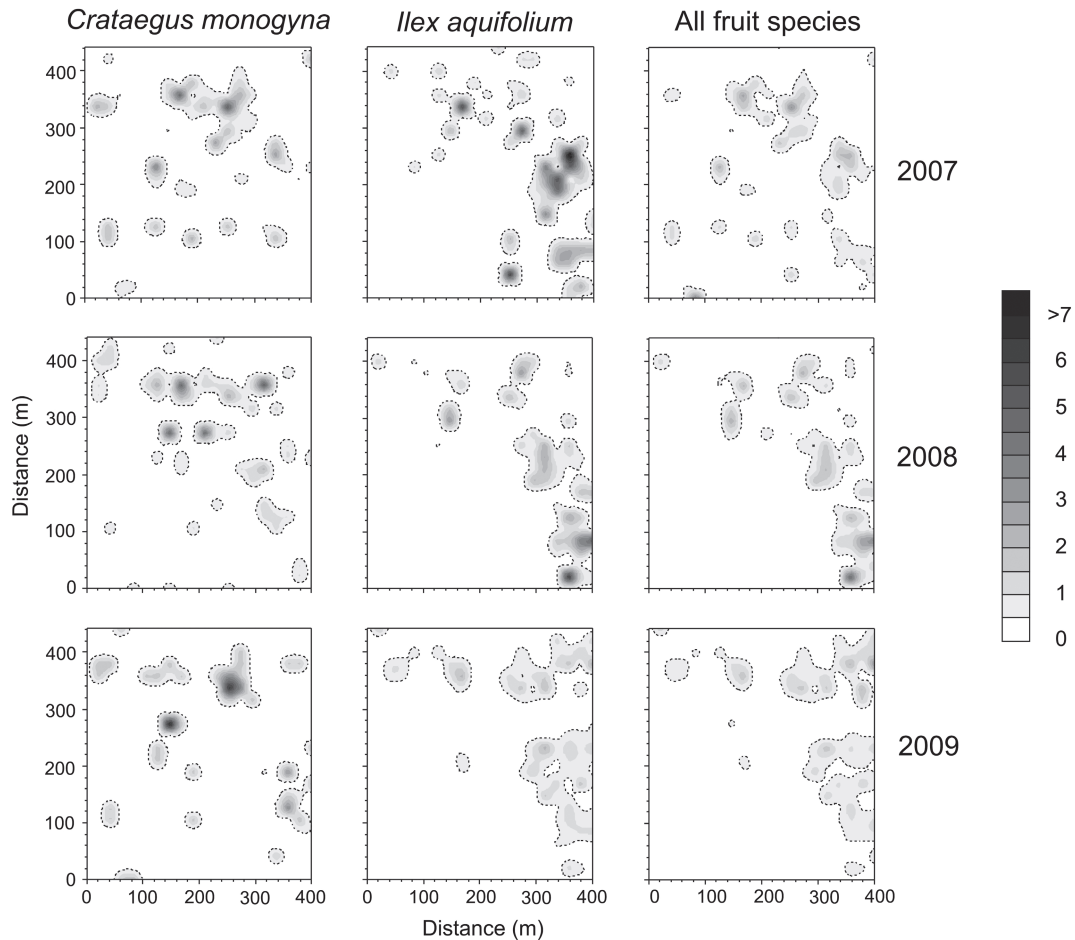


Figure 3. Distribution of fruit crops of *Crataegus monogyna*, *Ilex aquifolium*, and all fleshy-fruited trees, in the study plot across years. Grey-scaled contours represent the percentage of the whole fruit crop accounted for by each 20 × 20 m cell of the plot. Dashed lines surrounding the minimum value considered (0.5%) and the grey scale are shown.

exponential distribution, reciprocal link: L-R $\chi^2 = 34.4$, $p < 0.0001$, DF = 3). The proportion of resting observations in open microhabitats, relative to the total number of resting observations, was significantly larger in *T. viscivorus* and *T. philomelos* than in *T. merula* and *T. iliacus* (0.24, 0.10, 0.07 and 0.03, respectively; contingency analysis: L-R $\chi^2 = 67.8$, $p < 0.0001$, DF = 3).

Different birds showed different spatial distributions across the plot (Table 1, Fig. 4). The distributions of

T. viscivorus and *T. philomelos* were less aggregated and more widespread across the plot (especially towards the southwestern sector) than those of *T. iliacus* and *T. merula*, which were much more aggregated and restricted to the northeastern sector (Fig. 4). The relationships between the clustering indexes of each bird species and forest cover were all positive and significant, except for *T. viscivorus* in 2007 (Table 1). In fact, the response of *T. viscivorus* to forest cover tended to be, on average, weaker than for other

Table 1. Degree of spatial aggregation in the abundance of fruits and frugivorous thrushes across years, estimated by the index of aggregation (Ia) and the corresponding significance level (n.s. = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$). The strength of the relationship between the point-based clustering indexes of these abundances and that of forest cover, estimated from the coefficients (\pm SE) of simultaneous autoregressive models (SARc; $n = 440$ cells; significance levels correspond to associated t-values) are also shown.

	2007		2008		2009	
	Ia	SARc	Ia	SARc	Ia	SARc
Fruits						
<i>Crataegus monogyna</i>	1.68**	-0.02 \pm 0.02 n.s.	1.84***	0.01 \pm 0.02 n.s.	1.50**	0.02 \pm 0.02 n.s.
<i>Ilex aquifolium</i>	2.51***	0.12 \pm 0.02***	2.58***	0.15 \pm 0.02***	3.56***	0.23 \pm 0.03***
Thrushes						
<i>Turdus merula</i>	1.50**	0.09 \pm 0.02***	3.44***	0.40 \pm 0.03***	2.59***	0.27 \pm 0.03***
<i>Turdus iliacus</i>	1.68**	0.11 \pm 0.02***	3.09***	0.29 \pm 0.02***	3.42***	0.37 \pm 0.03***
<i>Turdus philomelos</i>	1.35*	0.07 \pm 0.01***	2.46***	0.20 \pm 0.02***	2.74***	0.22 \pm 0.03***
<i>Turdus viscivorus</i>	1.28 n.s.	-0.02 \pm 0.02 n.s.	2.38***	0.21 \pm 0.03***	2.36***	0.23 \pm 0.03***

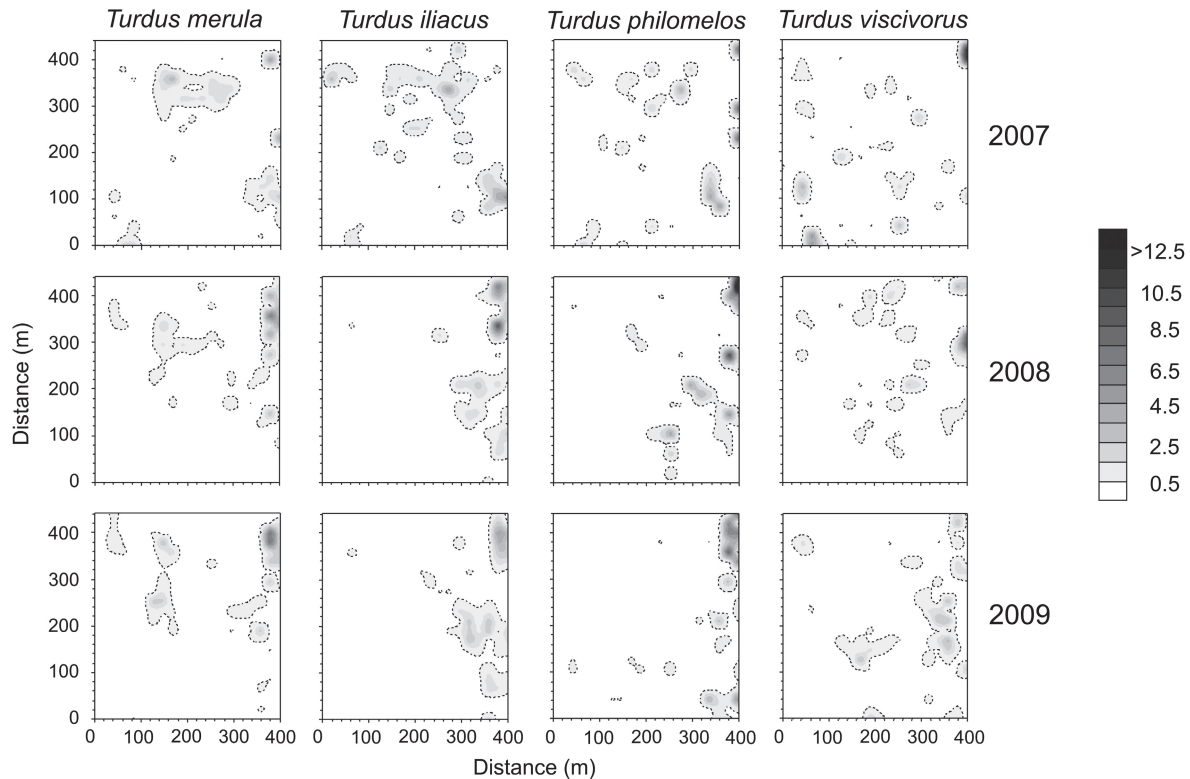


Figure 4. Distribution of the abundances of different bird species in the study plot across years. Grey-scaled contours represent the percentage of bird observations relative to the cumulative number of birds per 10 h, accounted for by each cell of the plot. Dashed lines surrounding the minimum value considered (0.5%) and the grey scale are shown.

thrushes. Stronger than the differences between species were the differences between years in the degree of spatial aggregation and the relatedness to forest cover. For example, the SAR coefficients between the clustering indexes of forest cover and bird abundance varied less between species ($cv = 29.3$) than between years ($cv = 59.6$). All species showed lower indexes of aggregation and lower SAR coefficients with regard to forest cover in 2007 than in 2008 and 2009 (Table 1, Fig. 4).

The degree of clumpiness in total bird abundance was always explained by the simultaneous effect of the distribution of forest cover and fruit abundance (Table 2). However, the degree of predictability and the relative weight of forest cover and fruit availability strongly varied between years. In 2007, the spatial patterns of forest cover and fruit availability explained a lower proportion of the spatial distribution of birds within the plot, and bird

patchiness depends more on fruits than on forest cover. The following years, a large proportion of bird patchiness was explained, almost exclusively, by forest cover in 2008, and forest cover and, secondarily, fruit availability in 2009.

Patterns of seed dispersal

The average magnitude of seed dispersal in the plot was similar in 2007 and 2009, with, respectively, 15.8 ± 1.7 and 18.7 ± 3.9 seeds per sampling quadrat (GLM, Poisson distribution, log link: L-R $\chi^2 = 0.08$, $p = 0.77$, $DF = 1$). However, the distribution of frequencies of seed abundance differed between years, with median and maximum numbers of seeds per quadrat of 2.7 and 410 in 2007, and 0.5 and 994 in 2009, respectively (Median test: $\chi^2 = 15.37$, $p < 0.0001$, $DF = 1$). The specific composition of the seed

Table 2. Summary of the spatial simultaneous autoregressive models (SAR) considering the clustering indexes of forest cover and fruit abundance as predictor variables, and those of bird abundance as response variable, for different years ($n = 440$). The total variance explained by the predictors (r^2), the degree of significance of the whole model (F-value based), the value (\pm SE) of the regression coefficients of each predictor, and their degree of significance (t-value based), are also shown (n.s. = $p > 0.05$; *** = $p < 0.001$).

Year	r^2	F-value	Factor	Coefficient (\pm SE)	Stand. coef.	t
2007	0.30	96.93***	forest cover	0.16 ± 0.02	0.27	5.15***
			fruit abundance	0.36 ± 0.05	0.33	7.52***
2008	0.52	236.44***	forest cover	0.42 ± 0.04	0.59	12.21***
			fruit abundance	0.02 ± 0.06	0.01	0.29 n.s.
2009	0.60	317.85***	forest cover	0.33 ± 0.03	0.50	9.76***
			fruit abundance	0.20 ± 0.04	0.24	4.72***

rain changed between years (Fig. 2C), with the abundance of *I. aquifolium* and *T. baccata* increasing but that of *C. monogyna* decreasing from 2007 to 2009 (Supplementary material Appendix 4, Table A4). The abundances of *C. monogyna*, *I. aquifolium* and *T. baccata* seeds were correlated across sampling stations, in both study years (all pairwise Spearman correlations between species were $r > 0.22$, $p < 0.0001$, estimated after Dutilleul's correction for spatial autocorrelation).

Seed rain was patchy in both study years, although patchiness was weaker in 2007 ($I_a = 1.49$, $p < 0.05$) than in 2009 ($I_a = 1.85$, $p < 0.001$). The spatial distribution of dispersed seeds mirrored that of forest cover (Fig. 5), but this concordance was weaker in 2007 (SAR coefficient: 0.18 ± 0.06 , $t = 2.93$, $p = 0.004$, $r^2 = 0.14$, $n = 125$) than in 2009 (SAR coefficient: 0.26 ± 0.04 , $t = 7.08$, $p < 0.0001$, $r^2 = 0.44$, $n = 125$).

Quadrats in covered microhabitats almost always received some seed (91.6% of 299 quadrats), whereas seeds only occurred in a third of open quadrats (32.3% of 681). The percentage of seed occurrence decreased from 2007 (62.9%) to 2009 (38.4%). This decrease was sharper in open (44.0 to 22.9%) than in covered (94.9 to 86.8%) microhabitat quadrats. Both microhabitat (spatial logistic regression coefficient: 2.40 ± 0.33 ; $t = 10.0$, $p < 0.001$, $DF = 1$), year (SLR coefficient: -0.49 ± 0.17 ; $t = -2.82$, $p < 0.01$, $DF = 1$) and microhabitat \times year interaction (SLR coefficient: -0.39 ± 0.18 ; $t = -1.75$, $p < 0.05$, $DF = 1$) had significant effects on the probability of seed deposition.

Discussion

Response of the plant–frugivore assemblage and seed dispersal function to habitat loss

We evaluated a plant–frugivore assemblage and its derived ecosystem function, seed dispersal, along a gradient of anthropogenic disturbance in the Cantabrian forest. Forest loss had a strong effect on landscape-scale distribution of fruits and birds. These effects entailed a decay of the seed dispersal, evidenced by a decrease in both the magnitude and the clumpiness of seed rain from continuous forest to the heathland–pasture matrix. Similar functional decays have been reported for both tropical (Lehouck et al. 2009a, Moran et al. 2009) and Mediterranean (Santos and Tellería 1994) forest ecosystems. Furthermore, the effect of forest loss on seed dispersal was also evident at the small scale, as seed deposition was much less frequent in the open microhabitats than under trees.

Our study evidenced strong temporal variability in the components of the plant–frugivore assemblage, as the abundances of fruit and bird species changed across years. In the case of fruits, this temporal mosaic was related to *I. aquifolium* masting processes (Guitián and Bermejo 2006). In the case of thrushes, although our measurements of bird abundance were rough estimates of population size, inter-annual variation could derive from population changes caused by winter hardness or hunting pressure in other parts of the wintering area (Herrera 1998, Guitián and Bermejo 2006). We cannot exclude some fruit tracking

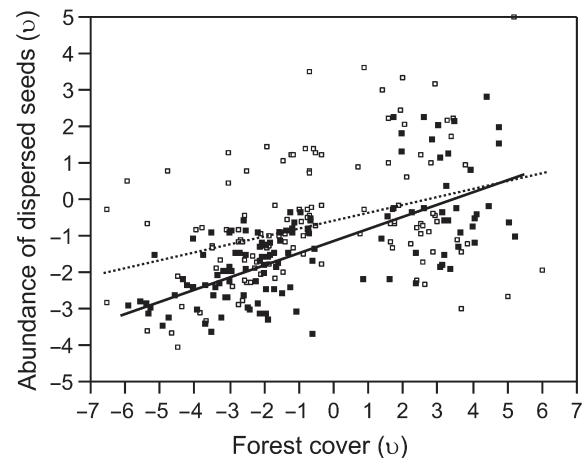


Figure 5. Response of seed dispersal to forest cover. For each sampling point in the study plot in different years (2007, white dots; 2009, black dots), dots represent the values of SADIE-provided clustering indexes (v) for the abundance of dispersed seeds and forest cover. Lines of regressions between the clustering indexes of forest cover and abundance of dispersed seeds are also represented (2007, dashed line; 2009, continuous line). Regressions differ in elevation ($t = 3.27$, $p < 0.05$, $n = 247$) and slope ($t = -2.37$, $p < 0.05$, $n = 246$).

across years, as bird activity in our locale increased from 2007 to 2009, mirroring fruit availability (but see Guitián and Bermejo 2006).

The spatial patterns of seed dispersal also varied between years. Relative to 2009, seed rain in 2007 was more widespread across the plot and less dependent on forest cover (Fig. 5). Moreover, seed deposition was more likely in open microhabitats in 2007 than in 2009. In other words, the constraining effects of habitat loss on the spatial patterns of seed dispersal were buffered in 2007. Considering that seed dispersal by birds drives tree recruitment in the Cantabrian forests (García et al. 2005c, Herrera and García 2010), we would interpret this buffering effect as an increased probability of tree recovery in the deforested matrix, and, hence, a major determinant of forest resilience to anthropogenic change.

Redundancy and response diversity within the plant–frugivore assemblage

Our results show that frugivore diet was more variable between years than between species (but see Guitián and Bermejo 2006, Martínez et al. 2008). In 2007, when fruiting display was dominated by *C. monogyna*, all bird species largely consumed this plant resource. In 2008 and 2009, the proportion of *I. aquifolium* increased greatly in the diet of thrushes, especially for the more abundant *T. iliacus*. Thus, diet composition was dominated by the more abundant fruiting species every year, suggesting that thrushes also tracked the inter-annual variability in fruiting composition (Carnicer et al. 2009). These similarities in diet between frugivores, together with the strong inter-annual variability, could contribute to the larger seed deposition in forest-devoid sectors in 2007, since all bird species fed on the more abundant – but also the most widely

distributed – *C. monogyna* fruits during this year. Thus, diet could be a source of functional redundancy with an effect on seed dispersal resilience. However, given that seed deposition is strongly determined by post-foraging behavior (Jordano and Schupp 2000), the role of diet variability is obviously entangled in the effect of fruit spatial distribution on frugivore movement.

Frugivorous thrushes showed inter-specific differences in post-foraging distances, with *T. viscivorus* and *T. philomelos* showing larger distances than *T. merula* and *T. iliacus* (Jordano and Schupp 2000, Martínez et al. 2008). Foraging distances may have an ultimate effect on dispersal distances, with broader-range frugivores generating wider seed-deposition patterns (Spiegel and Nathan 2007). However, the differences in foraging distances observed here did not seem to have a strong effect on the inter-annual changes in seed dispersal, given that in 2007 we found a wider seed rain even with no larger relative abundances of broader-range thrushes.

The differential response of frugivore species to the same gradient of disturbance may lead to some seed deposition in those more degraded landscape sectors (Santos et al. 1999). In our case, we found differences between thrushes in the frequency of use of open microhabitats, and in the degree of spatial match between forest cover and bird abundance. From both processes, *T. viscivorus* emerged as the species with the stronger ability to overcome the barriers imposed by forest loss (Jordano and Schupp 2000, Martínez et al. 2008). Nevertheless, the differences between species seemed weaker than the differences between years in the response to habitat loss, as all species were more frequent in the low-covered landscape sectors in 2007, but progressively restricted to high-covered areas in 2008 and 2009 (Fig. 4). Thus, we found increased dispersal to open microhabitats and to low-covered landscape sectors even with no strong changes in the relative abundance of species with a larger ability to cope with forest loss. Hence, rather than being derived from response diversity, we should interpret seed dispersal resilience in our study system as a consequence of the response by the whole frugivore assemblage.

Fruits and thrushes as components of ecological memory

We found a clear spatial response of the whole frugivore assemblage to forest cover and fruit availability across the landscape, since the clumpiness of bird abundance was explained by these habitat features across years. Nevertheless, the relative role of resource abundance vs that of forest cover differed between years. Namely, fruit availability effect was stronger in 2007, when *C. monogyna* dominated the fruiting landscape across the whole plot (i.e. fruits were even abundant in small patches and remnant trees; Fig. 3), than in the other years, when *I. aquifolium* crops increased and far fewer fruits were proportionally available out of large forest patches. We interpret the change in the relative effects of fruit availability to be the consequence of a stronger fruit-resource tracking that led thrushes to overcome their reluctance to enter into deforested areas, where they are

more exposed to their predators (García et al. 2011). Similar effects of scattered resources have been described for other frugivores in fragmented landscapes (Lehouck et al. 2009b, Breitbach et al. 2010). More importantly, the changes in the relative strength of fruit tracking encompassed the differences across years in the response of seed rain to the gradient of habitat loss. Namely, the stronger the response to fruit availability by the whole frugivore assemblage, independently of forest cover, the larger the proportion of seeds reaching low-covered areas. We may thus conclude that fruit-resource tracking may have a strong impact on the resilience of seed dispersal to habitat loss.

Ecological memory represents the historical component of ecosystem resilience, i.e. the biological information that remains after disturbance, enabling the re-establishment of functions (Nyström and Folke 2001). In our case, a forest affected by habitat loss, ecological memory derives from those traits and features enabling seeds to reach deforested areas and start woodland recovery. Among various possible traits, the capability of trees to bear large crops over a long life-span, generating different fruiting templates on the same landscape across years, and to persist in the more degraded sectors of habitat, together with the ability of birds to track for fruits across space and time, would make it possible to broaden seed dispersal across the landscape. Of the various potential features, small forest patches and isolated trees would drive the trajectories of birds tracking for fruits through the deforested matrix. Moreover, ecological memory depends on the interaction between organisms and environmental features that operate as biological legacies, mobile links and support areas. In our case, fruiting trees inhabiting small forest patches, or even isolated within the deforested matrix (mostly *C. monogyna*), are biological legacies that attract frugivorous bird to feed or perch on them, and hence, operate as nucleation foci for seed dispersal and recruitment (Elmqvist et al. 2001, Herrera and García 2009). Frugivorous thrushes, by moving from forest stands towards the deforested matrix, are mobile links that connect patches suffering different degrees of degradation via seed deposition (Lundberg and Moberg 2003, García et al. 2010). And finally, fruiting trees dominating large forest patches (mostly *I. aquifolium*) are support organisms producing large seed outputs to be transferred by birds across the landscape (Elmqvist et al. 2001). In sum, our study evidences the usefulness of biological legacies, mobile links and support organisms, to typify functional groups – and hence to represent functional diversity – within species assemblages (Folke et al. 2004).

Concluding remarks

Our study suggests that resilience of seed dispersal to habitat loss depends mostly on the functioning of the whole plant–frugivore assemblage, rather than on the functional redundancy and/or response diversity of frugivore species. However, we can exclude neither stronger effects of these forms of frugivore singularity in systems showing greater variability in frugivore composition than that found here, nor the potential effects of other frugivore traits driving

dispersal effectiveness (e.g. those determining the treatment of seeds in the gut and the number of seeds dispersed). In any case, we would surmise that the effect of fruit tracking process on seed dispersal resilience shown here may be generalized to other temperate and tropical systems, frequently composed of highly mobile frugivores but currently affected by habitat loss and fragmentation (Lehouck et al. 2009b, Breitbach et al. 2010, González-Varo 2010). Similarly, resource tracking by mobile consumers might be a major source of resilience of many trophic functions to different types of human-induced disturbances (e.g. insects tracking for flowers and maintaining pollination under habitat loss, carnivores tracking for ungulates and controlling grazing under over-hunting, parasitoids tracking for out-breaking prey and maintaining pest control under climate change; Lundberg and Moberg 2003, Kremen et al. 2007). Thus, we encourage the consideration of trophic processes as drivers of the response of many species assemblages, suppliers of ecosystem services, to the new environmental mosaics generated by anthropogenic global change.

Acknowledgements – We thank J. Rodríguez, J. Rodríguez-Pérez, V. Rivera, C. Guardado, and R. Pérez, for technical support in field and lab work, and V. Lendrum for linguistic advice. Funding was provided by European Social Fund and Spanish Ministry of Science (FPI grants to DM and JMH, CGL2008-01275 and CGL2011-28430 grants to DG), and CONICET and FONCYT (PIP 114-200801-00276 grant to JMM).

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Supplementary material (Appendix E7519 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.