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Spatial networks of fleshy-fruited trees drive the flow of avian seed dispersal through a landscape

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Summary

1. Seed dispersal by animals leads to plant genes, individuals and species flowing across the landscape, but this process has been seldom seen as the explicit result of structural or landscape connectivity.

2. For two years, we studied avian seed dispersal of fleshy-fruited trees in a secondary forest of the northern Iberian Peninsula, considering the areas under the canopies of fruiting trees as hubs of seed deposition.

3. Using graph-theory models, we set a spatially explicit network in a continuous landscape, with individual fruiting trees as nodes and expected frugivore movements as links between nodes. We calculated the contribution of each tree to network connectivity, finding strong inter-annual variability derived from tree properties (position, fruit crop and species).

4. Trees contributing the most to connectivity accumulated larger seed clumps under their canopies, demonstrating agreement between a network structural connectivity and the functional connectivity of seed dispersal flow. This pattern, however, is accentuated when the large-scale distribution of fruiting crops closely matches that of individual trees, suggesting between-year variation in resource tracking by avian frugivores.

5. Our findings reveal connectivity to be an emerging property of plant-disperser systems, operating at the scale of individual fruiting plants, but contingent on the yearly, large-scale templates of fruiting crops.

Key-words: *Crataegus monogyna*, dispersal hubs, functional connectivity, *Ilex aquifolium*, landscape ecology, plant–frugivore interactions, seed rain, structural connectivity, *Turdus* spp.

Introduction

Connectivity is the property of ecological systems whereby flows of information through space, time and hierarchical levels of organization are maintained (Baguette *et al.* 2013). In spatial terms, connectivity means that the distribution of ecological objects with respect to their weight, abundance and degree of isolation modulates ecological flow. The so-called structural connectivity describes the potential flow of information of a given landscape, and it is the sum of the spatial relationship between elements (i.e. patches of habitat or resources) and is described by likely physical relationships between them, whereas 'functional connectivity' represents the actual flux of ecological processes, such as organism dispersal or nutrient transfer, across these spatial elements (Fagan & Calabrese 2006; Baguette *et al.* 2013). Structural connectivity is easier to assess than functional connectivity, even when it is estimated with some synthetic measures of the spatial behaviour of organisms, to decide which landscape elements may be connected or not by organisms' movement (e.g. animal home-range size). Nevertheless, structure-based measures may provide incorrect estimates of actual ecological flows, given that functional connectivity inherently incorporates the species-based properties of mobile organisms, which are highly variable over short and long time-scales (Taylor, Fahrig & With 2006; Baguette & Dyck 2007). Thus, there is a strong move to demonstrate the link between structural and functional connectivity by explicitly assessing the variation in key ecological functions across the observed gradients of structural connectivity (Fagan & Calabrese 2006; Baguette *et al.* 2013). This is especially relevant to predict how and in which conditions landscape spatial structure maintains the ecological flows (Taylor, Fahrig & With 2006) and the population dynamics of organisms in real-world landscapes (Wiegand *et al.* 1999).

Seed dispersal is a key process for the dynamics of plant populations and communities, because it provides the

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movement of genes, individual seeds and plant species across the landscape (Jordano 2007). The consequences on plant populations of such a movement of seeds are considered to depend on its magnitude and directionality, that is, whether it mostly occurs within landscape patches (e.g. Spiegel & Nathan 2007), between locally associated patches (e.g. Prasad & Sukumar 2010; Morales *et al.* 2012) or between groups of habitat patches enhanced by stepping stones (Herrera & García 2009; Carlo *et al.* 2013). Nevertheless, seed dispersal has seldom been viewed as a flow resulting from connectivity (but see Soons *et al.* 2005), and empirical evidence on how landscape structure shapes the flux of individual seeds and species is still lacking. In the case of animal-dispersed fleshy-fruited species, it has been hypothesized that individual fruiting plants may act as elements that promote seed flow (Carlo, Aukema & Morales 2007), resulting from the active tracking by animals of fruit and cover resources (García, Zamora & Amico 2011; Carlo *et al.* 2013). Frugivores drop many seeds under plant canopies acting as nucleation foci (e.g. Clark *et al.* 2004; Blendinger, Blake & Loiselle 2011), and this seed deposition may be highly contingent on the individual plant location relative to co-fruiting partners (Saracco, Collazo & Groom 2004; Morales & Carlo 2006; Morales *et al.* 2012). Additionally, fleshy-fruited plants can produce complex yearly patterns of fruit crop distribution and species-based availability of fruits (e.g. mast fruiting), which leads to the hypothesis that the relative role of each individual plant on seed dispersal flow may strongly vary between fruiting events, even within the same landscape (e.g. García *et al.* 2013).

Here, we demonstrate that fleshy-fruited trees drive seed dispersal flow using an integrative framework of structural or landscape connectivity. By means of a graph-theory approach (Dale & Fortin 2010), we were able to decompose a heterogeneous landscape into spatially explicit, discrete nodes (fleshy-fruited trees) and the links between them (connections expected from frugivore movements), aiming to infer the effects of functional connectivity on seed dispersal from seed deposition patterns. We applied this approach to the secondary forest of the Cantabrian Range, where frugivorous birds are known to track resources across yearly mosaics of individual fruiting trees (García *et al.* 2013). In fact, the characteristics of the neighbourhood of individual fruiting trees, such as the surrounding abundance of fruits of the same or of other species, influence the frugivory rate at the tree level (Martínez, García & Herrera 2014). We thus hypothesize that these neighbourhood effects would cascade into the magnitude of seed deposition below individual trees. In other words, the relative position and the fruit crop size of individual trees would be features conditioning the seed flow among fruiting trees, and hence throughout the whole forest landscape. Specifically, the present work aimed to verify (i) the structural connectivity provided by fleshy-fruited trees and (ii) the relationship between structural connectivity and the abundance of avian-dispersed seeds (i.e. the functional connectivity of seed dispersal). We interpret the potential changes in functional connectivity between years in relation to landscape-scale variations in fruiting patterns.

Materials and methods

STUDY SYSTEM

Our study system comprises the assemblage of fleshy-fruited trees of the secondary forest in the Cantabrian Range (N Iberian Peninsula) and their avian frugivore guild. This forest is highly fragmented and dominated by fleshy-fruited trees, mostly Holly (*Ilex aquifolium;* 65·8% of fleshy-fruited trees in our study plot), Hawthorn (*Crataegus monogyna*; 25·5%) and Yew (*Taxus baccata*; 4·0%). All these species ripen in autumn (October to November). Hawthorns and female Yews produce single-seeded fruits, whereas female hollies two to four seeds (pyrenes) per fruit (García, Obeso & Martínez 2005); while yew trees do not produce 'true' fruits, we consider herein their fleshy arils to be functionally equivalent to angiosperm fruits. Average fruit crops for individual trees are ca. 2700, 2200 and 3900 fruits for holly, hawthorn and yew, respectively (D. García, unpubl. data). Strong inter-annual differences in fruit production are typical, both within (i.e. masting vs. non-masting events) and between tree species (García *et al.* 2013). The core of the frugivore guild is dominated by wintering thrushes (*Turdus* spp.). In the Cantabrian Range, wintering thrushes are almost exclusively frugivores and feed mostly on the dominant fleshy-fruited species (Martínez, García & Obeso 2008). Their daily activity is dominated by foraging for fruits and resting on tree perches, with only occasional landing on open ground (García *et al.* 2013). Namely, fleshy-fruited canopies typically account for more than 75% of perching events in the Cantabrian secondary forests (García *et al.* 2013; see also Martínez, García & Obeso 2008). Flocking behaviour is typical when moving between perching trees and fruiting patches. Thrushes are legitimate seed dispersers of fleshy-fruited trees as seeds are deposited intact in faeces, which are mostly defecated when birds are perching or just taking off from perches (authors' pers. obs.). The small-scale distribution of seeds mirrors the spatial patterns of bird movement, with >80% seeds occurring below trees and <20% appearing in open microhabitats such as rocks and pastures (García & Martínez 2012; García *et al.* 2013). After deposition by birds, seeds may suffer predation by rodents (*Apodemus* spp.) and predation frequency peaks in late winter (García, Obeso & Martínez 2005). Rodents do not act as seed dispersers (García, Obeso & Martínez 2005).

STUDY SITE

The study site was located in the Sierra de Peña Mayor (900 m a.s.l., Asturias region, N Spain; Fig. 1), a mountain range where secondary forest is intermingled with meadows, heathland and limestone rocky outcrops. We set up a 400 × 440 m rectangular plot in which the amount of forest cover ranges from densely covered sectors in the NE to areas of scant cover and isolated remnant trees in the SW (Fig. 1). Spatial segregation of fleshy-fruited trees exists in our study site (Herrera & García 2009; García *et al.* 2013). Namely, *C. monogyna* trees occur across the whole study plot (i.e. from the deforested matrix to larger forest fragments), whereas *I. aquifolium* and *T. baccata* trees mainly locate in forest patches (Fig. 1). From September to February, we carried out two field surveys in consecutive fruiting periods: 2009–2010 and 2010–2011 (hereafter 2009 and 2010, respectively). Further information about this site can be found elsewhere (García *et al.* 2013).

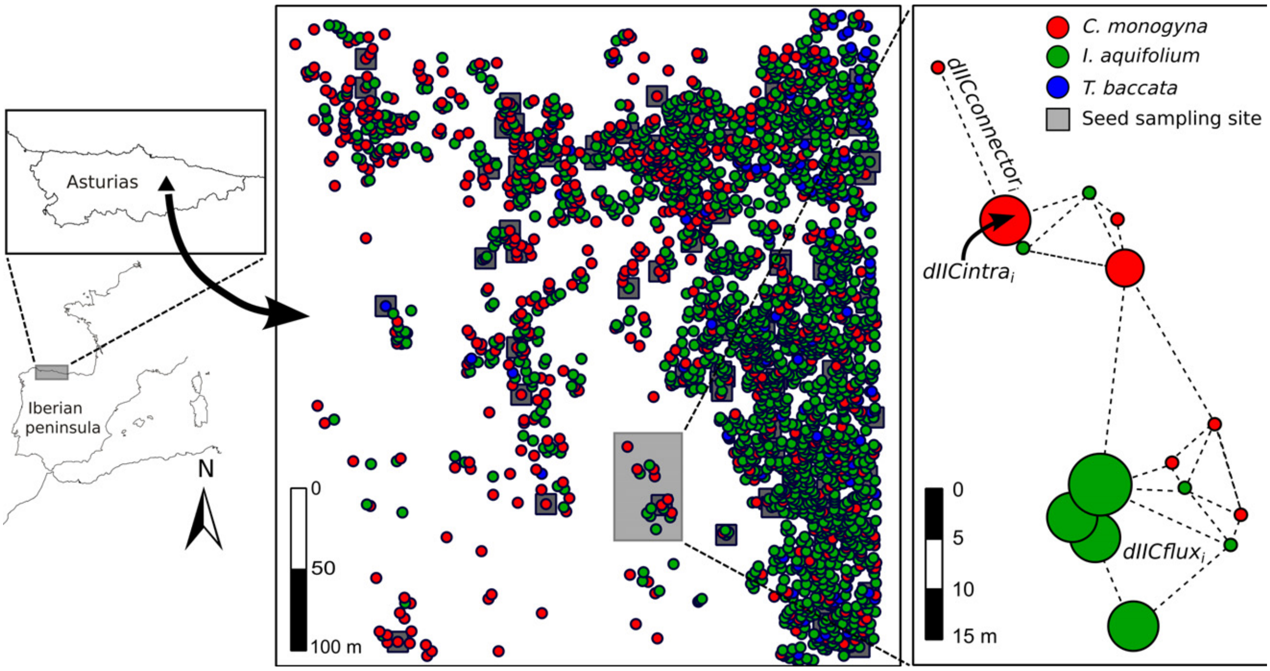

Fig. 1. Location of the study site (left panels) and the distribution of fleshy-fruited trees in the study plot (midpanel). Circles represent the position of fleshy-fruited trees ($n = 2384$ trees, species defined by colours). Seed sampling stations ($n = 87$ quadrats, located below fleshy-fruited trees) are set in grey squares. The right panel illustrates a zoomed landscape portion defined by a spatially explicit network that considers each tree as a node (circles) connected by links (dashed lines). Node size represents fruit crop. Two nodes are directly linked if their Euclidean distance is <50 m (only some potential links are shown, for clarity).

DATA COLLECTION OF SPATIAL DISTRIBUTION OF TREES AND FRUIT CROP

We developed a Geographical Information System (GIS, ArcGIS 9·3) based on a recent (2011) 1:5000-scale orthophotograph of the study plot. At the beginning of the fruiting season (from September to October), we traversed the entire plot visually recording the standing crop of all fleshy-fruited trees by means of a semi-quantitative Fruiting Abundance Index (FAI; considering six intervals: 0 = without fruits; 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10 000; 5 ≥ 10 001) (Saracco, Collazo & Groom 2004). All data on position, species and FAI of individual trees were incorporated into the GIS platform.

SEED RAIN DATA COLLECTION

The species-based abundances of dispersed seeds were estimated from sampling stations (50 × 50-cm quadrats) located below the canopy of fleshy-fruited trees (Fig. 1). These stations were a subset of a larger sampling set involving 2200 quadrats uniformly distributed across the whole plot and separated from each other by at least 2 m (García & Martínez 2012). In our case, we selected those stations unequivocally located below monospecific canopies of individual trees belonging to the three most abundant fleshy-fruited species in our study plot, namely 24 stations under *C. monogyna*, 59 under *I. aquifolium* and four under *T. baccata*; sample sizes mirrored the relative species-based abundance of these fleshy-fruited trees in the whole plot ($\chi^2 = 6$, d.f. = 4, $P = 0{\cdot}199$). For each year, we estimated the number of dispersed seeds per tree species in each sampling station as the sum of seeds found in two consecutive surveys (late November and mid-January). During the two fruiting years, we collected all bird-dispersed seeds in sampling stations during two field surveys (November and January). These seeds included both intact seeds and those showing signs of post-dispersal predation by rodents (seed husks or empty coats). The proportion of rodent-predated seeds found in sampling surveys was low (3·84% in 2009, and 2·63% in 2010, relative to the total number of dispersed seeds) and independent of the spatial distribution of bird-dispersed seeds (García, Zamora & Amico 2011). For each station, we calculated the seed abundance as the cumulative number of seeds deposited through the season.

MEASURES OF STRUCTURAL CONNECTIVITY PROVIDED BY FLESHY-FRUITED TREES

We considered that individual fleshy-fruited trees were interconnected by the flux of seed dispersal by avian frugivores when moving from one tree to another, and used graph-theory models to quantify the structural or landscape connectivity of our continuous study site for seed dispersal (Dale & Fortin 2010). The graph perspective conceives the landscape as a network of nodes (in our case, trees) connected between nodes (links between nodes), meaning that a connection between two nodes implies flux of information or 'structural connectivity' within the landscape (i.e. the movement of seeds). Indeed, the application of network-based models and metrics has been explicitly encouraged for the resolution of ecological questions that require characterization of connectivity at relatively large scales (Fagan & Calabrese 2006).

We ranked individual nodes based on the metrics calculated by the so-called methodology of 'patch-removal experiments', which uses theoretical experiments to assess the node importance within the landscape (Bodin & Saura 2010). Such metrics are calculated after sequentially removing each individual node and calculating their resulting effect on the overall connectivity metric (Saura & Pascual-Hortal 2007; Saura & Rubio 2010); in other words, nodes are ranked according to how much the connectivity metric decreases when they are removed (Bodin & Saura 2010). The metrics are the following: first, *NL* represents the number of links each node has, given a specific threshold distance. Second, the integral index of connectivity (*IIC*) and the probability of connectivity (*PC*) are global measures of connectivity accounting for certain landscape properties (i.e. dependent on node attributes, classically measured as habitat availability at the landscape scale). While *IIC* is a binary index based on a simplified connection model between nodes at a threshold distance, *PC* is a probabilistic connection allowing a continuous modulation of the connection strength (i.e. based on the distance decay function between nodes). To identify critical elements within a network, the relative contribution of the node *i* to the overall connectivity can also be calculated from the percentage of variation in, for instance, *IIC* caused after the removal of the node *i* from the landscape

$$dIIC_i = 100 \times \frac{IIC - \mathrm{ICC}_{remove,i}}{\mathrm{ICC}} \qquad \text{eqn 1}$$

where $dIIC_i$ is the relative contribution of the element *i* within the landscape to the overall *IIC*, after removing element *i* from the landscape. Similar relative contributions can also be calculated for *NL* (dNL_i) and *PC* (dPC_i). It should be noted that $dIIC_i$ and $dIIC_i$ were conceived for its use as a relative metric aimed to evaluate the importance of and/or changes in landscape elements and thus vary with the number of elements per landscape (Saura & Rubio 2010). The absolute values of *PC* are of less interest since very low values of $dIIC_i$ or dPC_i may be obtained when the node attributes (e.g. habitat availability or fruit crop of each node) are very small compared with the network topology of the entire landscape (Saura & Rubio 2010).

Network metrics can be further partitioned into three separate fractions that quantify the different ways in which nodes and links contribute to overall connectivity; this approach has the advantage that latter metrics are measured in the same units and can be directly compared and summed within a unifying framework (Saura & Rubio 2010). For instance, $dIIC_i$ can be partitioned into:

$$dIIC_i = dIICintra_i + dIICflux_i + dIICconnector_i \qquad \text{eqn 2}$$

where $dIICintra_i$ is the contribution of node *i* in terms of intrapatch connectivity (based on node attributes, such as habitat availability or fruit crop) and does not depend on either links or network topology. $dIICflux_i$ corresponds to the area-weighted dispersal flux through the connections of node *i* to, or from, all of the other nodes in the landscape when *i* is either the starting or ending node of that connection or flux. Hence, $dIICflux_i$ depends on both the node's attributes (i.e. fruit crop of each tree) as well as its position within the network topology. In other words, $dIICflux_i$ measures how attributes of a given node are well connected to the rest of them (in terms of the amount of flux based on node attributes; Saura & Rubio 2010). Finally, $dIICconnector_i$ is the contribution of the node or link *i* to the connectivity between other nodes and depends only on the topological position of a node or a link in the network. when *dIICconnectori* fraction is high is key to maintain connectivity between groups of nodes and/or few nodes with high attributes (e.g. patches with high habitat availability or fruit crop) and is useful to detect nodes acting as stepping stones that facilitate the dispersal flow in the landscape (Saura & Rubio 2010).

GRAPH PARAMETERIZATION OF THE FLOW OF SEED DISPERSAL BETWEEN FLESHY-FRUITED TREES

We constructed a spatially explicit network within the limits of our study plot, where fleshy-fruited trees represented nodes, and the between-tree distances the links potentially connecting each node (Fig. 1). Due to computational limitations (Saura & Torne 2009), we restricted our analysis to *I. aquifolium*, *C. monogyna* and *T. baccata* ($n = 2384$), which represented 68·4% of all trees in our study plot and accumulated more than 70% of perching events by frugivorous thrushes (García *et al.* 2013). Translated into a graph-theory model, we assumed that tree nodes were exclusively differentiated by the individual fruit crop (i.e. estimated from FAI, see above); in other words, we expected frugivorous thrushes to be more attracted to individual trees with large fruiting crops (Herrera, Morales & García 2011). Seed transfer between tree species existed (García, Martínez & Obeso 2007), and we considered it reasonable to assume that the probability of between-tree seed dispersal (i.e. links between tree nodes) was independent of species identity. Additionally, non-fruiting individuals (such as *I. aquifolium* and *T. baccata* males) can still be used as perches by avian frugivores, as the densities of dispersed seeds could be similar to those deposited under female trees (Martínez, García & Obeso 2008); we thus assigned an arbitrary value of FAI = 0·5 as a low-attribute value for non-fruiting trees (i.e. nodes with attribute values of 0·0 are not connected with other nodes; Saura & Torne 2009).

We further established a distance threshold to characterize the potential links between trees, based on the distribution of flying distances between consecutive perches of the frugivorous thrushes recorded in our study site. Specifically, we found that 95% of distance bounds between perches were below 50 m (García *et al.* 2013; Morales *et al.* 2013), and we thus set a distance threshold of 50 m for binary indexes (*dNL* and *dIIC*). We calculated probabilistic indexes (*dPC*) dependent on distance-based probabilities between links (Saura & Torne 2009). In our case, we parameterized a negative exponential function, corresponding to a median of 15 m flying distance between two perches with a probability of 0·5 (Morales *et al.* 2013). We thus calculated the relative structural connectivity of the tree *i* to the overall topology, with the metrics of *NL*, *IIC* and *PC* (eqn 1), aiming to identify those better functionally connected trees (with higher metric values) that potentially capture most of the flow of seed dispersal. For $dIIC_i$ and dPC_i, we further computed the three fractions decomposed by the overall contributions on intrapatch, flux and connector (eqn 2). We calculated structural connectivity metrics with Conefor 2·6 (Saura & Torne 2009; Saura & Rubio 2010). In addition, we used generalized linear models (GLMs) to test the variability of fruit crop, *dNL*, *dIIC* and *dPC* explained by the effects of 'Fleshy-fruited species' and 'Year' as categorical variables. Variables were fitted to Poisson (fruit crop) and Gaussian error distributions (*dNL*, *dIIC* and *dPC*) and log- and identity link functions, respectively.

RELATIONSHIP BETWEEN LANDSCAPE CONNECTIVITY AND SEED DISPERSAL

We performed statistical analyses aiming to explain seed abundance under trees (i.e. functional connectivity of seed dispersal) as a response to the structural connectivity generated by individual fleshy-fruited trees (decomposed by spatially explicit metrics of graph-theory models; see above). We performed two models: first, we explained the variables of seed dispersal based on the relative contribution of individual trees (eqn 1). Second, we analysed seed abundance as a function of the relative structural connectivity fraction of individual trees (eqn 2).

Using seed abundance as dependent variable, we compared a set of candidate models incorporating independent variables based on resources (fruit crop measured as FAI), landscape connectivity metrics (*dNL*, *dIIC* and *dPC*) or fractions of those connectivity metrics (e.g. *dIICintra*, *dIICflux*, *dIICconnector*). Models included 'Year', 'Fleshy-fruited species' (except *T. baccata* because of the low sample size, $n = 4$), each of the resource-connectivity independent variables and their interactions (e.g. 'Year' × 'Connectivity metrics'). We did not include variables of fruit crop and landscape connectivity in the same candidate models due to the fact that latter variables were highly correlated (i.e. r^2 >0·840). Analyses were fitted to GLMs, following zero-inflated Poisson error distributions and log-link functions with the *pscl* library (R Development Core Team, 2012). We tested all model subsets as the result of all possible combinations of (independent) variables, selected the 'best model' as being the one with the lowest Akaike Information Criterion (AIC) and checked the spatial autocorrelation of the 'best model' residuals by means of Moran's I test using the *spdep* library (R Development Core Team, 2012).

Results

YEARLY FRUIT CROP AND ITS EFFECT ON STRUCTURAL CONNECTIVITY

We found strong inter-annual differences in the distribution of fruit crops, due to fruiting differences between species. For instance, fruiting in 2009 was strongly segregated in space, as most fruiting trees concentrated in high forest-cover areas (the NE of the study plot). Comparatively, in 2010, fleshy-fruited trees were more evenly distributed across the whole landscape (spanning from isolated trees to those inside the forest; see Fig. S1 in Supporting information). Fruit crop was proportionally higher in 2009 for *I. aquifolium* and higher in 2010 for *C. monogyna* and did not vary between years for *T. baccata* (Fig. 2a and Table S1, Supporting information). *I. aquifolium* and *C. monogyna* had proportionally more and less *NL*, respectively (Fig. 2b and Table S2, Supporting information). Yearly differences in the distribution of fruit crops cascaded into the metrics describing structural connectivity contributions of individual trees. For *dIIC* and *dPC*, *I. aquifolium* trees had more structural connectivity in 2009, whereas *C. monogyna* and *T. baccata* trees were better connected in 2010 (Fig. 2c and 2d , and Tables S2, S3 and S4).

FUNCTIONAL CONNECTIVITY OF FLESHY-FRUITED TREES AND SEED DISPERSAL

Below trees, the abundance of dispersed seeds was three-fold higher in 2009 compared with 2010 (Fig. 2e), but was 25% less diverse (Fig. 2f). *T. baccata* trees received more seeds in 2010 below their canopies, followed by *I. aquifolium* and *T. baccatta* in 2009. *C. monogyna* trees received a low amount of dispersed seeds in both years (Fig. 2e).

From the univariate models of fruit crop, *NL*, *dIIC* and *dPC,* we found that tree contribution to *dPC* best predicted (lowest AIC) seed abundance (Table 1). Trees with higher *dPC* had higher seed abundance below them (Fig. 3), and this connectivity metric was the most important factor explaining seed abundance (see Table S5, Supporting information). Between-year variability on *dPC* also explained an important fraction of the variability of the seed rain below trees (Table S5). For instance, tree *dPC* in 2010 resulted in relatively lower seed abundance. Residuals of the *dPC* model showed no spatial autocorrelation (Moran's test: I = 4·28*10-5, P = 0·367).

With our combination of parameters, *dPC* decomposition suggested that most of the relative contribution of fleshy-fruited trees depended on *dPCflux* (98·6%, both years averaged), followed by *dPCintra* and *dPCconnector* (Table

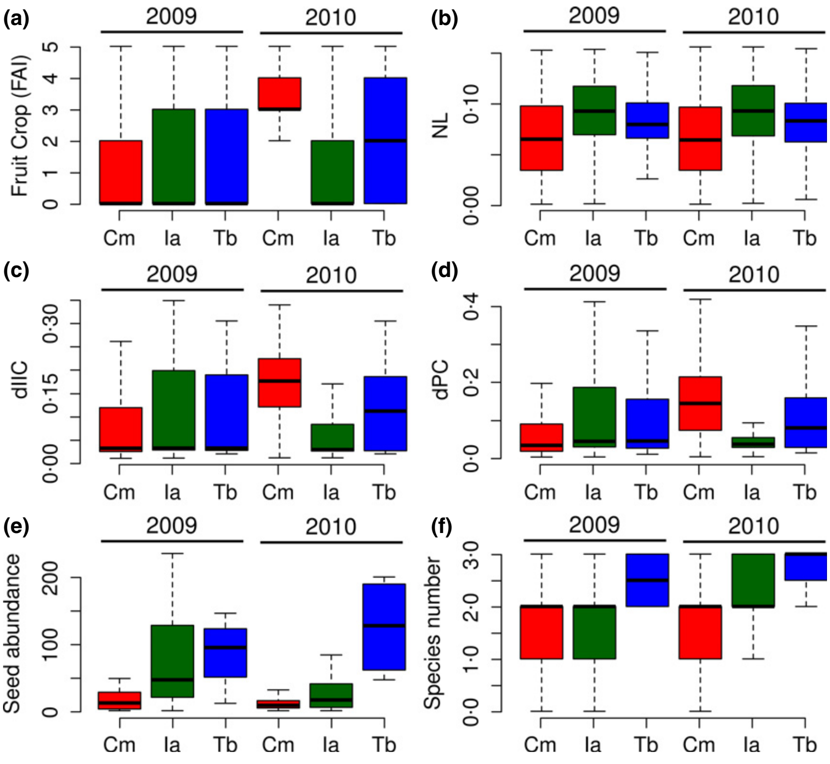

Fig. 2. Measures of (a) fruit crop (semi-quantitative Fruiting Abundance Index, FAI), (b) number of links (*NL*), (c) integral index of connectivity (*IIC*), (d) the probability of connectivity (*PC*), (e) seed arrival and (f) number of fleshy-fruited species in quadrats below trees, by fleshy-fruited species and years. Details about studied metrics are in the main text. a–d boxplots summarize the metrics of all fleshy-fruited trees in the study plot (n = 2384 trees), whereas e-f boxplots measures of sampled trees (n = 87 quadrats below trees). Fleshy-fruited species are *Crataegus monogyna* (Cm; n = 658 for a–d metrics and n = 24 for d–f), *Ilex aquifolium* (Ia; n = 1627 and n = 59, respectively) and *Taxus baccata* (Tb; n = 103 and n = 4, respectively).

S6, Supporting information). Trees with higher *dPC*intra and *dPC*flux, but lower *dPC*connector, received higher numbers of dispersed seeds below them (Fig. 4). Considering fixed factors, Year accounted for the largest variability explained by the model (Table S6). There were yearly and species-based differences in the effects of *dPC* components on seed abundance: trees with more *dPC*intra in 2010 had less seeds, and *dPCflux* and *dPCconnector* of *I. aquifolium* had relatively more seeds (Fig. 4).

Discussion

In this work, we have explained seed dispersal across a fragmented landscape by considering the network relationships between neighbour fleshy-fruited trees and the large-scale patterns of fruiting. We demonstrate that the individual characteristics of trees (species identity, fruit crop, spatial position) scale-up, by means of non-additive contributions, to an emerging property (structural connectivity) that ultimately drives seed dispersal by frugivorous birds. By relating this sort of tree-mediated structural connectivity to seed deposition patterns, we further evidence the actual functional connectivity of the studied landscape in terms of seed dispersal flow. We also show that the yearly variations in tree traits (fruit crops) lead to changes in the resource landscape for frugivores, modulating the imprint of tree network on the ecological function of seed dispersal.

Table 1. Summary of the set of candidate models fitting the abundance of dispersed seeds by fruit crop (Fruiting Abundance Index) and connectivity metrics (*dNL*, *dIIC* and *dPC*). In every model, we also include as independent variables ‘Year’ (2009 and 2010) and ‘Fleshy-fruited species’ (*Crataegus monogyna* and *Ilex aquifolium*), and the two-way interactions between independent variables. Dependent variables were fitted to a zero-inflated Poisson distribution. ΔAIC was the difference in the Akaike Information Criterion (AIC) values between each model and the low-AIC model (i.e. ΔAIC = 0·0 was the model with lowest AIC, showed in the last row)

Model	Log-likelihood	ΔAIC	Resid. d.f.
Fruit crop	−4232	−375·7	147
dNL	−4641	−625·9	147
dIIC-	−4107	−1445·1	147
dPC	−3919	0·0	147

FUNCTIONAL CONNECTIVITY OF SEED DISPERSAL ESTIMATED FROM GRAPH-THEORY MODELS

The spatial pattern of fruiting plants and the availability of frugivores are considered mainstream in predicting the variation in frugivory and seed dispersal between individual plants (Saracco, Collazo & Groom 2004; Morales & Carlo 2006; Morales *et al.* 2012). In fact, it has been hypothesized that frugivore activity may concentrate on ‘frugivory hubs’ (Carlo, Aukema & Morales 2007), specific neighbourhoods with plants interrelated by frugivore movements, likely leaving an imprint on landscape-scale seed dispersal patterns. In our case, we show that seed deposition increased in those neighbourhoods whose spatial structure facilitated the movement of birds among fruiting trees, demonstrating the existence of frugivory hubs from the functional outcome (i.e. seed dispersal) of the tree network.

This spatial network emerged from a graph-theory model that identified the relative role of each individual tree in terms of contribution to landscape or structural connectivity. Whereas our approach links individual trees based on observations of frugivore movements (i.e. ‘source tree’ perspective), we fail to characterize the long-distance dispersal events and precise location of the source and destination trees (Jordano 2007). Genetic tools (i.e. ‘target tree’ perspective) can overcome latter methodological caveats but still could have problems when the number of source trees is large or when source trees are close (i.e. overlapping their potential target areas; Jordano 2007). A previous study in our system, using seed labelling by stable-isotope tools, estimated a low frequency of effective long-distance movements (Carlo *et al.* 2013), suggesting

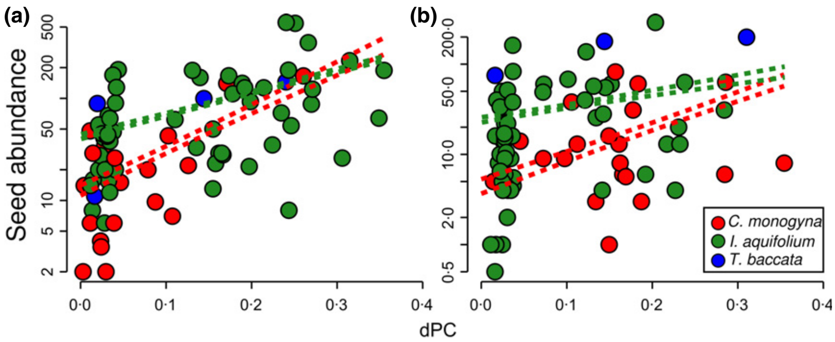

Fig. 3. Relationship between seed abundance and the contribution of each individual tree to network connectivity (*dPC*). 2009 (a) and 2010 (b). For each year and metric, trees are represented by dots (species defined by colours as in Fig. 1). For each panel, lines represent fitted values of the best-fitting model (see Table S5 in Supplementary information); fitted values for *Crataegus monogyna* were shown in black and for *Ilex aquifolium* in grey. Data for *Taxus baccata* trees are represented but not included in analyses (*n* = 4). Note the different scales of the x- and y-axes (log scaled).

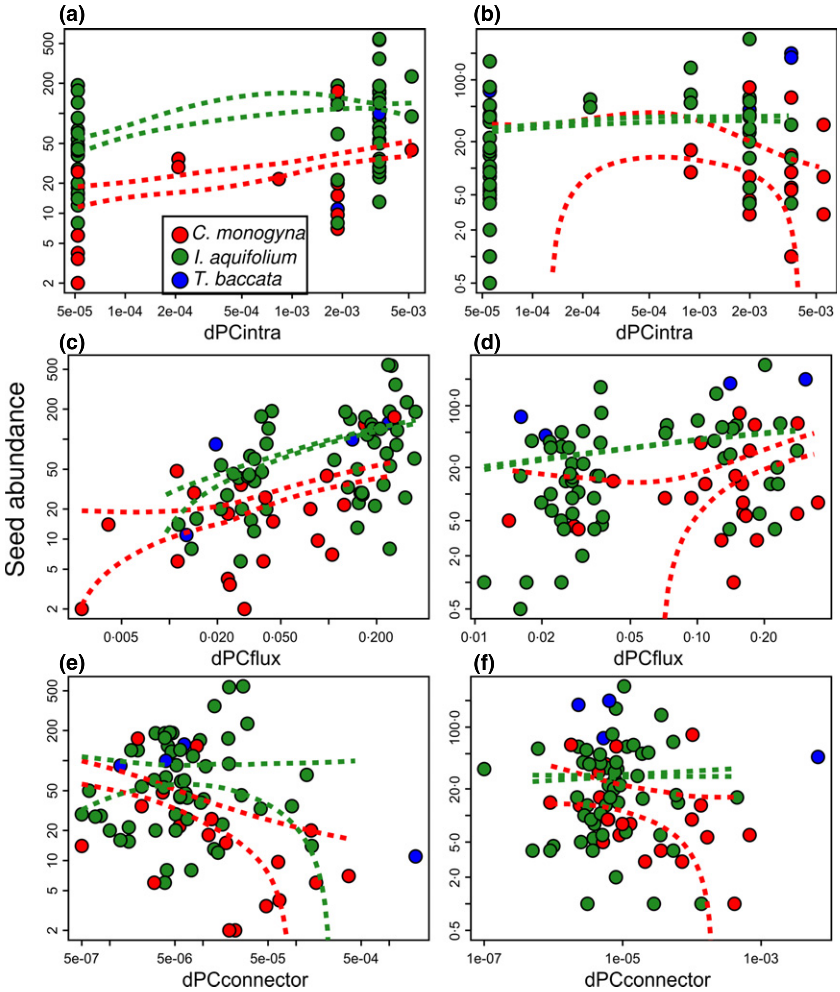

Fig. 4. Relationship between seed abundance and the contribution of each individual tree to *dPC* fractions, for 2009 (a, c, e), and 2010 (b, d, f). Connectivity fractions were decomposed by dPCintrai (a, b), *dPC*fluxi (c, d) and *dP* Cconnectori (e, f). Lines represent fitted values of the best-fitting model (see Table S6). For further conventions, see Fig. 3.

that our parameterization is well suited to account for the most frequent, short-distance and recurrent movements of frugivorous birds, and their likely effect on seed deposition below trees. In fact, seed dispersal in our system is commonly biased to areas under tree canopies (especially those holding fleshy fruits), and this habitat type concentrates a huge portion of total seed rain (Carlo *et al.* 2013; García *et al.* 2013). Thus, by focusing on fruiting trees as network nodes, we are representing major trends of landscape-scale seed dispersal flow, with a major influence on the recruitment of fleshy-fruited trees (García, Martínez & Obeso 2007; Herrera & García 2009; García *et al.* 2013). In any case, our work provides a straightforward description of seed dispersal flow derived from the frugivore displacements between trees, highlighting the role of birds as connectors (i.e. 'mobile links') of ecological information important for tree population dynamics (García *et al.* 2013).

INTER-ANNUAL VARIABILITY IN FRUIT CROP PATTERNS AND THE DILUTION OF SEED DISPERSAL FUNCTIONAL CONNECTIVITY

We here show that the two years studied represented contrasting layouts of the fruiting landscape. Namely, *I. aquifolium* masted in 2009 and that created a highly predictable, large-scale fruit distribution, which essentially mimicked forest cover (see also García *et al.* 2013). This led *I. aquifolium* trees to contribute much to the potential connectivity. In 2010, by contrast, a more heterogeneous pattern of fruiting emerged due to the joint effects of (i) the spatial singularity of *C. monogyna* trees (i.e. numerous individuals scattered across the study plot, irrespective of forest gradient; García *et al.* 2013), (ii) a proportionally higher/heavier fruiting of those *C. monogyna* trees isolated in the deforested matrix and (iii) a non-masting *I. aquifolium* year. This fruiting template was translated into a proportionally higher contribution of *C. monogyna* trees to structural connectivity. Interestingly, we found a stronger contribution to landscape connectivity and seed deposition below canopies for *T. baccata* trees in 2010, despite no differences in yearly fruiting crop in this species (see Fig. 2). This fact suggests that structural connectivity could result exclusively from the spatial structure of the surrounding 'fruiting landscape' and that may translate into functional connectivity (i.e. higher seed deposition below better connected trees). We would argue that yearly changes in large-scale fruiting patterns cascade into differences in functional connectivity for seed dispersal due to variations in the sensitivity of frugivores when tracking for fruit resources.

In fact, frugivorous thrushes are known to forage in a scale-dependent manner, adapting their tracking response to the changes in heterogeneity in fruiting resources (García, Zamora & Amico 2011). In 2009, resources (forest and fruits) were spatially congruent, and thus, frugivorous birds mostly tracked fruits inside the forest (García & Martínez 2012; García *et al.* 2013). *I. aquifolium* monopolized the seed rain in that year, and thus, the abundance of dispersed seeds below trees was threefold higher in 2009 compared with 2010 (i.e. on average holly fruits have c. three seeds). Hence, as a consequence of the concentration of frugivore activity in fruit-rich forest patches, the abundance of dispersed seeds under canopies depended on how well connected individual fleshy-fruited trees were. Indeed, the decomposition of structural connectivity components further highlighted the relative importance of big-crop-size, well-connected trees (i.e. high *dPC*flux values). In contrast, in 2010, when forest and fruits did not spatially agree, birds probably tracked for fruits at a broader scale and also provisioned from the big-crop-size *C. monogyna* trees scattered through the deforested matrix (see García *et al.* 2013 for a similar pattern in previous years for the same system). This change in the scale of foraging would have weakened the association between structural connectivity and seed abundance (badly connected matrix trees did not receive fewer seeds than well-connected forest ones; see also Herrera & García 2009). Finally, the structural connectivity decomposition also suggested that *C. monogyna* played a role in the change of frugivore foraging scale in 2010 as *dPC*flux was higher for this species during this year and had a positive effect on seed deposition.

The dilution of functional connectivity effects shown here could also be related to inter-annual variations in the composition of the frugivore guild since there may be strong functional differences between frugivore species (Jordano 2007). In our study system, thrush species have distinctive responses to resources (García *et al.* 2013; Morales *et al.* 2013), and yearly based variability in frugivore guild composition exists (García *et al.* 2013). Nevertheless, the effects of intraguild variability seem to be less important than the response of the whole frugivore assemblage to fruit production changes in determining the differences between years in large-scale patterns of seed rain (e.g. García *et al.* 2013). We would thus emphasize fruiting mosaics as a major source of contingency of large-scale seed rain patterns generated by frugivores with plastic activity responses.

Concluding remarks

We empirically demonstrate here that the connectivity for seed dispersal is a systemic property emerging from the relative non-additive contributions of individual trees and frugivores. We also emphasize that the existence of current links between structural and functional connectivity shapes tree population dynamics and that functional connectivity results from the plastic response of mobile frugivores to habitat spatial templates (Baguette & Dyck 2007; Baguette *et al.* 2013). In other words, a dynamic landscape of fruiting resources alters frugivore response, breaking the link between structural and functional connectivity for seed dispersal. Functional connectivity estimates, based on how each organism views the landscape across time (Baguette & Dyck 2007), need to be referred to the meaningful scales of the landscape at which ecological processes mostly operate (Wiegand *et al.* 1999). Promising methodologies based on a) genetic and stable-isotope tools (Baguette *et al.* 2013) and b) cost-distance and individual-based models (Baguette & Dyck 2007) could certainly lead to more accurate estimates of how organisms move throughout fragmented and dynamic landscapes. We would argue that these findings may be generalized to many ecological functions derived from spatially explicit trophic processes, especially those involving sessile organisms that perform as resource patches for mobile consumers (e.g. plant–animal interactions; Fortuna *et al.* 2008, 2009). Integrating this sort of spatially explicit networks with those accounting for the topology of trophic interactions (by means of 'graphs of graphs'; Dale & Fortin 2010) is a prerequisite to fully understanding the biodiversity response to human-caused landscape change (Hagen, Kissling & Rasmussen 2012).

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Supporting Information

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

Appendix S1 Additional results of the yearly fruit crop distribution and GLM analyses comparing fruit crop and connectivity metrics between tree species and years.

Fig. S1. Distribution of fleshy-fruited trees in the study plot by years.

Table S1. Results of the GLM analysis on fruit crop affected by years and fleshy-fruited species

Table S2. Results of the GLM analysis on the number of links affected by years and fleshy-fruited species

Table S3. Results of the GLM analysis on the integral index of connectivity of each tree affected by years and fleshy-fruited species

Table S4. Results of the GLM analysis on the integral probability of connectivity of each tree of each tree affected by years and fleshy-fruited species

Table S5. Parameter estimates for the GLM analysis on seed abundance (response variable) affected by the probability of connectivity of each fleshy-fruited tree, year and fleshy-fruited species

Table S6. Parameter estimates for the GLM analysis on seed abundance (response variable) affected by dPC fractions (i.e. dPCflux, dPCintro dPCconnect), year and fleshy-fruited species