Differential effects of fruit availability and habitat cover for frugivore-mediated seed dispersal in a heterogeneous landscape

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Summary

1. We investigated the effect of forest cover and fruit availability on frugivore-mediated seed dispersal of the ornithochorous tree *Crataegus monogyna* in highly heterogeneous secondary-growth forests of the Cantabrian Range (NW Spain).

2. During 2006 and 2007, we collected dispersed *Crataegus* seeds from 283 sampling stations in a 400×440 m study plot in which forest cover varied from dense to scant. Dispersal kernels were characterized with an extended version of the inverse modelling framework that incorporates the effect of the local environment at the source and the influence of all those environments that seeds potentially encountered during their dispersal path.

3. We found that forest cover and fruit abundance had opposite influences on dispersal patterns. Plants growing in cells with denser cover dispersed more seeds and at larger average distances than those from more sparsely covered cells, while mean dispersal distance and the probability of long-distance dispersal decreased with increasing abundance of fleshy fruits. However, the relative influence of these factors changed between study years, as forest cover had a weak effect on seed dispersal in the second year when fruits were scarcer and more heterogeneously distributed across the landscape.

4. Habitat resistance to seed movement increased with increasing forest cover. Consequently, cells with high forest cover in a matrix of sparse tree density were predicted to intercept a substantial amount of seeds.

5. *Synthesis.* Our results suggest that the local environment at a seed's source and, to a lesser extent, all those environments that seeds potentially encounter during their dispersal path can have pervasive effects on frugivore-mediated seed dispersal kernels in heterogeneous landscapes. They also highlight the fact that not just forest cover, but also the underlying fruit-resource distribution, needs to be considered to understand how environmental heterogeneity affects seed dispersal patterns. Our findings could be extended to landscapes subjected to anthropogenic disturbance such as fragmentation. Thus, the consideration of fruit-resource distribution seems essential for establishing the relationship between landscape pattern and the spatial behaviour of frugivores, and in turn, for explaining frugivore-mediated seed dispersal in fragmented landscapes.

Key-words: Cantabrian Range, *Crataegus monogyna*, dispersal, frugivore behaviour, habitat fragmentation, heterogeneity, plant–animal interactions, seed dispersal kernels

Introduction

Seed dispersal is a critical process as both the structure and dynamics of plant populations and communities can be strongly affected by the spatial template established by dispersed seeds (for reviews see Nathan & Muller-Landau 2000;

Levine & Murrell 2003). In many tropical and temperate ecosystems, a large proportion of plant species rely on fruit-eating animals (hereafter frugivores) for dispersal services (Herrera 2002). For these species, the probability of propagules leaving their parent plant, the ability to cross boundaries between habitat types, and the distance moved from their origin, largely depend on the abundance and spatial behaviour of frugivores (e.g. Clark *et al.* 2005; Westcott *et al.* 2005; Morales & Carlo

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2006; Russo, Portnoy & Augspurger 2006; Carlo & Morales 2008). Accordingly, in addition to plant species-specific traits, both seed removal probabilities and seeds' spatial distribution away from parent plants are also related to spatial environmental factors such as the availability of suitable food, shelter and climatic conditions for frugivore (e.g. Saracco *et al.* 2005; García & Chacoff 2007). However, our understanding of how environmental variables influence frugivore behaviour in spatially heterogeneous landscapes and the subsequent effects on seed dispersal patterns remains limited.

Recent studies show that environmental heterogeneity strongly conditions frugivore-mediated seed dispersal; for example, García & Chacoff (2007) found that fruit removal on *Crataegus monogyna* trees was strongly related to the nature of the neighbourhood surrounding source plants, with higher seed dispersal probabilities for plants growing in neighbourhoods with a higher degree of protective canopy. Additionally, theoretical studies based on simulations of bird foraging behaviour show that seed dispersal patterns are sensitive to the landscape-level degree of aggregation of fruiting plants and that the existence of neighbouring plants facilitates seed removal (Morales & Carlo 2006; Carlo & Morales 2008). However, despite these empirical and theoretical findings, there is a lack of integrative studies simultaneously assessing the relative importance of these neighbourhood- and landscape-level environmental effects on seed dispersal patterns. More importantly, the research literature has commonly neglected the fact that for frugivorous animals, movement decisions might simply reflect underlying fruit-resource distribution, rather than the influence of habitat cover itself (Lehouck *et al.* 2009; González-Varo 2010; Herrera & García 2010). In fact, the influence of both the amount of habitat cover and its spatial arrangement on frugivore behaviour may even be inconsistent over time because of spatiotemporal variations in fruit availability (Herrera & García 2009). Therefore, this inattention to underlying fruit-resource distribution may result in an incomplete and temporally inconsistent picture for predicting frugivore activity on, and therefore the subsequent seed dispersal patterns of, plants populating heterogeneous landscapes.

In this study, we explore the effect of two environmental variables, forest cover and fruit-resource availability, on seed dispersal kernels of the bird-dispersed tree *Crataegus monogyna* Jacq. (*Crataegus* hereafter) in highly heterogeneous secondary-growth forests of the historically human-managed Cantabrian Range (NW Spain). A common way to characterize seed dispersal patterns is by means of the inverse modelling (IM) approach. This estimates the seed dispersal kernel (i.e. the probability density function of the location of seed deposition with respect to the source, *sensu* Nathan & Muller-Landau 2000) based on the spatial distribution and fecundity of potential mother plants and the number of dispersed seeds arriving at traps of known location (Canham & Uriarte 2006). However, as we sought to evaluate the effects of environmental heterogeneity on seed dispersal kernels, we used an extended version of the IM framework recently developed by Schurr, Steinitz & Nathan (2008) that enabled us to explicitly incorpo-

rate the potential influence of the source's local environment as well as that of all the environments that seeds might have encountered during their dispersal path. Specifically, in this study, we are seeking to discover: (i) whether the local environment in which seed sources are located, or the environments the seed encounters along its dispersal path, is the most relevant environmental factor driving the dispersal process, (ii) how environmental variables (i.e. amount of forest cover and fruit availability) affect the seed dispersal process, (iii) if the amount of forest cover or the presence of fleshy fruits is the most important environmental variable for explaining seed dispersal kernels and (iv) whether dispersal kernels are affected by interannual variations in community-wide fruit availability.

STUDY AREA AND STUDY PLOT

Field work took place in the Sierra de Peña Mayor-Trigueiro (43°17′N–5°30′W), a mid-elevation mountain of the Cantabrian Range (Asturias, Spain). The site exhibits a karstic physiognomy, with limestone outcrops alternating with areas of shallow soil. Dominant canopy trees in the Sierra de Peña Mayor-Trigueiro include beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.), mainly occurring in a few large patches of hardwood forests adjacent to smaller, fringe areas of secondary-growth forests which are mainly populated by fleshy-fruited plant species such as holly (*Ilex aquifolium* L.) hawthorn (*Crategus monogyna* Jacq.) and yew (*Taxus baccata* L.). Owing to the high anthropogenic use for livestock grazing, secondary-growth forests in the Sierra de Peña Mayor-Trigueiro (and indeed across the Cantabrian Range in general) can be considered as woodland pastures, and they are characterized by low forest cover (*c.* 30%) embedded in a matrix of human-promoted stony pastures and heathlands (García *et al.* 2005).

To evaluate the role of forest cover and fruit availability on seed dispersal patterns of *Crataegus* along an increasing gradient of environmental heterogeneity, a 400 × 440 m rectangular plot was chosen in one such secondary-growth forest in September 2006 (Figs 1 and S1). Forest cover within the study plot overall was low (*c.* 27%), although it ranged from dense to scant, with forest patches strongly differing in size, shape and degree of isolation. Findings from previous studies assured the suitability of the extent of this spatial framework for accurately covering both the spatial grain of the movements of thrushes (*Turdus*) that are the main seed dispersers of the study species in this site (see *Dispersal system* below; Martínez, García & Obeso 2008), as well as the spatial scale of their response to forest cover (García & Chacoff 2007; Herrera & García 2010). Hence, our study plot accurately represented the spatial heterogeneity of secondary-growth forests in the Cantabrian Range, as well as the spatial scale at which the frugivore-mediated seed dispersal process occurs.

DISPERSAL SYSTEM

We studied seed dispersal of *Crataegus*, which was chosen as it is the most frequent tree species in our study site and is found
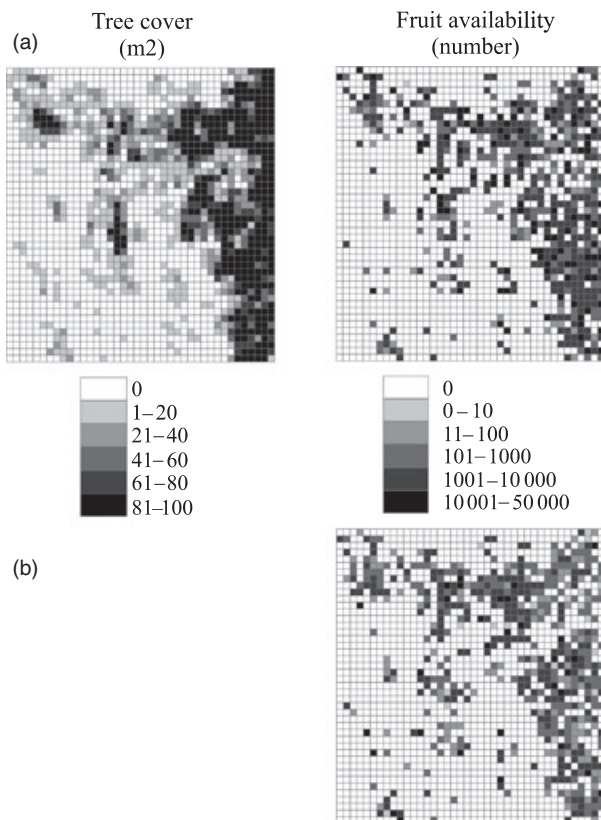
Tree cover (m2)

(a)

Fruit availability (number)

0
1–20
21–40
41–60
61–80
81–100

0
0–10
11–100
101–1000
1001–10 000
10 001–50 000

(b)

Fig. 1. Map of the study plot showing tree cover (m^2; left panel) and fruit abundance distribution from all fruiting trees (number of fruits; right panels) projected on a 10×10 m cell in 2006 (a) and 2007 (b). Note the spatiotemporal variation in the template of fruit abundance between years.

in a wide range of conditions, from trees embedded in the forest to completely isolated trees in the nonforested matrix. In this way, we ensured the presence of study plants across the complete gradient of spatial heterogeneity. *Crataegus* is a shrub or small tree native to Europe, north-west Africa and western Asia that commonly grows up to 10 m in height. Fruits are oval, small (*c*. 1 cm long), red when ripe and seem berry-like, but are in fact, structurally, a pome containing a single seed. In our study site, the fruits of this species are mainly consumed by resident thrushes (black-bird *Turdus merula*, song-thrush *T. philomelos* and mistle-thrush *T. viscivorus*) and overwintering migrants of the same and other species (e.g. fieldfare *T. pilaris* and redwing *T. iliacus*; Martínez, García & Obeso 2008). Thrushes account for almost all the animal-generated seed rain and act as legitimate seed dispersers (*sensu* Jordano 2000) as they swallow the whole fruit and then regurgitate or defecate the seeds undamaged, clean of any pulp and viable. Foxes (*Vulpes vulpes*) and badgers (*Meles meles*) may also occasionally consume fruits from basal branches or fruits fallen to the ground. However, their contribution to the total, animal-generated seed rain has previously been shown to be negligible, especially with reference to *Crataegus* (Martínez, García & Obeso 2008). Thrushes are highly vagrant flocking birds, able to move long distances across the local landscape, but when foraging in forest patches, they display short aver-

age flight distances (33.5 m) and only a low frequency of flight distances over 100 m (< 14%, Martínez, García & Obeso 2008).

SEED SAMPLING

In September of 2006 and 2007, we placed a total of 283 seed sampling stations within the 400×440 m study plot, distributed using a stratified design to ensure different distances from target trees and to cover the entire extent of the study plot (see Fig. S1 in Supporting Information for details on the spatial distribution of sampling stations). At each sampling station, we established a permanent 50×50 cm ground quadrat, in which we collected all dispersed *Crataegus* seeds in successive fortnightly surveys from September to January. We used the cumulative number of dispersed seeds within each sampling station throughout the dispersal season in further analysis. We considered losses of dispersed seeds from sampling stations to be low given that postdispersal seed predation mostly occurs in late winter and is consistently low in *Crataegus* relative to other co-occurring species (García, Obeso & Martínez 2005a). In fact, even during late winter, seed removal rates estimated from experimental seed depots adjacent to sampling quadrats were always below 10% in both study years, and statistically independent to the density of seeds and the distance to source trees (*authors' unpublished data*; see also García, Obeso & Martínez 2005b). A few seeds were found with seed coats gnawed by rodents. We counted these as dispersed seeds, based on the assumption that rodents had found and gnawed them post-dispersal; rodents do not act as seed dispersers for *Crataegus* (see Alcántara *et al.* 2000 for a similar procedure; García, Obeso & Martínez 2005a). Previous work in the same study site comparing seed deposition between open and excluded-to-predators sampling stations evidenced negligible losses of seeds for *Crataegus* (García, Obeso & Martínez 2005b). Hence, we considered our method of seed collection to provide an estimate of seed deposition reliable enough for the evaluation of dispersal kernels (see Martínez & González-Taboada 2009 for a similar procedure).

FRUITING TREES DISTRIBUTION AND ENVIRONMENTAL CORRELATES

Prior to the seed sampling seasons of 2006 and 2007, we mapped all the individual trees of all species within the study plot. Furthermore, the individual fruit production of each tree was scored using a ripe fruit abundance index (FAI). FAI was visually estimated by means of a semi-logarithmic scale: 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10 000; 5 > 10 000 (see Herrera & García 2010 for a similar procedure). The spatial position and fruit production of each individual tree and the spatial position of all sampling stations were entered in a GIS platform (ARCGIS 9.0, ESRI® ARCMAP™, Redlands, California, USA) for subsequent analysis.

The approach proposed by Schurr, Steinitz & Nathan (2008) to study the influence on seed dispersal kernels of both

the source's local environment (hereafter *source effects*) and all those environments potentially crossed by the seeds during the dispersal path (*path effects*) is based on the sampling of environmental variables from a spatially discrete grid (Fig. 1). Thus, we incorporated into the aforementioned GIS, a layer consisting of a grid of 1760 10×10 m cells superimposed on the 400×440 m extent of the study plot (Fig. 1). We selected this cell size as it provides a good representation of the spatial grain at which forest cover surrounding source trees affects seed-disperser foraging response in our study site (García & Chacoff 2007). Using the most recent digital cartography of the study site (i.e. 2004), we obtained the amount of forest cover (in m^2, irrespective of tree species) for each cell, which was used for both study years. Based on our extensive knowledge of the study site and the detailed identification of each individual tree within the study plot, we were able to ensure that there were no differences in either the amount or the spatial patterning of forest cover between 2006 and 2007, which could have altered forest cover measurements. In 2006 and 2007, we obtained total fruit abundance (as a measure of fruit availability for frugivores) for each cell, calculated as the sum of the crop from all fruiting trees, regardless of their species identity. Crop sizes were extrapolated from FAI ranks, using an allometric function fitted to the actual crop size of a sub-sample of trees ($y = 1.765 \exp(1.924 \text{ FAI})$; $R^2 = 0.80$; $N = 136$). We estimated the crop size of this sub-sample in September of each study year by counting all ripe fruits on 15 randomly selected fruiting branches, and the number of fruiting branches per tree, then extrapolating the number of fruits to the whole tree crown (see Herrera & García 2009 for a similar procedure).

FITTING SEED DISPERSAL KERNELS

Our first aim was to fit seed dispersal kernels, irrespective of environmental effects, by means of the standard IM framework. We used this framework as a null, or baseline, model whereby no environmental variables affect seed dispersal kernels. Seed arrival at each plot under this approach is modelled as the sum of the seed shadows from all individual seed sources, and it is a function of the distances r_{st}, from a given sampling station t, to all seed sources s, individual plant fecundities Q and a dispersal kernel f. Thus, the expected number of seeds arriving at a given sampling station t of area At was denoted as:

$$\hat{S}_t(G, r_t, A_t; \beta) = \sum_s Q_s(G_s; \beta_{fec}) f(r_{st}; \beta_{disp}) A_t$$

where r_{st} is a matrix containing the distances between each seed sampling station and sources, β is a vector of model parameters containing both fecundity parameters β_{fec} and dispersal parameters β_{disp}, and G is a vector of plant fecundity measures for each source s. Plant fecundity is commonly modelled as an allometric equation of the diameter at breast height (d.b.h.) of each adult tree (e.g. Martínez & González-Taboada 2009). However, we

used the allometric function described earlier (i.e. $y = 1.765 \exp(1.924 \text{ FAI})$) as a more accurate measure to estimate the individual plant fecundity of each potential source plant. The observed number of seeds arriving at each sampling station was assumed to follow a negative binomial distribution because seed rain was found to be more variable than in a Poisson distribution. Accordingly, we made the overdispersion parameter (o) of the negative binomial a linear function (with a log link) of the amount of forest cover in the cell where each sampling station was located.

From among the candidate kernels used for modelling seed dispersal patterns, we chose the two-parameter 2Dt kernel (Clark *et al.* 1999). The 2Dt kernel seems highly suitable in animal-mediated seed dispersal because of its ability to account for both local and long-distance dispersal (Clark *et al.* 1999). Thus, it is able to fit the typically convex shape near the source tree but also the expected 'fat tail' for frugivore-mediated seed dispersal kernels (e.g. Clark *et al.* 2005).

ACCOUNTING FOR SOURCE AND PATH EFFECTS ON SEED DISPERSAL KERNELS

We used the extended version of the traditional IM framework proposed by Schurr, Steinitz & Nathan (2008) to test the influence of environmental heterogeneity on *Crataegus* seed dispersal kernels. We modelled plant fecundity, and kernel scale and shape as functions of either forest cover or fruit availability in the cell where mother plants were located. Furthermore, the effects of the environments potentially encountered by seeds during their dispersal path were described by transforming physical space between seed sampling stations and source plants into 'movement space' (*sensu* Schurr, Steinitz & Nathan 2008). Under this approach, distances in high-resistance environments (i.e. low seed permeability) are enlarged relative to distances in lower resistance environments; for example, bird-dispersed seeds will presumably face increased resistance through covered habitats because birds commonly use tree cover as a stop-over in which to rest or protect themselves while flying across the landscape (e.g. Debussche & Lepart 1992; Herrera & García 2009). Similar effects of forest cover on the movement of seeds can be expected in the case of wind-dispersed seeds as seeds may be intercepted by trees (Schurr, Steinitz & Nathan 2008). Detailed information on the incorporation of source and path effects into the traditional IM approach can be found in Appendix S1 (see also Schurr, Steinitz & Nathan 2008).

All models were fitted by maximum likelihood in the R software (*bbmle* package; R Development Core Team 2005). We built all potential combinations, i.e. alternating cover and fruit availability as environmental variables depicting source and path effects. We used the parameter estimates of the best models to explore how source and path effects affect seed dispersal kernels of *Crataegus* trees. The relative merits of the different models were compared using Akaike Information Criterion (AIC, Burnham & Anderson 1998).

Results

FOREST COVER, FRUIT ABUNDANCE AND SEED DISPERSAL

Forest cover averaged $24.45 \pm 0.8\%$ (mean $\pm$ SE) per 10×10 m cell ($N = 1760$) and ranged from 0 to complete cover, showing a rough gradient across the study plot (Fig. 1). Mean fruit number per cell showed a sharp reduction from 2042.5 ± 130.8 (range 0–41 391) in 2006, to 924.8 ± 76.4 (range 0–39 610) in 2007. Nevertheless, we collected more dispersed seeds in 2007 than in 2006, with a total of 2546 (average density per 50×50 cm sampling station 5.4 ± 0.72) and 3896 (7.7 ± 0.92) seeds, respectively. This was probably due to the strong interannual variations in the abundance of seed dispersers (*authors' unpublished data*). There were very weak correlations between forest cover and fruit abundance per cell in 2006 ($R^2 = 0.09$, $F_{1,889} = 88.4$, $P < 0.001$) and in 2007 ($R^2 = 0.09$, $F_{1,889} = 167.8$, $P < 0.001$).

DISPERSAL KERNELS

Dispersal kernels estimated by the standard IM procedure (i.e. with no consideration of habitat features) provided the worst fit in both 2006 and 2007 (Tables 1 and S1). The consideration of source and path effects greatly improved model performance in both study years, highlighting the importance of the source's local environment as well as the environments encountered by moving seeds along their potential dispersal path. These effects were dominated by forest cover during 2006, when overall fruit abundance was high, but fruit abundance was better at explaining seed dispersal variability during 2007, the less productive year.

We used the parameter estimates of the best model for each year to explore source and path effects on seed dispersal kernels of *Crataegus*. According to these models, tree cover was the main environmental variable driving source effects in 2006 (Table 1). Both the fecundity (*b*) and the scale (*u*) parameters

increased with increasing forest cover (Table 1). Plants growing in cells with denser cover dispersed more seeds and at larger mean dispersal distances than those from more sparsely covered cells (Fig. 2). However, despite increased average dispersal distance, the shape parameter was higher in more densely covered cells, indicating that seed dispersal probability decreased with distance at a slower rate for trees in locations with lower cover relative to those in neighbourhoods with denser cover (Fig. 2).

In 2006, forest cover was also the main environmental variable affecting seed movement across the landscape (Tables 1 and S1). In this year, habitat resistance to seed movement increased with increasing forest cover. Consequently, grid-cells with high forest cover in a matrix of sparse tree density were predicted to intercept a substantial amount of seeds.

In 2007, the models including source effects alone fitted better than those also including path effects (Table 1). During this particular year, fruit abundance was the main environmental variable determining source effects, and both the fecundity parameter *b* ($\beta_{b1} = -1.02$; Table 1) and the scale parameter *u* ($\beta_{u1} = -0.13$; Table 1) were lower in cells with a high amount of fruits. However, unlike in 2006, the shape parameter *p* ($\beta_{p1} = 0.75$; Table 1) was higher in cells with a higher amount of fruits, suggesting that at least in 2007, the number of dispersed seeds, their average dispersal distance and the probability of seeds being at larger distances from source trees decreased with increasing abundance of fleshy fruits (Fig. 3).

The inclusion of forest cover to model the overdispersion parameter *o* improved standard models in 2006 (ΔAIC = 36.5) and 2007 (ΔAIC = 129.3). In both years, the variability of seed deposition rates in a given sampling station was lower in cells with a high amount of forest cover than in more sparsely covered locations (Table 1).

Discussion

We examined the environmental effects on seed dispersal kernels of *Crataegus* in secondary-growth forests in the

Table 1. Parameter estimates, negative log-likelihood and AIC values for the best-fit model in each four categories (including path and source effects, with only source effects, with only path effects, and models without environmental effects). Models come from a global analysis fitting tree cover and fruit availability as source and/or path effects and are ordered according to increasing AIC values (see also Table S1)

	Source	Path	β_{b0}	β_{b1}	β_{o0}*	β_{o1}*	$\beta_{\mu0}$	$\beta_{\mu1}$	β_{p0}	β_{p1}	β_{w1}	$-\ln L$	AIC
2006	Cover	Cover	−0.69	0.48	1.58	−0.95	2.16	8.77	−2.18	6.61	0.10	−698.7	1414.2
	Fruit	–	5.16	−0.43	1.60	−0.98	7.27	−0.40	8.14	−0.99	–	−700.1	1418.2
	–	Fruit	7.16	–	1.32	–	4.37	–	−0.30	–	0.01	−702.6	1422.8
	–	–	–	–	1.45	–	4.47	–	−0.44	–	–	−727.2	1460.4
2007	Fruit	–	8.20	−1.02	1.28	−0.06	17.29	−0.13	6.02	0.75	–	−794.8	1608.0
	Fruit	Fruit	8.10	−1.00	1.30	−0.06	16.55	0.68	4.83	1.67	−0.04	−796.5	1611.0
	Cover	–	−3.88	11.13	1.40	−0.77	4.43	−1.28	4.03	−12.76	–	−802.8	1621.6
	–	Cover	3.94	–	1.14	–	1.33	–	−7.71	–	0.08	−813.5	1637.0
	–	–	–	–	1.23	–	4.42	–	−0.54	–	–	−885.0	1776.0

*Modelled by accounting for the amount of forest cover where each source tree was located (see text for details).
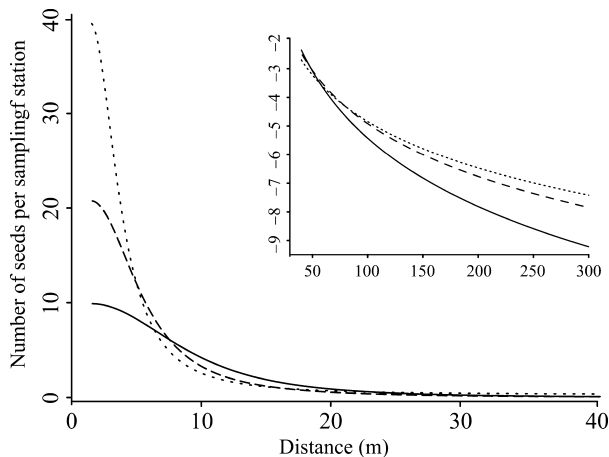AIC, Akaike Information Criterion.

Fig. 2. Source effects driven by forest cover on the dispersal kernels of *Crataegus monogyna* as predicted by the best model in 2006. Figures represent the seed dispersal kernel for plants growing in areas of high (100 m^2; solid line), medium (50 m^2; hatched line) and low forest cover (1 m^2; dotted line). The lines correspond to a tree dispersing 20000 seeds. *Inset* graph shows the same probability densities in log scale for longer distances.

Cantabrian Range (NW Spain). These environmental effects were explored by explicitly accounting for the amount of forest cover and fruit availability in the local environment where source plants were located as well as in those environments a seed potentially encountered along its dispersal path. We found that both forest cover and fruit abundance affected seed dispersal kernels, but their relative importance changed between years. This was apparently related to the strong inter-annual variation in community-wide fruit availability, as forest cover had a weak effect on seed dispersal kernels in the second study year when fruits were scarcer and more heterogeneously distributed across the landscape. In addition, we found that forest cover and fruit abundance had opposite influences on dispersal patterns during the two study years. Our results suggest that the local environment of the source and, to a lesser extent, all those environments that seeds might have encountered during their dispersal path can have pervasive effects on

seed dispersal kernels of bird-dispersed trees in spatially heterogeneous landscapes. More importantly, they highlight that both forest cover and fruit availability need to be considered to understand the underlying mechanisms by which environmental heterogeneity affects frugivore-mediated seed dispersal patterns. In this sense, we found that it is in fact spatiotemporal variations in fruit availability which determine which of the environmental variables (forest cover or fruit availability for frugivores) has the greater effect on seed dispersal patterns for frugivore-mediated seed dispersed plants in heterogeneous landscapes.

SOURCE AND PATH EFFECTS ON SEED DISPERSAL KERNELS

The seed dispersal kernels of *Crataegus* were strongly related to the local environment of the source. In line with previous studies, this finding suggests that the nature of the neighbourhood (i.e. the source effects) is a key feature for predicting seed dispersal patterns in heterogeneous landscapes (e.g. García & Chacoff 2007; Carlo & Morales 2008). However, our work goes further as it disentangles the relative influences of forest cover and fruit availability for frugivores as source effects on seed dispersal patterns (see also Herrera & García 2010). As previous works have also shown, forest cover had positive effects on the number of dispersed seeds, which is likely to be related to the higher frequency of bird visits to fruiting plants within high-cover neighbourhoods (García & Chacoff 2007). Conversely, the higher the fruit availability around source plants, the lower the amount of dispersed seeds. This presumably reflects plant–plant competition regarding seed dispersal, at least at this spatial scale, because of the presence of cofruiting individuals of the same and other species (e.g. Saracco *et al.* 2005; but see also Carlo & Morales 2008).

Forest cover was the main environmental feature driving source effects on seed dispersal patterns in 2006 when plants growing in denser-cover locations exhibited, on average, larger mean dispersal distances. This result strongly matches patterns of resource tracking by frugivorous thrushes: actively
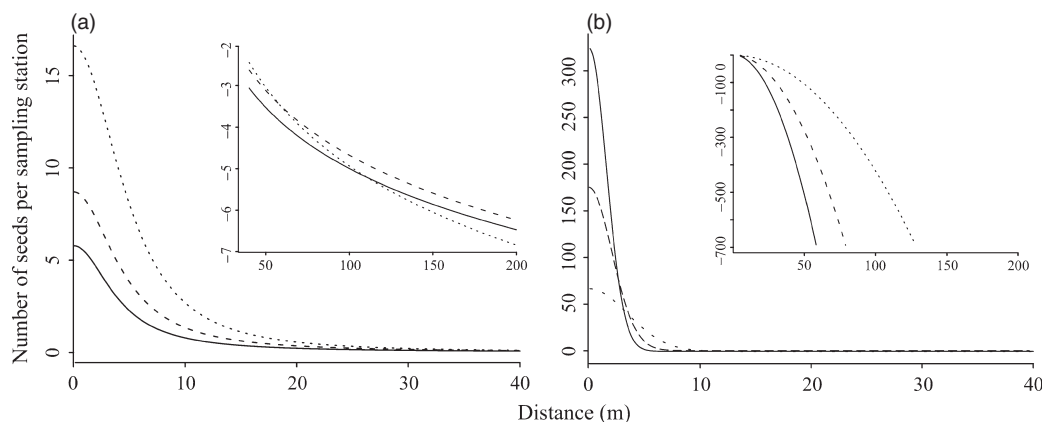

Fig. 3. Source effects driven by fruit abundance on the dispersal kernels of *Crataegus monogyna* as predicted by the best model in 2006 (left panel) and 2007 (right panel). Figures represent the seed dispersal kernel for plants growing in areas of high (60 000 fruits; solid line), medium (30 000 fruits; hatched line) and low abundance (10 000 fruits; dotted line). The lines correspond to a tree dispersing 20 000 seeds. *Insets* in each graph show the same probability densities in log scale for longer distances.

searching for neighbourhoods with higher forest cover across the landscape and, once within them, commonly moving among individual fruiting trees (*authors' unpublished data*). More importantly, we found that seed dispersal probability decreased with distance from the parent plant at a slower rate for trees in sparser-cover locations relative to those in denser-cover locations. This finding has previously been predicted for both wind- and animal-dispersed plants (Nathan 2006), but as far we are aware, this is the first empirical evidence testing this theoretical prediction for frugivore-dispersed plants (Morales & Carlo 2006; Carlo & Morales 2008). In our case, increased probabilities of dispersal events at larger distances seem to be related to the gradient of environmental heterogeneity in our study site, whereby the distance between source trees increases from denser- to sparser-cover areas. This, in turn, would lead to frugivores making wider displacements over the whole landscape, especially when using sparse cover locations such as isolated trees or clumps of trees across the nonforested matrix. These findings suggest a potential trade-off in the effects of forest cover on seed dispersal that may have significant ecological and evolutionary consequences. Increased long-distance dispersal is responsible for the ability of plant populations to attain fast migration rates, and thus, despite diminished average seed dispersal distance, plants in sparser-cover locations may be able to respond more efficiently to rapid environmental changes relative to those growing in denser-cover neighbourhoods (Clark, Macklin & Wood 1998).

Our results also evidenced that forest cover was not the only factor driving source effects on seed dispersal kernels. Indeed, in 2007, the availability of fruits around source trees was the main environmental feature affecting seed dispersal patterns. The most plausible explanation for this shift towards fruit availability as the main descriptor of source effects is the sharp reduction in both the total amount and the spatial predictability of community-wide fruit resources across the studied landscape (much higher in 2006 than in 2007). As fruit availability for frugivores decreases, frugivores will tend to visit plants located in neighbourhoods rich in fruits more frequently (Saracco *et al.* 2005; García & Chacoff 2007), and therefore their foraging decisions will be better explained by the presence of cofruiting individuals rather than by the protective canopy itself (Herrera & García 2010). Our results thus agree with theoretical predictions arguing that small-scale neighbourhood effects (i.e. the modelled source effects) might be controlled by large-scale processes (the interannual changes in landscape-scale fruit distribution; Carlo & Morales 2008). They also demonstrate empirically the existence of spatiotemporal changes in the neighbourhood-dependent rates of fruit removal and seed dispersal in fleshy-fruited plant communities (Carlo, Aukema & Morales 2007).

We found evidence of path effects only in 2006, probably due to the strong decrease in fruit availability at the landscape scale in 2007. In 2006, tree cover was the main environmental feature conditioning the ability of seeds to travel through the landscape once they leave source trees and habitat resistance to seed movement increased with increasing forest cover. This is not surprising given the habit of frugivores to use tree cover as a resting or protective stop-over while flying through the landscape (e.g. Debussche & Lepart 1992; Herrera & García 2009). However, it is important to consider that the source-path model explicitly assumes that path effects depend only on the environments crossed by the straight line extending from the source to the deposition site (Schurr, Steinitz & Nathan 2008). This might be somewhat unrealistic in the case of animal-dispersed plants as frugivores carrying seeds tend to follow complex trajectories after feeding in source trees (Russo, Portnoy & Augspurger 2006). Thus, without direct evidences from real-bird movements, path effects on seed dispersal kernels must be interpreted with caution.

Conclusions

We showed that both forest cover and fruit availability for frugivores are relevant environmental features in determining the seed dispersal of zoochorous plants in spatially heterogeneous landscapes. Indeed, our findings suggest that under certain environmental conditions, fruit availability for frugivores could even be a more important descriptor of dispersal than forest cover itself (Herrera & García 2010). These statements can be extended to heterogeneous landscapes that, as in our case, are subjected to anthropogenic habitat disturbance such as fragmentation. Habitat fragmentation promotes discontinuities in the spatial distribution of the remaining habitat cover and fruit resources, something which has been suggested to strongly influence foraging patterns of frugivores and therefore seed dispersal patterns (Lehouck *et al.* 2009; González-Varo 2010; Herrera & García 2010). However, as far we know, there is no previous empirical evidence on the relative influence of habitat cover and fruit availability on seed dispersal kernels for plants populating fragmented landscapes. In this sense, our results suggest that human-promoted heterogeneous landscapes should be viewed from a wider perspective than that of 'human perception' where they are typically considered a static, discrete reality of habitat *vs.* nonhabitat scenario (Fischer & Lindenmayer 2006). This approach may be too simplistic because, as we have found, spatial and temporal changes in environmental features, besides habitat cover, are actually influencing habitat suitability for dispersal processes. In our case, not all available habitat cover was always suitable for maintaining the seed dispersal process of *Crataegus*, as, in some years, parts of this habitat cover were of poor-quality for frugivorous birds, i.e. empty of target resources such as fleshy fruits. Therefore, the consideration of fruit-resource distribution is essential when addressing the relationship between landscape patterns and ecological processes in real-world landscapes, and subsequently, to fully understand frugivore-mediated seed dispersal in disturbed landscapes.

Acknowledgements

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Supporting Information

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

Appendix S1. Model fitting and parameter estimation describing source and path effects.

Table S1. Parameter estimates and model fit of each model developed.

Figure S1. Location of the study plot and sampling station at the Sierra de Peña Mayor (NW Spain).

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