Research

Consistency and reciprocity of indirect interactions between tree species mediated by frugivorous birds

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Despite the recognized importance of indirect plant–plant interactions for community structure, we still need to improve our current knowledge on how their outcomes are consistent in space and time, as well as reciprocal between participating species. These caveats are especially relevant in the case of indirect interactions mediated by animals, whose behavior may show high variability. We studied consistency and reciprocity of frugivore-mediated interactions between fleshy-fruited trees. For three years we examined the influence of crop size and neighborhood characteristics (con- and heterospecific fruit abundance and forest cover) on frugivory rates on *Crataegus monogyna* and *Ilex aquifolium*, two coexisting species in the secondary forests of the Cantabrian range that share a guild of frugivorous birds. Crop size and neighborhood characteristics influenced frugivory on *C. monogyna* and *I. aquifolium*. Both con- and heterospecific fruit abundance affected frugivory, evidencing the occurrence of indirect interactions between trees, although the strength and sign of these effects varied between tree species as well as across years within species. By showing complex temporal patterns in the consistency and reciprocity of indirect interactions, this study emphasizes the need for multispecific, long-term studies to assess the actual contribution of animal-mediated plant–plant indirect interactions to community dynamics.

Direct interactions (i.e. those where the effect of one species is transmitted without intermediaries to another), maybe by being more conspicuous or intuitive, have been the center of most studies of plant–plant interactions. However indirect interactions, in which the effect of one species on another is mediated by a third (Wootton 1994; for example, a plant species that suffers increased herbivory due to its co-occurrence with another, highly palatable, species; Barbosa et al. 2009), have been revealed as community drivers of equal, or even greater importance than direct interactions (Holt 1984, Strauss 1991, Schoener 1993, Vandermeer et al. 1995, Bailey and Whitham 2007). Nevertheless, despite this recognized relevance, a general community framework is still short on information on how consistent, and how reciprocal among participating species, the outcomes of plant–plant indirect interactions are (Holt and Lawton 1994, Chaneton and Bonsall 2000).

Following on from early studies, it has been shown that the effects of indirect interactions are not necessarily constant across space (Holt 1984, 1988) or time (Holt and Lawton 1994, Miriti 2006), disappearing or even changing their sign, and leading to variations in community dynamics (Holt 1984). For example, Kitzberger and collaborators (2007) found, during a bamboo masting event in the Patagonian forest, that the initial positive effects of bamboo seeds on those of *Nothofagus* and *Autrocedrus* became

negative after three months. Moreover, reciprocity in the performance of indirect effects, defined, in a broad sense, as the ocurrence of two-way indirect interactions between species, irrespective of their sign, is also important. Different community dynamics are expected when indirect interactions simultaneously affect all participants rather than simply a single species (Chaneton and Bonsall 2000). Caccia et al. (2006) evidenced that the presence of the mice-preferred *Austrocedrus* seeds increased predation on the seeds of *Nothofagus*, but there was not a reciprocal effect of *Nothofagus seeds* on those of *Austrocedrus*. Nevertheless, very few of the studies focusing on indirect interactions have actually considered reciprocity (Chaneton and Bonsall 2000). The assessment of consistency and reciprocity is especially pertinent in those plant–plant relationships mediated by animal species. Given that animals may respond to spatio-temporal variation in environmental conditions, irrespective of plant response, and may interact simultaneously with co-occurring plants (at least in the case of generalist consumers), low consistency but high reciprocity may be expected for most animal-mediated, indirect plant–plant interactions.

Frugivory has a key role in plant community dynamics (Wang and Smith 2002, Levine and Murrell 2003). Fruit removal is the first filter as to the relative number of propagules that many plant species introduce into the community.

Removal of the fruits from one plant will not only depend on the traits of the species, but also on the surrounding environmental context, which is frequently shaped by the occurrence of other plant species (Carlo et al. 2007). Thus, plant–plant interactions mediated by frugivores will emerge as a result of, first, the wide generalism of plant–frugivore assemblages (with many plant species sharing frugivores within the community, Bascompte et al. 2003, Donatti et al. 2011) and, second, the ability of frugivores to optimize their foraging by selecting collective fruiting patches over individual fruiting plants (Sallabanks 1993, García and Ortíz-Pulido 2004). In fact, this scale-dependent behavior generates neighborhood effects (Sargent 1990, Carlo et al. 2007). For a given plant, these effects may mean apparent competition if the presence of fruiting neighbors leads to a decrease in fruit removal from that plant (Manasse and Howe 1983, Alcántara et al. 1997, Saracco et al. 2005), whereas they will, conversely, imply apparent mutualism if the result is an increase in fruit removal (Sargent 1990, Carlo and Aukema 2005, Blendinger et al. 2008). These variations in frugivory patterns may be translated into imbalances in the magnitude of seed dispersal for the different plant species, presumably cascading down through the subsequent stages of their regeneration cycles (Levine and Murrell 2003), and potentially leading to variations in plant species populations and community dynamics (Hubbell et al. 2001, Wang and Smith 2002).

In this work, we study the consistency and the reciprocity of frugivore-mediated, plant–plant interactions, defined as those involving both intra- and interspecific effects within tree neighborhoods. For this purpose we monitored the influence of neighboring fruit production on fruit removal in two co-occurring species of fleshy-fruited trees linked by a shared guild of frugivorous birds for three years. Neighborhood effects were estimated by taking into account that individual removal rates may also be affected by plant traits (crop size; Sallabanks 1993) and by other features of the surrounding context (forest cover acting as protection; Sapir et al. 2004). Specifically, we tested the occurrence of apparent competition and mutualism mediated by shared frugivores through answering the following questions: 1) How variable across species and years were fruit removal rates, individual crop sizes and the production of con- and heterospecific fruits (as neighborhood characteristics which potentially influence birds' foraging activity)?; and 2) Which environmental features (crop size, neighborhood) affected frugivory rate across species and years, and how (positive or negatively)? We expected that the inherent variability of fruit-frugivore interactions, derived from interannual changes in fruit crop and frugivore abundances (Levey and Benkman 1999, Jordano 2000), would also occur in our system, potentially affecting consistency and reciprocity of the frugivore-mediated indirect interactions.

Material and methods

Study system

Our study system was the temperate secondary forest of the Cantabrian mountain range (northern Spain). This is a common but low-cover habitat (García et al. 2013) occurring as fringe patches adjacent to mature stands (mainly composed by *Fagus sylvatica*), and as variable-sized fragments, or even isolated remnant trees, embedded in a dominant ($>70\%$ cover) matrix of stony pastures and heathland (*Erica* spp., *Ulex europaeus*). Secondary forest is dominated by the fleshy-fruited trees hawthorn *Crataegus monogyna*, holly *Ilex aquifolium,* yew *Taxus baccata*, rowan *Sorbus aucuparia* and whitebeam *Sorbus aria*, as well as hazel *Corylus avellana*. We chose *C. monogyna* and *I. aquifolium* as study species since they are the main tree species in the study area, in terms of cover and fruit production, and their fruits show an overlapping ripening period in early autumn, staying on the tree until mid-winter. 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* (Martínez et al. 2008). *Turdus pilaris*, *T. iliacus* and *T. torquatus* are over-wintering species in northern Spain, whereas *T. merula*, *T. viscivorus* and *T. philomelos* are species with resident populations that are joined by individual overwintering migrants. All thrushes swallow the entire fruits, expelling the intact seeds in their feces thereby acting as legitimate seed dispersers (Jordano 2000). These six bird species are the major seed dispersers for both *C. monogyna* and *I. aquifolium* in the secondary forests of the Cantabrian Range (García et al. 2005). The plant–frugivore system studied is characterized by strong between-year variability, in terms of both fruit production and bird abundance (García et al. 2013). The importance of the different fruit species in the diet of thrushes relates to the relative abundance of each fruit species each year, with thrushes mostly feeding on the fruit species which is most abundant in a particular year, suggesting low specific diet selection (García et al. 2013).

Study site

This study was carried out in the Sierra de Peña Mayor (1000 m a.s.l.; 43°17′59″N, 5°20′29″W Asturias, northwest Spain). At this site, secondary forest is intermingled with mature forests, meadows, heathlands and limestone rocky outcrops. The study was conducted within a 17.6 ha rectangular plot (Fig. 1) over three consecutive years: the autumn-winter season in 2007–2008, 2008–2009 and 2009–2010 (hereafter, respectively 2007, 2008 and 2009). The plot was selected to represent a gradient of secondary forest cover, from dense forest areas to scattered trees isolated within the non-forest matrix, hence providing a wide range of neighborhood characteristics for individual trees, both in terms of forest cover and fruit abundance.

Frugivory

At the beginning of the fruiting season of each year (October), we selected 16 individual fruiting trees (hereafter focal trees) of each species. They were distributed throughout the entire plot to reflect a complete range of neighborhood characteristics in the field, from isolated trees to trees embedded in forest fruit-rich patches (Fig. 1). The identity of focal trees changed from one year to another
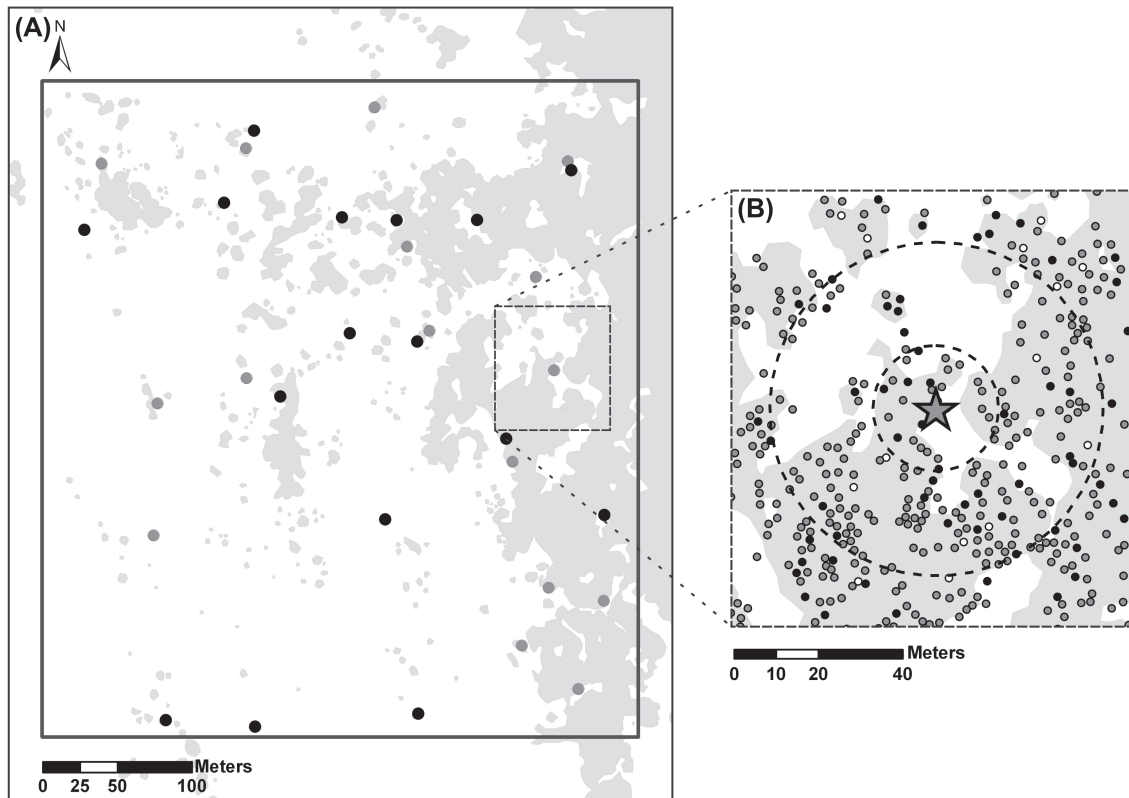
Figure 1. (A) Map of the study plot in 2008 sampling period, showing focal trees (black dots: *Crataegus monogyna; gray dots: Ilex aquifolium*) and the extent of forest cover (light gray area). (B) A detail of the inner circle (15 m radius) and outer ring (15 to 40 m radius), both indicated with a dashed line, chosen to represent ecological neigborhoods around a central focal tree (dark grey star). Fleshy-fruited trees are represented as dots (black: *C. monogyna*; dark gray: *I. aquifolium*; white: *Taxus baccata*).

as many trees failed to bear fruits in consecutive years (Supplementary material Appendix 1). Before the fruit consumption by birds began, for each focal tree, we counted the number of fruits on 15 branches (arbitrarily distributed through the whole accessible crown of the tree) and the total number of branches per tree. We estimated the individual crop size by multiplying the average number of fruits per branch by the number of branches per tree. At the same time, we labeled five fruiting branches per tree, and counted the initial number of fruits. To avoid bias in frugivory estimations, labeled branches were selected so as to be arbitrarily distributed through the whole accessible crown of the tree, and to contain from 60 to 120 fruits. When standing fruits are removed by Cantabrian thrushes, their stalks remain attached to the branch for a long time afterwards (authors' personal observation; Supplementary material Appendix 2 Fig. A2), whereas when fruits fall to the ground through natural abscission or the action of wind or rain, their stalks fall with them. This enabled us to distinguish fruits picked and removed by thrushes from those falling to the ground through abiotic causes. Labeled branches were surveyed fortnightly from October to February of each sampling season, and the number of standing fruits and the number of bare stalks remaining on branches were recorded each time. Bare stalks were removed with scissors after each survey to avoid recounting. For each tree, we estimated frugivory as a fruit removal rate by considering the labeled branches and dividing the number of

bare stalks observed throughout the season by the initial number of standing fruits. For further methodological details of frugivory estimation see Supplementary material Appendix 2.

Neighborhood metrics

In October of each sampling season, we surveyed the entire plot, mapping all trees and identifying them at the species level. Fleshy-fruited species on the plot were mainly represented by *C. monogyna* and *I. aquifolium,* accompanied by a small number of *T. baccata* individuals. For each fruiting individual of these species, we visually estimated the number of standing fruits by using a semi-logarithmic scale (fruit abundance index FAI: $1 = 1$–10 fruits; $2 = 11$–100; $3 = 101$–1000; $4 = 1001$–10000; $5 > 10000$). In the study system and site, fruiting of all individuals of the different species studied is synchronous and ripening occurs within 1–2 months (although fruits remain attached to trees for a further 1–3 months; García et al. 2013). Thus, we considered that a single sampling of fruit abundance at the beginning of the season provided an appropriate estimate of the spatial arrangement of fruit resources for thrushes.

We developed a geographic information system of the study area (GIS, ArcGIS9) based on a 1:5000-scale orthophotograph. Layers with precise geo-referenced information about the position and the crop size of all mapped trees (including focal trees) were generated. We generated

another GIS layer representing forest cover by carefully digitizing the extent and shape of all tree cover from the orthophotograph (Fig. 1).

To measure neighborhood characteristics, we used GIS to delimit two non-overlapping sectors around each focal tree (Fig. 1): an inner circle of 15-m radius (hereafter R15) and a surrounding ring with a circumference ranging from 15 to 40 m radii (hereafter R15–40). We considered that each of these two sectors represented a neighborhood context at a different spatial scale (Hubbell et al. 2001, García and Chacoff 2007). As neighborhood metrics for each sector, we calculated forest cover (m²) and the abundance of fruits of *C. monogyna*, *I. aquifolium* and *T. baccata* i.e. the sum of crop sizes of all fruiting trees per species. Crop sizes were extrapolated from FAI ranks, taking into account the fit between the actual crop size of a sub-sample of trees (estimated as described for focal trees) and FAI, by following an allometric equation (actual crop size = 1.765 exp(1.924 FAI); $R^2 = 0.80$; n = 136; Herrera et al. 2011).

Statistical analysis

Between-year variations in removal rates, crop sizes and abundance of different fruits at R15 and R15–40 of focal trees were tested by using generalized linear models (GLMs), with a normal error distribution and a log link function. In addition we performed the same analyses for forest cover at R15 and R15–40 to assess whether focal trees represented similar neighborhood gradients, year on year, within the whole gradient of forest cover across the study plot (Supplementary material Appendix 1). Independent analyses were performed for each focal species.

We also used GLMs to analyze the effects of crop size and neighborhood parameters on frugivory. Independent models were built for each 'species' × 'year' combination, given that a different set of focal trees were sampled every year, and that strong between-year variation in total and relative fruit abundances have been found in the study system (García et al. 2013). Each model incorporated the crop size of the focal tree, the amount of forest cover (m²) and the number of *C. monogyna*, *I. aquifolium* and *T. baccata* fruits as predictor variables. Due to the scarcity of adult fruiting trees of the species in the plot, it was only possible to incorporate *T. baccata* fruit abundance in models at the R15–40 extent. Instead of the raw values of forest cover, the residuals of the linear regression between fruit abundance (predictor) and forest cover (response) were incorporated in the models. In this way, we sought to avoid the potential effects of non-independence between predictors in the multivariate models (Quinn and Keough 2002; Pearson correlation forest cover – fruit abundance: $r = 0.77$, $p < 0.0001$, n = 96) while achieving a measure of forest cover variability that was independent of fruit abundance (as many trees such as hazel, male holly, and male yew, do not bear fleshy-fruits; see Hargis et al. 1998, Villard et al. 1999 for a similar procedure in forest fragmentation studies). We assumed that this residual variable represented the protection of frugivorous birds against their own predators, as it accounted for the effects of forest cover independent of food provision (García et al. 2011).

The GLMs were constructed with Normal error distribution for the response variable (frugivory). We tested different link functions and raw and log transformed data on predictor variables to find the best-fit model for each case, as judged by deviance G^2 as a goodness-of-fit statistic (lower values indicating a better fit; Quinn and Keough 2002). All statistical analyses were performed with JMP 7.0 (SAS Inst.).

Results

We found strong variation between years in frugivory rates, individual crop sizes and most neighborhood characteristics (GLM: $\chi^2 > 2.92$, n = 48, for all tests; Fig. 2). The average proportion of removed fruits per plant in *Ilex aquifolium* increased from 2007 to 2009, but intermediate values were observed in *Crataegus monogyna* in all years. The crop size of focal trees and the abundance of fruits in their neighborhoods differed significantly between years in both species. *Crataegus monogyna* and *I. aquifolium* fruit abundances showed opposite tendencies: while the former decreased from 2007 to 2008, the latter increased. No between years variations were found in the abundance of *Taxus baccata* fruits. The values of forest cover around both species at either R15 or R15–40 neighborhood scales were similar between years (Supplementary material Appendix 1 Fig. A1).

Crop size and neighborhood effects on frugivory

GLM models showed significant effects of crop size and neighborhood characteristics on the fruit removal rates of *C. monogyna* and *I. aquifolium*. Crop size and forest cover effects were, however, inconsistent in time (Table 1). The abundance of fruits in the neighborhood significantly affected fruit removal rate in focal trees in all study cases (species by year combinations). The effects of the different neighbor fruits on frugivory varied across years, both in occurrence and sign (Table 1, Fig. 3). We also found that the between year consistency of these neighborhood effects was not similar for *C. monogyna* and *I. aquifolium* (Table 1, Fig. 3). Neighborhood effects varied not only between years and species, but also between scales for each species within year (Table 1).

Discussion

Indirect interactions between plants have traditionally been considered as important drivers of plant community dynamics (Bailey and Whitham 2007). In this study, we widen the current framework of plant–plant indirect interactions by showing how shared plant consumers may lead to reciprocal indirect effects between plant species, which can change from negative (competitive) to positive (mutualistic). Specifically, we show that the reproductive success of fleshy-fruited trees, estimated as the rate of fruit removal by legitimate dispersers, was determined not only by intrinsic plant traits, but also by the presence of con- and heterospecific fruiting trees in the neighborhood of individual
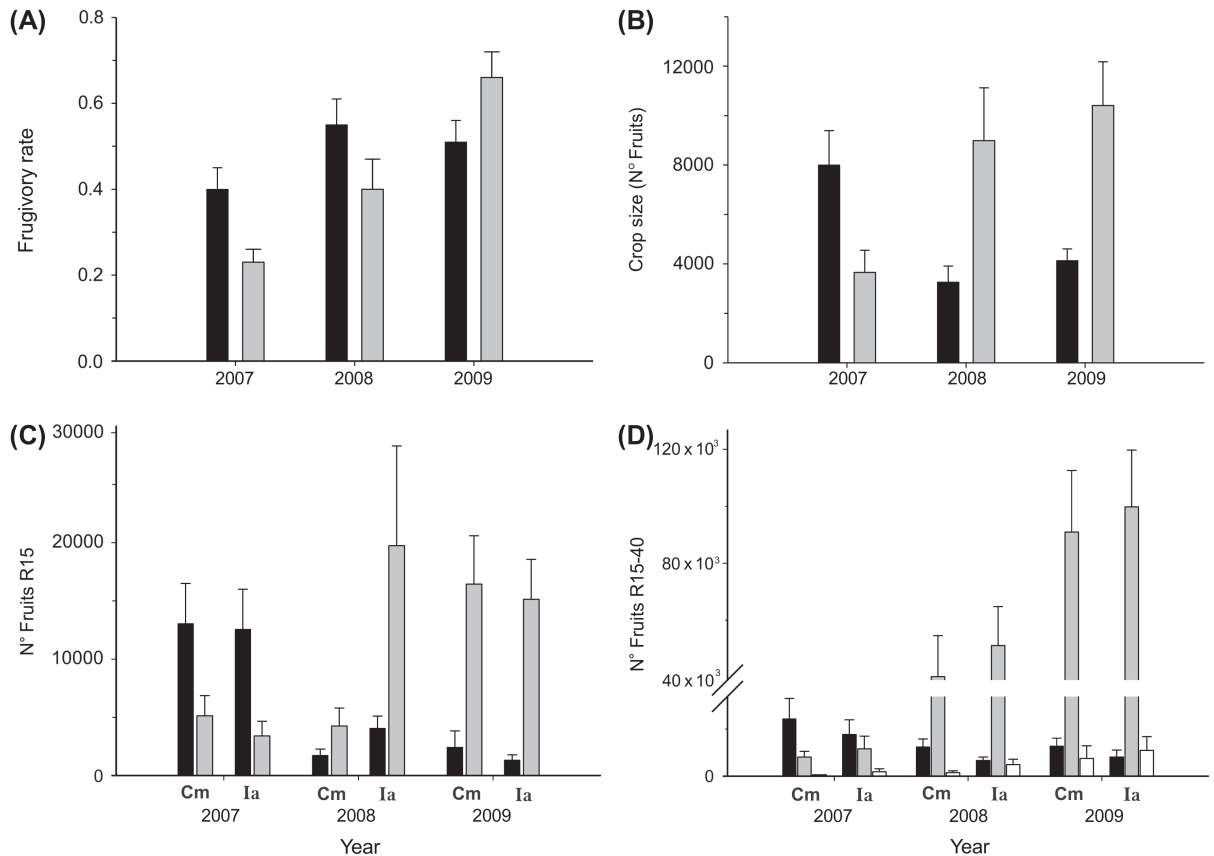
Figure 2. (A) Mean frugivory rate (proportion of fruits removed from labeled branches) on focal trees (n = 16) ± standard error (SE) on *Crataegus monogyna* (black bars) and *Ilex aquifolium* (grey bars) for the three years studied. (B) Mean crop size (number of fruits produced) on focal trees (n = 16) ± SE on *C. monogyna* (black) and *I. aquifolium* (gray) for the three years studied. (C) and (D) Mean fruit abundance ± SE of the different species producing fruits in the inner circle (15 m radius, R15) and outer ring (15 to 40 m, R15–40 radius), respectively, chosen to represent ecological neighborhoods of *C. monogyna* (Cm) and *I. aquifolium* (Ia) focal trees (n = 16). *C. monogyna* fruits are represented by black bars, *I. aquifolium* by gray bars and *T. baccata* by white bars (no *T. baccata* fruits were found in any R15).

plants (Manasse and Howe 1983, Alcántara et al. 1997, Saracco et al. 2005). By reciprocally influencing frugivore visitation and fruit consumption, neighbor trees may generate apparent mutualistic and competitive processes with the potential to shape tree recruitment and, hence, community dynamics (Carlo et al. 2007, Sasal and Morales 2013). Nevertheless, the ultimate, community-level consequences of these indirect interactions will strongly depend on how constant in time (Holt and Barfield 2003, Kitzberger et al. 2007), and generalized across species, their effects are (Chaneton and Bonsall 2000). Here, by studying two plant species over three consecutive years, we overcome the limitations of single-species or short-term studies and assess frugivore-mediated interactions in terms of species reciprocity and temporal consistency. In the following sections, we interpret the plant–plant interaction outcomes by looking at birds as a resource for plant reproduction, but discuss the contingencies of these interactions by considering how frugivores react to fruit resources and habitat structure.

Crop size effects

Crop size is frequently a major determinant of frugivory rate as frugivores are disproportionally attracted to plants

with big crops, because these are more conspicuous or more profitable (Sallabanks 1993, Blendinger et al. 2008) and we expected these mechanisms to be operating in the cases of *Crataegus monogyna* and *Ilex aquifolium* (see also Martínez et al. 2007). However, the crop size effects found in the present study varied between years. Birds did remove proportionally more fruits from those trees bearing bigger crops in 2007 (Table 1), a year in which the total local fruit abundance was comparatively smaller and fruiting trees were more heterogeneously distributed across the landscape (García et al. 2013). These two facts might have led thrushes to optimize their foraging by selecting where to feed at a very fine spatial scale: the individual tree. However, we found negative effects of crop size on frugivory rate (*I. aquifolium* in 2009, a year of very high fruit production; Fig. 2D). This situation suggests satiation effects, as proposed by Hampe (2008), with higher overall crop production resulting in a decreased proportion of fruits being consumed.

Forest cover effects

Frugivorous birds often concentrate their activity on high-cover forest patches, searching for perching places and

Table1. Summary of GLM models evaluating the effect of crop size and neighborhood characteristics on the frugivory rate of *Crataegus monogyna* and *Ilex aquifolium* trees in different years. Predictor variables include the crop size of the focal tree, and forest cover and the abundance of fleshy fruits of different species (Cm: *C. monogyna*; Ia: *I. aquifolium*; Tb: *Taxus baccata*) in the inner circle, (radius 15 m, R15) and outer ring (radius 15 to 40 m, R15–40), which were chosen to represent different ecological neighborhoods. No *Taxus baccata* fruits were found at R15 in any year so this factor was not taken into consideration in the models. The case was the same in 2007–2008 around *C. monogyna* at R15–40. In all models: normal distribution, log link function, degrees of freedom (DF) = 8 (except in *C. monogyna* in 2007 where DF = 7), $\chi^2 > 2.2$ and $p < 0.05$. Raw predictor variables were used in the models except for *C. monogyna* 2008–2009 and 2009–2010 where the best fit was found to be with log transformed variables. The maximum likelihood estimates (*estimate*, in bold when $p < 0.05$) and χ^2–values testing the partial effect of each predictor variable on the model are shown. *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$.

Parameter	2007–2008 Estimate	χ^2	2008–2009 Estimate	χ^2	2009–2010 Estimate	χ^2
C. monogyna						
Crop size	**8.38 × 10⁻⁵**	10.60***	**0.19**	3.99*	0.04	0.04
R15						
Forest cover	**4.33 × 10⁻³**	10.09**	0.05	0.09	−0.09	0.18
Fruits Cm	**−1.50 × 10⁻⁵**	3.85*	**−0.16**	5.55*	−0.03	0.79
Fruits Ia	**2.33 × 10⁻⁵**	3.49*	**0.08**	6.16*	**0.08**	5.19*
R15–40						
Forest cover	**−5.84 × 10⁻⁴**	7.45**	−0.05	0.11	−0.40	3.13
Fruits Cm	**−1.90 × 10⁻⁵**	11.07***	**0.19**	4.09*	0.01	0.09
Fruits Ia	−1.82 × 10⁻⁵	1.46	−0.04	2.59	0.04	0.70
Fruits Tb	–	–	**0.09**	6.40*	−0.04	1.55
I. aquifolium						
Crop size	**5.03 × 10⁻⁵**	8.91**	7.73 × 10⁻⁶	<0.01	**−4.20 × 0⁻⁵**	5.95*
R15						
Forest cover	**4.19 × 10⁻³**	34.88***	−8.73 × 10⁻³	0.16	**2.31 × 10⁻³**	6.49 *
Fruits Cm	**−1.67 × 10⁻⁵**	6.65**	−3.04 × 10⁻⁴	2.94	**1.31 × 10⁻⁴**	3.77*
Fruits Ia	**1.54 × 10⁻⁴**	26.73***	**−2.72 × 10⁻⁴**	8.19**	1.42 × 10⁻⁵	2.30
R15–40						
Forest cover	**−4.84 × 10⁻⁴**	27.22***	−1.12 × 10⁻³	0.44	−3.66 × 10⁻⁵	0.07
Fruits Cm	−3.42 × 10⁻⁶	0.87	**3.13 × 10⁻⁴**	7.26**	−1.59 × 10⁻⁵	2.49
Fruits Ia	**−5.34 × 10⁻⁶**	3.55*	3.38 × 10⁻⁶	0.45	−2.23 × 10⁻⁶	2.63
Fruits Tb	**−1.63 × 10⁻⁴**	26.46***	**1.11 × 10⁻³**	9.30**	**−2.56 × 10⁻⁵**	11.00***

protection from predators (Sapir et al. 2004, García et al. 2011), leading to fruiting trees in dense neighborhoods having higher visitation rates. In our case, the amount of forest cover in the immediate vicinity of the fruiting tree positively influenced fruit removal in *C. monogyna* and *I. aquifolium*. These results corroborate previous findings from indirect measurements of bird activity, like seed deposition, within the same system, which suggest an effect of forest cover independent of fruit abundance (Martínez et al. 2008, Herrera et al. 2011). Similarly, we show here that forest cover influence varied strongly between years, not exerting an influence on frugivory by birds in every year (Herrera et al. 2011, García et al. 2013; see also Caccia et al. 2006 for a similar results on seed predation). Forest cover extent was constant over time in the study plot and around the focal trees (Supplementary material Appendix 1). Thus, the dilution of forest cover effects must be related to variations in other neighborhood features like fruit availability (Herrera et al. 2011) or other ecological factors not considered by our design, like the abundance of predators of frugivorous birds (Howe 1979).

Indirect interactions between fruiting neighbors

Our results show that, while feeding on individual *C. monogyna* and *I. aquifolium* trees, birds were influenced by the presence of con- and heterospecific fruits in the immediate vicinity. As judged from the sign of the relationship between neighboring fruit abundance and fruit removal, *C. monogyna* only competed with conspecific neighbors, whereas *I. aquifolium* suffered both intra- and interspecific apparent competition. However, we also found apparent mutualism, as birds fed more on *C. monogyna* trees when they were surrounded by many *I. aquifolium* fruits. By contrast, mutualism in *I. aquifolium* was performed by con- and heterospecific plants, as was the case for this species in relation to apparent competition. Even though other studies have revealed these indirect interactions (Alcántara et al. 1997, Blendinger et al. 2008), we are not aware of previous evidence of the influence of con- and heterospecific fruiting neighborhoods on different co-occurring focal species within a community.

We also found that different co-occurring plant species showed different patterns of temporal consistency (Fig. 3). Some interaction outcomes were consistent between years in *C. monogyna*, which was affected by interspecific facilitation each year and, simultaneously, by intraspecific competition in two out of the three years of the study. Conversely, in *I. aquifolium,* the influence of con- and heterospecific neighbors varied between years in both occurrence and sign. We cannot explain these temporal inconsistencies based on the scenarios proposed for direct interactions, such as those linked to strong environmental biotic variations (e.g. competition–facilitation transitions along stress gradients; Pugnaire and Luque 2001, Holzapfel et al. 2006), or those derived from variations associated
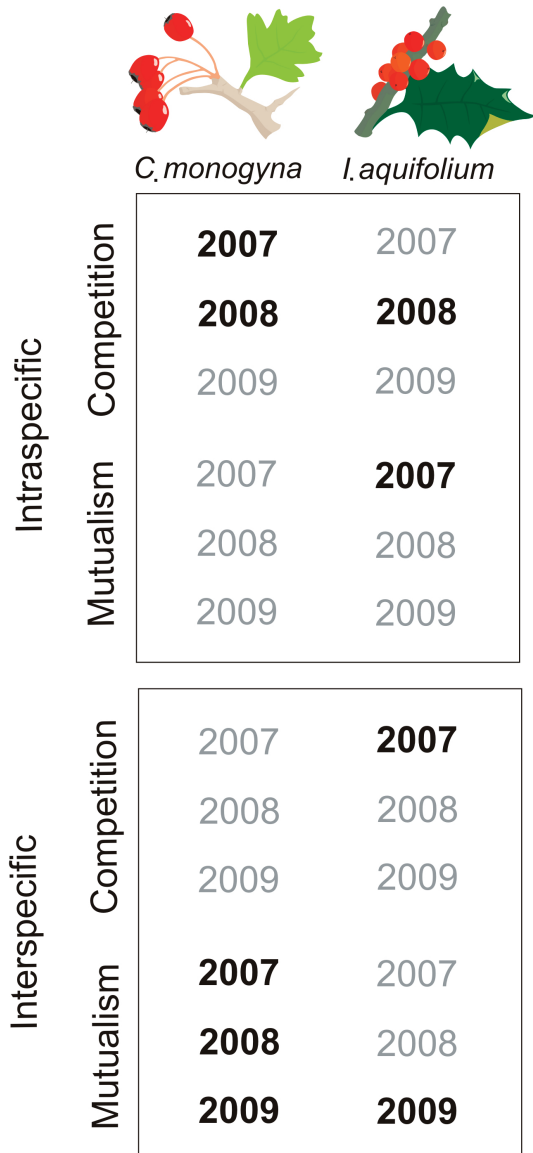
Figure 3. Summary of observed intra- and interspecific neighborhood indirect interactions on *Crataegus monogyna* and *Ilex aquifolium* in different years, interpreted from the effect of fruit abundance at R15 neighborhood and frugivory rate (in bold black, years with significant effect; in gray, years with no effect). Consistency in the intra- and interspecific effects can be seen by following the vertical columns. Reciprocity in interspecific effects can be seen in the lower square. Artwork by Daniel Martínez.

with the ontogenetic development of interacting plants (Miriti 2006). We would thus argue here that the temporal patterns shown in the present work must derive from the between year variation in the large-scale characteristics of the whole plant–frugivore system. In this sense, the abundances of both fruits and thrushes and their landscape-scale spatial distribution changed between years (García et al. 2013), which means that frugivores have to cope with quite different neighborhoods from year to year. Namely, frugivores will be conditioned to optimize their foraging according to different fruiting scenarios, both at the neighborhood and the landscape scale, and thus the role of the different neighborhood characteristics may not be

the same across years (Van Ommeren and Whitham 2002, Kitzberger et al. 2007, García et al 2013). With regard to the inter-specific discordances in consistency patterns, they do not seem to be related with any of the ecological factors considered in this study. We suggest that minor phenological mismatches (with *C. monogyna* ripening earlier than *I. aquifolium*), combined with variations in the bird community through the season (with migratory species arriving sequentially), could underpin the differential frugivory outcomes between plant species.

Even though new studies of indirect interactions have been published following that by Chaneton and Bonsall (2000), who reported on the paucity of research relating to reciprocity in indirect interactions, this still remains a poorly explored matter. We have found no evidence of any study considering reciprocity in the indirect effects between fruiting plants (but see Östman and Ives 2003 and Caccia et al. 2006 for good examples of insect and seed predation respectively). We, however, did find reciprocity in the performance of indirect interactions in our study systems (Fig. 3). While feeding on *C. monogyna,* birds are influenced by the fruits of neighbor *I. aquifolium* trees, and, reciprocally, hawthorn fruits influence bird foraging on holly trees (Fig. 3). Nonetheless, this reciprocity also changed between years, both in terms of occurrence and in the symmetry of the effects (same or different sign). Its coexistence with *I. aquifolium,* consistently enhanced frugivory on *C. monogyna*, while the effect of this latter species on the former showed considerable variability. We would expect that consistency in the outcomes of one species, even with no long-term reciprocity, would lead to demographic imbalances between species (similar to that suggested by Schnurr et al. 2004 and Caccia et al. 2006), ultimately promoting coexistence, with *C. monogyna* individuals reproducing better when surrounded by few conspecifics but by many *I. aquifolium*.

Finally, our multi-scaled neighborhood approach also enabled us to observe the inconsistent outcomes (occurrence and sign) of frugivore-mediated interactions across spatial scales. These inconsistencies suggest that landscape features differentially determine frugivore foraging decisions at different scales (García and Ortíz-Pulido 2004, García et al. 2011). In our study, considering a broader scale also meant that we could show the effects of another plant species involved in the indirect interactions, *Taxus baccata* (Table 1)*,* which had not been detected in the immediate neighborhood due to its scattered distribution through the landscape.

Concluding remarks

In this study we have shown that even within a small assemblage of fleshy-fruited plants and their shared frugivores, environmental variability led to a high degree of complexity in the outcome of indirect interactions between tree species at neighborhood and landscape scales. Over a short time scale important variations in the consistency and reciprocity of these indirect effects found, with species dependent singularities. We argue that these results, based on a straightforward fruit–frugivore case study, may be applied to many other temperate and tropical systems, hosting both richer and more generalist plant–frugivore

assemblages, and also to other interactions mediated by animal consumers, such as pollination.

Short-term, species-centered studies are useful tools for identifying the factors determining the occurrence of indirect interactions, but usually fail to reveal the balances which determine their consistency. In addition, the reciprocal and symmetrical effects for the different species involved in these interactions should not be taken for granted. Thus, if we aim to understand the real impact of indirect interactions on plant communities we need to explicitly consider the different sources of variability affecting them, by using long-term, multispecific approaches.

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