The effect of spatio-temporal variation in understanding the fruit crop size hypothesis

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In order to evaluate the 'fruit crop size' hypothesis, we analyzed the effect of fruit availability on the number of visits by birds and on the proportion of removed fruits, and on how much of the variation in the proportion of removed fruits could be explained by spatio-temporal variability. Fieldwork was done on the coast of the state of Veracruz, Mexico, using the small tree *Bursera fagaroides* (Burseraceae) and its frugivorous feeding assemblage, on four hills during four years. The number of fruits produced, the number of visits by birds, and the proportion of removed fruits varied between years with more than half an order of magnitude. The number of available fruits was associated to both the number of visits by birds and the proportion of fruits removed from each plant individual, and supports the fruit crop size hypothesis. However, the hypothesis varies in strength depending on total fruit production by the population per year and per hill. The spatio-temporal variation of the system was the effect of variation in the intensity of fructification between years and hills; the inclusion of spatio-temporal variability helped to explain most of the variation found in our results. The latter approach may explain the explain the conflicting results found by other authors in studies done in only one year or at one site, where variation is greatly reduced. Considering the number of published reports, a meta-analysis seems to be in order to determine the existence of a general effect between fruit production, the number of visits by birds and the proportion of fruits removed. If this is possible, we hypothesize that the association between fruit production and the number of visits by birds should be of low intensity.

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The influence exerted by fruit availability on the behaviour of frugivores has not been clearly established (Levey and Benkman 1999), which has caused that the 'fruit crop size' hypothesis has not been fully tested (Laska and Stiles 1994). This hypothesis states that plants producing larger fruit crops will attract higher numbers of potential fruit dispersal agents than plants producing smaller fruit crops, and, consequently, the former will have more seeds dispersed (Snow 1971, McKey 1975, Howe and Estabrook 1977, Laska and Stiles 1994). The 'fruit crop size' hypothesis can be divided into two related variants: (1) the absolute number of fruits removed from a plant will be larger in plants with larger crop sizes, and (2) the proportion of fruits removed will be larger in plants with larger fruit crop sizes (Laska and Stiles 1994). There is published evidence confirming the first variant ('absolute number of fruits removed', see Laska and Stiles 1994, for review). However, there is conflicting evidence in the case of the second variant ('proportion of fruits removed', e.g. Howe 1983, Manasse and Howe 1983, Davidar and Morton 1986, Denslow 1987, Jordano 1987, Foster 1990, Sargent 1990, Traveset 1994, Laska and Stiles 1994). We suggest that the conflicting evidence for the second variant could be explained if the spatio-temporal variation inherent to all systems of seed dispersal by vertebrates is considered (Sallabanks and Courtney 1993, Herrera et al. 1994, Herrera 1998a,

b). The aim of this study was to evaluate the second variant of the 'fruit crop size' hypothesis (i.e. the proportion of removed fruits) using the seed dispersal system of the small Neotropical tree *Bursera fagaroides* (Burseraceae) and its spatio-temporal variation. We were interested in the effect of fruit availability on the number of visits by birds and on the proportion of removed fruits, and on how much of the variation in the proportion of removed fruits could be explained by spatio-temporal variability.

Materials and methods

Fieldwork was done at Centro de Investigaciones Costeras La Mancha (CICOLMA), located on the coast of the state of Veracruz, Mexico (19° 36′ N, 96° 22′ W; elevation < 100 m). The climate is warm and subhumid; a rainy season occurs between June and September; total annual precipitation varies between 900 and 1800 mm; mean annual temperature is 24–26°C; and minimum temperature is 12.1°C (Rico-Gray et al. 1998). Fifty-four frugivorous birds and 33 ornithochorous plants have been reported for CICOLMA, and accumulated evidence suggests that monthly fruit richness determines the temporal richness of frugivorous birds at the landscape level; however, this pattern was not found for abundance of individual bird species vs fruit richness (Ortiz-Pulido et al. 1995, 2000, Ortiz-Pulido 2000a). We selected the frugivorous-ornithochorous system structured by *Bursera fagaroides* and its frugivorous feeding assemblage because of certain characteristics that facilitate its study. For example, the (1) small feeding assemblage (7 bird species), (2) small size of plant individuals (ca 2.5 m high, maximum 8 m), (3) open habitat (grasses) surrounded by tropical dry forest, (4) the shedding of leaves when in fruit, (5) synchronous fruit ripening once a year (January–May), (6) restricted distribution of plants in the site, (7) almost only species with ornithochorous fruits from January to May, and (8) that each fruit contains only one seed. For sampling we chose four hills with different environmental conditions (e.g. photosynthetic active radiation, humidity, temperature, shrub cover, exposure to incoming sea wind) (Ortiz-Pulido 2000b). We marked 59 female individuals of *B. fagaroides* and annually (1996–1999) counted the number of fruits produced (crop size) and the number of fruits removed, both in an area of 0.4 m² under the crown, and the number of bird visits (mean time of observation per plant per season = 4.5 h). To evaluate the effect of crop size on bird visits we used a 4 × 4 experimental design (years and slopes, respectively), factors were 'crossed' with unequal replication using 17, 17, 16, and 9 replicated observations for slopes H1, H2, H3 and H4, respectively, for the combination of the two factors. To

evaluate the effect of crop size on the proportion of removed fruits, we used a 3 × 4 design, because we did not count the number of fruits removed in 1999 (Ortiz-Pulido 2000b). The sampling unit for variables in the analyses were the individuals trees. These were observed every year in random order.

As we used 'count data', where '0' is a frequent value, the response variables fitted a Poisson (bird visits) or binomial distribution (proportion of removed fruits) (Crawley 1993). The variables were analyzed using the GLIM statistical package (Crawley 1993, Francis et al. 1993). Bird visits were analyzed using two-way ANOVA for Poisson-fitted data, with two factors (year, hill) and one covariable (fruit crop per tree). Proportion of removed fruits was analyzed using two-way ANOVA for binomial-fitted data, with two factors (year, hill), linking proportion of fruits removed to predictors by means of a logit link function. Because we were unable to find a statistical tool that would allow us to consider 'fruits per plant' as a covariable in the two-way ANOVA, we evaluated it as an offset variable in the model. Because our data were overdispersed, the results of the ANOVAs were corrected redefining the scalar parameter (based on Crawley 1993).

Results

The number of fruits produced, the number of visits by birds, and the proportion of removed fruits in *B. fagaroides* varies between years in more than half an order of magnitude (Fig. 1a, b, c). Highest fruit production per plant ($\bar{X} = 1120$) was registered in 1986, and lowest ($\bar{X} = 72$) in 1999 (Fig. 1a). Highest number of visits by birds ($\bar{X} = 1.3$) was registered in 1998, and lowest in 1999 ($\bar{X} = 0.2$) (Fig. 1b). Highest proportion of fruits were removed in 1996 ($\bar{X} = 31.8\%$) and 1997 ($\bar{X} = 36\%$) that in 1998 ($\bar{X} = 24.7\%$) (Fig. 1c).

The ANOVA used to analyze the number of visits by birds significantly explained 39.3% of the observed deviance (Table 1). The factors 'year' and 'hill' and the covariable 'fruit production per plant' significantly explained 10%, 14.1% and 3.6% of the deviance, respectively (Table 1). The 'year' × 'hill' and the 'year' × 'fruit production' interactions explained 8.1% and 3.50% of the deviance, respectively (Table 1). As the relationship between bird visits and crop size was not consistent between years (Fig. 2a), we found a significant effect of the 'year' × 'fruit production' interaction on the number of bird visits. The latter is similar to the result of the 'year' × 'hill' interaction, which was not consistent between hills per year (Fig. 2b).

The ANOVA used to analyze the proportions of fruits removed significantly explained 27.7% of the observed deviance. The factors 'year' and 'hill' signifi-

cantly explained 10.5% and 7.7% of the deviance, respectively (Table 2). The 'year' × 'hill' interaction explained 9.5% of the deviance (Table 2). The significant effect on the proportion of fruits removed for the interaction 'year' × 'hill' per plant means that the relationship removal-crop size is not consistent among hills (Fig. 1c). If 'fruits per plant' was exploratorily included in the model as an offset variable it explained directly 7.72% and indirectly 7.2% of the deviance in the data.
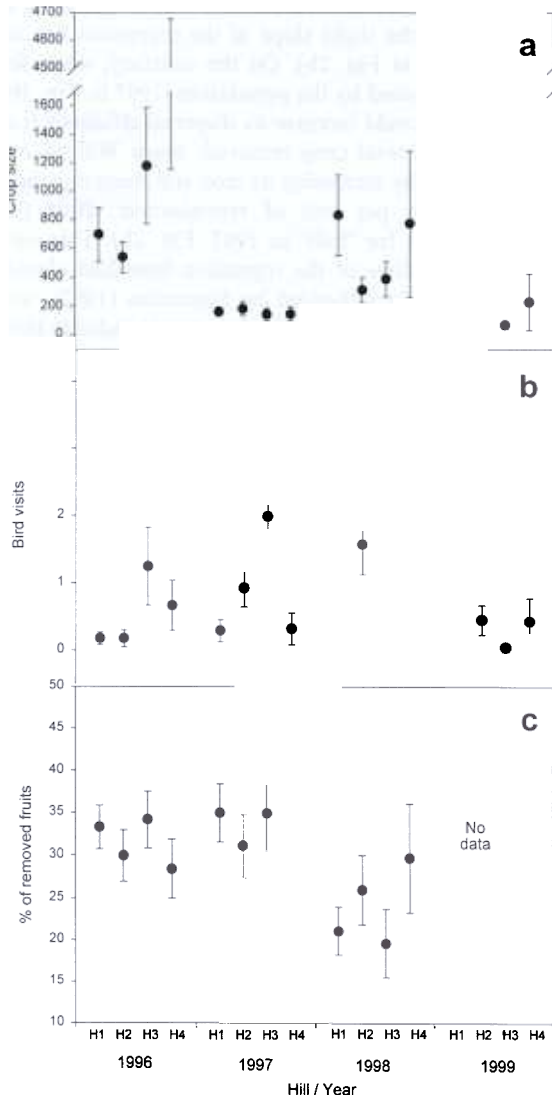

Fig. 1. (a) Annual variation in fruit set, (b) mean number of visits by birds, and (c) number of fruits removed, for individuals of *Bursera fagaroides* in four hills. A circle indicates the mean and the bars the standard error for each hill for each study year ('fruit removed' was not evaluated in 1999). Hills are indicated by a letter and number (e.g., H3).

Discussion

Our results on the seed dispersal system of *Bursera fagaroides* show that the number of available fruits was associated to both the number of visits by birds and the proportion of fruits removed from each plant individual, and support the fruit crop size hypothesis. However, they also suggest that the observed patterns were better explained if spatio-temporal variation is considered in the analysis. The effect of fruit production on the number of visits by birds was not large (7% considering direct and indirect effects), suggesting that this low-intensity association may explain the conflicting information reported elsewhere. For example, the correlation between fruit production and number of visits by birds was significant in *Virola surinamensis* (Myristicaceae) (Howe 1983, Manasse and Howe 1983), but the same correlation changed significance from year to year in *Allophylus edulis* (Sapindaceae) (Foster 1990); and no significant association was established for *Pistacia terebinthus* (Anacardiaceae) (Traveset 1994) or *Viburnum prunifolium* (Caprifoliaceae) (Laska and Stiles 1994). Similarly, the association between fruit production and the proportion of fruits removed, although clear in our study, has suffered from conflicting results. For example, there is a significant association between fruits produced and fruits removed in *Sambucus pubens* (Denslow 1987) and in *Viburnum dentatum* (Caprifoliaceae) (Sargent 1990), it is inconsistent for *Morus* trees (Moraceae) (Stapanian 1982), and it is not significant in *Virola surinamensis* (Myristicaceae) (Manasse and Howe 1983), *Olea europaea* (Oleaceae) (Jordano 1987), *V. prunifolium* (Laska and Stiles 1994), and six other plant species of Maryland, USA (Davidar and Morton 1986). Considering the number of published reports, a meta-analysis (Fernandez-Duque and Valeggia 1994, Arnqvist and Wooster 1995, Fernandez-Duque 1997) seems to be in order to determine the existence of a general effect between fruit production, the number of visits by birds and the production of fruits removed. If this is possible, we hypothesize that the association between fruit production and the number of visits by birds should be of low intensity.

Our results clearly show that the inclusion of spatio-temporal variability helped to explain most of the variation found in our results (35.7% for visits by birds and 27.8% for production of removed fruits). The latter approach may explain the conflicting results found by other authors in studies done in only one year or in one site, where variation is greatly reduced. Spatio-temporal variation has been mentioned in previous studies (e.g., Howe 1983, Levey 1988, Murray 1988, Willson and Whelan 1990, Loiselle and Blake 1991, Guitián et al. 1992, Jordano 1993, 1995, Sallabanks and Courtney 1993, Traveset 1995, Schupp and Fuentes 1995, Herrera 1998a, b), but few have indicated that its exclusion may be the source of confusing and unreal results in studies of seed dispersal (Herrera 1998a, b).

Table 1. Results of a two-way ANOVA (year, hill) with one covariable (fruit production per plant) for data fitting a Poisson distribution. The number of bird visits to plants was the response variables.

Factor	Df	Deviance	F	P	R^2
Year	3	30.38	8.76	0.0005	0.0998
Hill	3	42.94	12.22	0.0005	0.1410
Fruits per plants		10.89	9.42	0.005	0.0358
Y × H	9	24.77	2.38	0.05	0.0814
Y × H	3	10.55	3.04	0.05	0.0347
H × F	3	0.31	0.08	NS	0.0010
Y × H × F	9	11.14	1.07	NS	0.0366
Residual	204	176.46			

We suggest that the spatio-temporal variation of the studied system was an effect of the variation in the intensity of fructification of the individuals of *B. fagaroides* between years and hills (Fig. 1b). This variation in the system has a direct effect on the relationship established between the variables 'crop size-bird visits' per year (Fig. 2a) and 'crop size-proportion of removed fruits' per hill per year (Fig. 2b). The effect is clear when the slopes of the regression lines are compared. Thus the fruit crop size hypothesis varies in strength depending on total fruit production by the population per year and per hill (Fig. 2). It would seem that when more fruits are produced in the population (1996 in

Fig. 2. Relationship between crop size and visits by birds considering the interactions (a) 'year' × crop size', and (b) 'year' × 'hill'. The regression lines are adjusted to the origin. The legend at the end of each line indicates the year (in a) or the hill and year (in b, e.g., H1 96 = hill one for 1996). The dotted lines join regression lines to their legends.

Fig. 1b) it is not energetically convenient for an individual of *B. fagaroides* to produce many fruits, because it will not attract more birds due to an increment of its crop size (see the slight slope of the regression line for 'hills' in 1996 in Fig. 2b). On the contrary, when few fruits are produced by the population (1997 in Fig. 1b), an individual could increase its dispersal efficiency (i.e., the percent of total crop removed; sensu Willson and Whelan 1993) by increasing its crop size, receiving more visits by birds per unit of reproductive effort (see regression lines for 'hills' in 1997, Fig. 2b). This variability in the slope of the regression lines had already been partially hypothesized by Stapanian (1982), who mentioned that the slope of a line would indicate three levels of display efficiency: H, high efficiency, where a small total fruiting effort results in a high number of seeds dispersed (slopes > 50°); M, moderate efficiency, where an intermediate total fruiting effort result in equivalent seed dispersal (slopes ≈ 50°); and L, low efficiency, where a large total fruiting display is required for dispersal of few seeds (slopes < 50°). According to these categories, the *B. fagaroides* system exhibited low efficiency in 1996, moderate efficiency in 1998, and high efficiency in 1997 and 1999. An alternative, and probably complementary, view to explain the differences in slopes between years and hills is that in certain years and hills there are no birds, and thus it does not matter now much effort the trees of *B. fagaroides* put into producing fruits. For reasons that are not clear, absence of birds possibly occurred in hill 1 in 1998 and 1999, when no birds visited the plants (Fig. 2b).

As some authors have pointed out (e.g., Herrera 1998a, b, Levey and Benkman 1999), there is a need for long-term studies done in several sites before we can
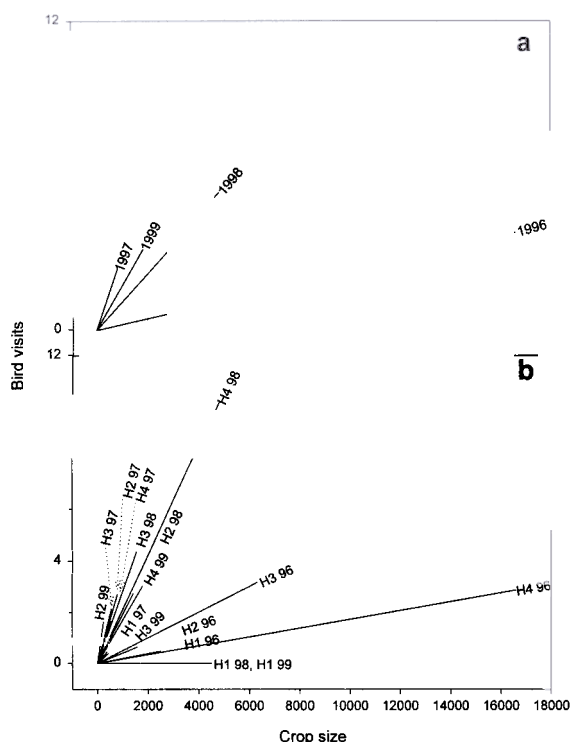
Table 2. Results of a two-way ANOVA (year, hill) for data fitting a binomial distribution. The proportion of fruits removed was the response variable.

Factor	df	Deviance	F	P	R^2
Year	2	25.54	11.67	0.0001	0.1053
Hill	3	18.61	5.66	0.005	0.0768
Y × H	6	23.11	3.52	0.005	0.0953
Residual	148	165.62			

reach clear conclusions on the functioning of seed dispersal systems. Finally, our results support the fruit crop size hypothesis, but suggest the need (1) to consider spatio-temporal variation in seed dispersal systems when evaluating the hypothesis, and (2) of a meta-analysis that may clearly determine the generality of this hypothesis.

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