Almazán-Núñez RC, Eguiarte LE, Arizmendi MdC, Corcuera P. 2016. *Myiarchus* flycatchers are the primary seed dispersers of *Bursera longipes* in a Mexican dry forest. PeerJ 4:e2126
https://doi.org/10.7717/peerj.2126

Myiarchus flycatchers are the primary seed dispersers of *Bursera longipes* in a Mexican dry forest: An overlooked coevolutionary process?

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We evaluated the seed dispersal of *Bursera longipes* by birds along a successional gradient of tropical dry forest (TDF) in southwestern Mexico. *B. longipes* is an endemic tree to the TDF in the Balsas basin. The relative abundance of frugivorous birds, their frequency of visits to *B. longipes* and the number of removed fruits were recorded at three study sites with different stages of forest succession (early, intermediate and mature) characterized by distinct floristic and structural elements. Flycatchers of the *Myiarchus* and *Tyrannus* genera removed the majority of fruits at each site. Overall, visits to *B. longipes* were less frequent at the early successional site. Birds that function as legitimate dispersers by consuming whole seeds and regurgitating or defecating intact seeds in the process also remove the pseudoaril from seeds, thereby facilitating the germination process. The highest germination percentages were recorded for seeds that passed through the digestive tract of two migratory flycatchers: *M. cinerascens* and *M. nutingii*. Perch plants, mainly composed of legumes (e.g., *Eysenhardtia polystachya, Acacia cochliacantha, Calliandra eryophylla, Mimosa polyantha*), serve also as nurse plants since the number of young individuals recruited from *B. longipes* was higher under these than expected by chance. This study shows that *Myiarchus* flycatchers are the most efficient seed dispersers of *B. longipes* across all successional stages. This suggests a close mutualistic relationship derived from adaptive processes and local specializations throughout the distribution of both taxa, as supported by the geographic mosaic theory of coevolution.

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Myiarchus flycatchers are the primary seed dispersers of *Bursera longipes* in a Mexican dry forest: An overlooked coevolutionary process?

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Abstract. We evaluated the seed dispersal of *Bursera longipes* by birds along a successional gradient of tropical dry forest (TDF) in southwestern Mexico. *B. longipes* is an endemic tree to the TDF in the Balsas basin. The relative abundance of frugivorous birds, their frequency of visits to *B. longipes* and the number of removed fruits were recorded at three study sites with different stages of forest succession (early, intermediate and mature) characterized by distinct floristic and structural elements. Flycatchers of the *Myiarchus* and *Tyrannus* genera removed the majority of fruits at each site. Overall, visits to *B. longipes* were less frequent at the early successional site. Birds that function as legitimate dispersers by consuming whole seeds and regurgitating or defecating intact seeds in the process also remove the pseudoaril from seeds, thereby facilitating the germination process. The highest germination percentages were recorded for seeds that passed through the digestive tract of two migratory flycatchers: *M. cinerascens* and *M. nutingii*. Perch plants, mainly composed of legumes (e.g., *Eysenhardtia polystachya, Acacia cochliacantha, Calliandra eryophylla, Mimosa polyantha*), serve also as nurse plants since the number of young individuals recruited from *B. longipes* was higher under these than expected by chance. This study shows that *Myiarchus* flycatchers are the most efficient seed dispersers of *B. longipes* across all successional stages. This suggests a close mutualistic relationship derived from adaptive processes and local specializations throughout the distribution of both taxa, as supported by the geographic mosaic theory of coevolution.

Key words: germination, establishment, flycatchers, nurse plants, restoration, coevolution.

Introduction

Biotic seed dispersal plays a central role in the spatial dynamics of plant populations (Spiegel & Nathan, 2007; Schupp, Jordano & Gómez, 2010; Forget et al., 2011; Jordano et al., 2011). Dispersion may encourage the establishment of plants since intraspecific competition is generally lower in sites distant from the parent plant (Godínez-Alvarez, Valiente-Banuet & Rojas-Martínez, 2002; Schupp, Milleron & Russo, 2002). Moreover, the incidence of pathogens and predators is usually reduced at new sites (Jordano et al., 2011, Obeso, Martínez & García, 2011).

In arid and semi-arid environments, biotic dispersal, germination and seedling establishment are critical phases of plant life cycles (Steenbergh & Lowe, 1969; Valiente-Banuet et al., 1991; Godínez-Alvarez & Valiente-Banuet, 1998; Orozco-Almanza et al., 2003; Padilla & Pugnaire, 2006). During the dry season, for example, seedlings face adverse factors, such as dry soil, direct sunlight and extreme temperatures (Godínez-Alvarez & Valiente-Banuet, 1998). However, dispersers aid in finding better conditions by depositing seeds in preferable microhabitats (i.e., under nurse plants) that promote germination and seedling survival (Pérez-Villafaña & Valiente-Banuet, 2009).

Inadequate agricultural practices have reduced the undisturbed area of tropical dry forests (TDF) in Mesoamerica to fragments at various successional stages (Quesada et al., 2009). Since the soil seed bank may be considerably reduced in disturbed fragments (Uhl, 1987; Martins & Engel, 2007), seed dispersal can play an important role in the recruitment of plants and hence contribute towards the composition and density of woody plants and the eventual restoration of these forests (Hammond, 1995; Peña-Claros & De Boo, 2002).

The vegetation of the Balsas basin in southwestern Mexico consists mainly of TDF (Rzedowski, 1978), and the dominant arboreal elements belong to the genus *Bursera,* Burseraceae (Rzedowski, Medina & Calderón de Rzedowski, 2005; Almazán-Núnez et al., 2012), whose fruits are a source of food for resident and migratory frugivorous and insectivorous birds during the dry season (Ortiz-Pulido & Rico-Gray, 2006; Ramos-Ordoñez & Arizmendi, 2011). Furthermore, the distribution of these birds in different successional stages of TDF is related to the presence of these trees (Almazán-Núñez et al., 2015). Although the role of insectivorous birds, such as flycatchers and vireos, as consumers and dispersers of *Bursera* spp. has been previously described (Greenberg, Foster & Márquez-Valdelamar, 1995; Hammond, 1995; Ortiz-Pulido & Rico-Gray, 2006; Ramos-Ordoñez & Arizmendi, 2011), there are few detailed reports on this subject. For instance, Ramos–Ordoñez & Arizmendi (2011) analyzed the seed dispersal of *B. morelensis*, while Ortiz-Pulido & Rico-Gray (2006) studied the same process in *B. fagaroides*, but no additional studies have been carried out in TDF to evaluate and compare biotic seed dispersal between sites with different degrees of disturbance (Hammond, 1995; Quesada et al., 2009).

Furthermore, the majority of studies on frugivory and seed dispersal have been limited to single locations (Ortiz-Pulido & Rico-Gray, 2006; Ramos-Ordoñez & Arizmendi, 2011), but patterns that are elusive at local scales may emerge in regional studies that cover areas with varying levels of disturbance or recovery (Carlo, Aukema & Morales, 2007). Frugivory and seed dispersal can also differ across a geographic mosaic, as interacting species may not necessarily have the same distribution (Thompson, 2005). That is, according to the mosaic of coevolution ideas, differential patterns of species distribution result in local specializations and interactions of varying degrees (Nuismer, 2006).

Moreover, studies that seek to understand patterns of biotic seed dispersal and seedling establishment in TDF at different levels of perturbation or seral stages, form the scientific basis for applied studies focusing on management and conservation strategies in these forests. In the TDF, native plants, particularly those from the Burseraceae family, are important in forest regeneration and can help to revert fragmentation (Ramos-Ordoñez, Arizmendi & Márquez-Guzmán, 2012).

The genus *Bursera* is a distinctive component of TDF in Mesoamerica, including ca. 107 species (De-Nova et al., 2012). Its distribution spans from northern Mexico to the northern region of South America (Becerra et al., 2012). The diversification of this genus has been related to the southward expansion of TDF in response to the elevation of the Sierra Madre del Sur and the Mexican Volcanic Belt (De-Nova et al., 2012). *Bursera* evolutionary history indicates that much of the biological richness of the Mesoamerican TDF derived from increased rates of speciation within habitats from the early Miocene to the Pliocene, due to marked arid regimes (Becerra, 2005; Dick & Wright, 2005). This scenario matches other hypotheses proposing that these lineages were mostly restricted to dry environments of Mexico and evolved during long periods of isolation (Valiente-Banuet et al., 2004).

In this study we describe the primary seed dispersal of *B. longipes* by frugivorous birds in a TDF of the Balsas basin of Guerrero. Belonging to the Simaruba sub-group of the diverse *Bursera* genus, *B. longipes* forms part of a larger clade that emerged in the Miocene just over 8.5 million years ago (De-Nova et al., 2012). This tree is a dominant species (Almazán-Núñez et al., 2012) in this biotic region, considered to be the center of diversification for this genus in Mesoamerica (Rzedowski, Medina & Calderón de Rzedowski, 2005). While *B. longipes* abundance increases in the most well-preserved sites, it also settles in disturbed areas (Rzedowski, Medina & Calderón de Rzedowski, 2005).

The questions of this study were: (1) Which bird species remove *B. longipes* seeds along the TDF successional mosaic? (2) Do seeds that pass through the tract of birds have higher germination rates than those that fall down from trees? (3) Are there differences in the quality of seeds dispersed by birds? (4) Does *B. longipes* need nurse plants to establish in different sites? (5) Do dispersal birds preferentially use nurse plants for perching in the successional mosaic?

Materials & Methods

Study sites

We conducted the study at three sites corresponding to different successional phases of TDF that have been largely unmanaged for varying periods of time since their last major disturbance (i.e., clear-cutting or burning). The three sites are described, as follows: (1) the early successional site (last disturbed *ca*. 20 y ago) consisted of vegetation regrowth but was once used for cattle ranching and, to a lesser extent, seasonal agriculture. (2) The intermediate successional site (last disturbed *ca*. 35 y ago) corresponded to a transitional phase between a mature forest and fragmented areas. The matrix surrounding the site consisted of pasture and seasonal corn and bean fields. This site was previously used for seasonal corn production and cattle ranching. Nonetheless, to a large extent, structural and floristic elements have developed so that they begin to mirror the original dry forest vegetation. (3) The mature successional stage is characterized by a closed canopy and the presence of a tree cover that is typical of mature dry forest (i.e., dominance of the *Bursera* spp.). This site has not experienced a large scale disturbance for more than 50 years.

Bursera longipes

Bursera longipes is endemic to TDF in the states of Mexico, Morelos, Puebla, Guerrero and Oaxaca in the Balsas basin (Fig. 1; Rzedowski, Medina & Calderón de Rzedowski, 2005). It is a deciduous species with trivalvate fruits that turn red at maturity. The seeds have a slightly orange pseudoaril (Guízar & Sanchez, 1991). The fruits are 1.3 ± 0.02 cm in length (the data represent mean ± SE) and 0.87 ± 0.04 cm in width, with a fresh weight of 0.62 ± 0.01 g (N = 100 fruits). The flowering season begins with the onset of the rainy season (May or June) and fruiting occurs in early June or from May–July. Most fruits ripen between November and May.

Seed dispersal effectiveness

The effectiveness of seed dispersal in each successional stage was estimated as proposed by Schupp (1993), by considering the quantity and quality components. The quantity was estimated based on the abundance of frugivorous birds, their frequency of visits to *B. longipes* tree and average number of fruits removed per visit. The quality was estimated based on the percentage of germination after seeds passed through the digestive system of birds, probability of seed deposition at nurse plants (adult plants that positively influence the recruitment of young seedlings) and the contribution of bird species to the establishment sites (Schupp, Jordano & Gómez, 2010). Seed dispersal effectiveness of each frugivore is calculated as the product of the components of quantity and quality, using the following subcomponents (Schupp, 1993): Effectiveness = relative abundance x frequency of visits x average number of removed fruits x seed germination x seed deposition probability x contribution of birds to the site of establishment.

Component of quantity

Relative abundance

The relative abundance of birds was estimated using nine mist nets (12 m long x 2.5 m wide) placed between *B. longipes* trees in each of the successional stages. The use of nets to capture birds was employed to corroborate and supplement information on species that feed on fruit and to capture data on birds' use of the habitat, relative abundance and feeding activities (Loiselle & Blake, 1999; Figueroa-Esquivel et al., 2009). Nets were placed during the months of greatest availability of mature *B. longipes* fruits (May and December 2010, from January–May, December 2011 and March–May 2012). During each period a total of 15 days of sampling per site was carried out. Mist nets remained open from 0700 to 1800 hours, resulting in a total of 1485 net-hours per site and 4455 net-hours for all sites.

For each species, the relative abundance was calculated based on the number of individuals captured per net hour, and the data were analyzed in a χ^2 contingency table to determine whether differences in number of individuals existed between sites. The null hypothesis in this case would be the existence of an equal number of individuals at each site.

Frequency of visits and average amount of removed fruit

The frequency of visits was determined by focal observations using binoculars (8 x 40 mm). These observations were randomly focused on seven *B. longipes* individuals with ripe fruits at each of the successional stages. The observations were made during January–May 2011 and March–May 2012 in both the morning (0700–1130 h) and afternoon (1600–1830 h) when bird activity is higher. A total of 70 hours of observation were recorded for each site (10 hours / tree), with a total of 210 hours for all three sites.

Each tree was observed at a distance of ~20 to 30 m for an observational period of 30 min, during which the visitor species, number of individuals per visit, total time per visit (from arrival to departure), number of visits and number of fruits eaten were recorded. The frequency of visits was analyzed in a χ^2 contingency table to determine differences between successional stages. The null hypothesis would indicate the existence of an equal number of visits between successional stages. The number of removed fruits was compared between sites with an unbalanced one-way ANOVA. For this analysis, data were transformed (log x + 1) to meet the assumptions of normality and homogeneity of variance.

Component of Quality

Seed germination

To determine the effect of the digestive system of birds on the proportion of germinated seeds, we used seeds obtained from the excrement of birds captured by the mist nets. These birds were placed in individual cages (40 x 40 cm) lined with mosquito netting and fed *ad libitum* with ripe *B. longipes* fruits for a day after capture. Retention time of seeds was estimated from the moment of fruit consumption until defecation. The premise is that longer retention times likely contribute to seeds being spread farther from the mother plant (Westcott & Graham, 2000). After evacuation, the feces were collected, and the birds were released. The techniques used to collect vomit and feces were non-invasive and it was no necessary to have a special authorization.

The viability of the seeds was tested with a flotation test, where floating seeds were considered nonviable due to the lack of embryonic development (Thompson, Grime & Mason, 1997). Viable seeds were washed with 10% sodium hypochlorite, planted in cotton on petri dishes at ambient temperature and moistened daily with distilled water. This procedure was

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performed to the following three treatments, representing seeds obtained from varying sources: a) control group 1: seeds with pseudoaril obtained directly from the trees, b) control group 2: seeds without pseudoaril obtained from trees and c) seeds that passed through the digestive system of collected birds.

For the final category, the germination experiment was performed only with bird species from which the largest number of seeds was obtained: *Myiarchus nuttingi* (*N* = 67), *Myiodynastes luteiventris* (*N* = 58), *Myiarchus cinerascens* (*N* = 33), *Melanerpes chrysogenys* (*N* = 29) and *Myiarchus tyrannulus* (*N* = 27). Meanwhile, a total of 50 seeds per site were used for each of the controls (fruits obtained from trees). Germination experiments were performed directly in the field, placing boxes with seeds of *B. longipes* under the canopy of nurse plants *Mimosa polyantha* and *Senna wislizenni*, which are commonly used by disperser birds for perching. The boxes were protected with mesh mosquito netting and boric acid was poured around the perimeter to avoid predation by ants. Over the course of 20 days, the boxes were checked daily to count the number of germinated seeds. Germination was indicated by the emergence of a radicle.

The time that seeds remained in the digestive system of birds and the proportion of germination were compared between treatment and controls groups with a one-way ANOVA, using as a null hypothesis the same proportion of germination for all treatments. The data on germination percentages were transformed to arcsine square root, as this is an appropriate technique for analyzing percentages and ratios (Sokal & Rohlf, 1987). Multiple comparisons were analyzed with a Tukey HSD. Analyses were performed in the SPSS 17.0 software (SPSS, 2008).

Seed deposition in secure sites (nurse plants)

The deposition of seeds under the cover of trees or shrubs (potential nurse plants) was estimated by focal observations to record the number of visits to these perching sites by birds after fruit consumption. To facilitate the monitoring of birds after they finished eating and departed to fly in another direction or roost on another plant, one person was dedicated to post-consumer observations. The number of visits to each of the following categories of perch plants was recorded: 1) Permanent, indicating that the individual remained in the same plant where they ate fruit, including displacement to the ends of branches. 2) *Mimosa* and *Acacia* trees and shrubs, which have been identified as potential nurse plants in semi-arid environments (Godínez-Álvarez & Valiente-Banuet, 1998). 3) Other tree or shrub plants, including nopals or cacti. Focal observations ended when eye contact with the observed individuals was lost.

A contingency table of χ^2 was used to compare the number of bird visits with each category of perch plant. The null hypothesis would indicate of an equal number of bird visits among all perch categories in the three successional stages. Standardized residuals were used to evaluate the preferential use by birds of certain perching sites (Valiente-Banuet et al., 1991; Godínez-Alvarez, Valiente-Banuet & Rojas-Martínez, 2002). These residuals are distributed around a mean of 0 with a standard deviation of 1, so any resulting value ≥ 2 (approximately 5% of the normal distribution) was considered to be a significant deviation.

The probability that the seeds were deposited in safe places (*Acacia* and *Mimosa* trees and shrubs) was determined by the proportion of frugivore visits to these perch plants in relationship to the total number of recorded visits.

Contribution of birds to seedling establishment in different successional stages

Two plots with a radius of 30 m (2 828 m^2 per plot) were randomly chosen in each of the successional sites. In each plot seedlings and young individuals of *B. longipes* (height <50 cm) were counted underneath trees or shrubs used by birds to roost after ingesting *B. longipes* fruits. The number of young *B. longipes* plantlings observed underneath nurse plants was compared to the number of individuals expected to be recruited at random, derived from examining a proportional area and counting *B. longipes* underneath all plants with a DBH ≥ 10 cm (Valiente-Banuet et al., 1991). The fulfillment of the null hypothesis would indicate a number of seedlings proportional to the coverage of woody plants for the two plots. Standardized residuals were obtained to analyze the significance. Plant cover was determined in a previous study corresponding to the study sites (Almazán-Nuñez et al., 2012).

Finally, each bird species was assigned a value of 0-1 according to their contribution towards the establishment of *B. longipes*. This value was estimated from observations of individuals of each bird species after feeding on *B. longipes* drupes, their flight destination, and number of visits to other plants. The maximum value was assigned to birds with the highest frequencies of flights to nurse plants under which the largest number of seedlings or young *B. longipes* individuals had been observed with respect what would be expected by chance, according to the standardized residuals for each plot.

Results

Component of quantity

Relative abundance

A total of 20 bird species were registered eating *B. longipes* fruits (Table 1). Differences in the abundance of bird species across the three successional stages were significant (X^2 = 48.26, df = 30, p < 0.05). *Melanerpes chrysogenys, Myiarchus cinerascens, Myiodynastes luteiventris* and *Icterus pustulatus* were abundant and present at all sites (Table 1). In the early successional stage the species with the highest relative abundance was *Spinus psaltria*, while flycatchers *Myiarchus tyrannulus* and *Tyrannus vociferans* were the most abundant in the mature stage.

Frequency of visits and number of removed fruits

The frequency of visits to remove fruit varied between sites ($X^2 = 54.78$, $df = 38$, $p < 0.05$). *Myiarchus tyrannulus* and *Tyrannus verticalis* were the most frequent visitors to the early successional site (Table 1), *T. vociferans* and *T. verticalis* to the intermediate site and *M. cinerascens* to the mature site. *Spinus psaltria* removed the greatest number of fruit at the early (5.00 ± 1.58) and intermediate (4.40 ± 0.51; Table 1) sites and *E. canicularis* at the mature site (11.00 ± 4.00).

Overall, 17.9% of the counted fruit was removed ($n = 825$) at the early site, 42.2% at the intermediate site and 39.9% at the mature site, although no significant differences were found among sites ($F_{2,275} = 1.57$, $p = 0.210$). The flycatcher *T. verticalis* remained for the longest time in the trees of the early site (6.78 ± 1.30 min), while in the intermediate site *T. vociferans* remained the longest (6.33 ± 1.13 min) and in the mature site *E. canicularis* did so (8.00 ± 4.00 min; Table 1).

Seed germination

The shortest average seed retention time from fruit intake until evacuation was recorded for *M. nuttingi* and the highest for *M. tyrannulus* (Table 2). The latter had the widest range in seed evacuation time (minimum = 10 min and maximum = 230 min). The shortest range corresponded to *M. luteiventris* (minimum = 12 min and maximum = 155 min; Table 2). However, these differences in retention time were not significant ($F_{4,122} = 0.98$, $p = 0.420$).

None of the seeds with pseudoaril (control group 1) germinated (Fig. 2). Seeds without pseudoaril (control group 2) had a germination rate of 10%. The seeds that passed through the digestive tract of *Myiarchus cinerascens* had the highest germination percentage (27%, $n = 33$), followed by *Myiarchus tyrannulus* (26%, $n = 27$), *Melanerpes chrysogenys* (24%, $n = 29$), *Myiarchus nuttingi* (15%, $n = 67$) and *Myiodynates luteiventris* (12%, $n = 58$) (Fig. 2). The resulting differences among treatments were significant ($F_{5,114} = 9.11$, $p < 0.001$). The Tukey HSD test indicated that the three bird species with the highest percentage of germination (*M. cinerascens*, *M. tyrannulus* and *M. chrysogenys*) significantly differed in the proportion of seeds germinated in the seeds without pseudoaril (control group 2, Fig. 3). However, significant differences were not found in the germination between seeds without pseudoaril (control group 2) seeds eaten by *M. nuttingi* and *M. luteiventris*.

Seed deposition in secure sites (*nurse plants*)

After consuming the fruits, the birds perched in three categories of plants (Fig. 4). The preference was for *Acacia* and *Mimosa* plants at all three sites ($X^2 = 22.98$, $df = 12$, $p < 0.05$; $X^2 = 55.33$, $df = 20$, $p < 0.05$; $X^2 = 54.98$, $df = 20$, $p < 0.05$ for the early, intermediate and mature sites respectively) (Fig. 4a-c). At the intermediate and mature sites, the flycatchers *M. nuttingi* and *M. tuberculifer* remained for the longest period of time in *Acacia* and *Mimosa* plants following feeding episodes, while *Tyrannus verticalis* and *Vireo gilvus* spent more time in trees where they obtainded the seeds. Thus, flycatchers of the genus *Myiarchus* were the most likely species to deposit *B. longipes* seeds beneath *Mimosa* and *Acacia* trees and shrubs throughout the three successional sites (Table 4).

Contribution of birds to the site of seedling establishment

The lowest density of *B. longipes* seedlings and non-reproductive individuals was found at the early site (0.002 ind / m2). The average height of plants was 54.07 ± 7.90 cm. At the intermediate and mature sites, the densities of seedlings and non-reproductive individuals were 0.007 ind / m2 and 0.008 ind / m2, with and average height of 50.93 ± 3.90 cm and 53.19 ± 3.80 cm, respectively, and did not differ significantly in density ($F_{2,5} = 0.89$, $p = 0.50$) or in average height ($F_{2,104} = 0.12$, $p = 0.89$).

At the early site, the number of seedlings and young *B. longipes* individuals was significantly higher underneath *Tecoma stans*, *Plocosperma buxifolium* and *Mimosa polyantha* plants (Table 3). At the intermediate site, the largest number of seedlings was found under *Mimosa polyantha* and *Calliandra eryophylla*, and for the mature site under *Eysenhardtia polystachya*, *Senna wislizeni*, *Sebastiana pavoniana* and *Acacia cochliacantha* (Table 3). *Acacia subangulata* was the only legume that presented a lower number of observed seedlings than expected by chance (Table 3).

The largest contribution to the establishment of *B. longipes* seedlings (that was calculated based on the number of flights to nurse plants with the largest number of observed seedlings with respect what would be expected by chance), was attributed to *M. cinerascens* at the early site and to *M. nuttingi* at the intermediate and mature sites (Table 4).

Effectiveness in seed dispersal

The effectiveness of seed dispersal was estimated for five bird species whose number of visits allowed for a reliable estimation, which varied depending on the site (Table 4). For other species, dispersion was not determined due to lack of defecated seeds or other subcomponents that would allow for assessment. At all sites the best dispersers belonged to the genus *Myiarchus*. At the early site, only *M. cinerascens* contributed to seed dispersion (Table 4), at the intermediate site, *M. nuttingi* was the largest contributor to seed dispersion while in the mature site, five species participated in seed dispersion, and *M. cinerascens* had the highest effectiveness (Table 4).

Discussion

The bird species involve in fruit consumption, removal and dispersion of *B. longipes* seeds were studied in terms of abundance and frequency of their visits to perching sites in the three study sites with different successional phases. *B. longipes* fruits were consumed by birds in all successional stages, but the identity of the species participating in seed dispersion, their importance and the plants used for perching after feeding varied among sites. Both abundance and the frequency of bird visits were lower in early successional site. This result concurs with the reports of Cordeiro & Howe (2003) and Figueroa-Esquivel et al., (2009), whom note that at disturbed sites the number frugivorous bird species and their relative abundance tends to decrease, due to the lower supply of resources.

Although several bird species removed many fruits and constantly visited *B. longipes* trees at all three sites, some of them did not contribute to the effective dispersal of its seeds. For example, *S. psaltria* and *E. canicularis* had the highest rate of fruit removal at all three sites. *S. psaltria* bits the seeds' pseudoaril, discarding the seeds underneath the parent plant that reduces the chances of germination and establishment, due to competition with other conspecifics (Jordano & Schupp, 2000; Bas, Pons & Gómez, 2005). *E. canicularis* destroyed or damaged the seeds upon handling them, thus their contribution to dispersion was negative. In addition, the mortality rate of plant seeds in species of the Malvaceae in the Neotropics has been shown to be high due to similar predation by birds related to this species (i.e., Psittacidae; Francisco et al., (2008)).

Previously it was suggested that species of the *Tyrannidae* family, particularly from the *Myiarchus* genus, despite being largely insectivorous, could be the main legitimate dispersers of *Bursera* fruits (Ramos-Ordonez & Arizmendi, 2011). In our study, *ca.* 70% of the seeds at the three sites were removed by Tyrannidae. *Myiarchus spp*. individuals, whose behavior is less gregarious compared with other birds that also consume *B. longipes* fruits (e.g., genus *Tyrannus, Eupsittula, Spinus*), removed about 30% of fruits at all of the sites. Two of these species are latitudinal migratory (*M. cinerascens* and *M. nuttingi*), and others two make local altitudinal migrations (*M. tuberculifer* and *M. tyrannulus*).

In the case of the first two flycatchers, the ripening time of *B. longipes* fruits coincides with the winter presence of these birds. In winter, energy demands increase (Telleria, Ramírez & Pérez-Tris, 2005) and the fruits of *Bursera* spp. represent a source of lipids, which are present in the pseudoaril overlaying the seeds (Ramos-Ordoñez, Arizmendi & Márquez-Guzmán, 2012). The distribution pattern of *M. tuberculifer* and *M. tyrannulus* apparently is determined by the supply of *Bursera* fruits (Almazán-Núñez et al., 2015), as the two bird species were only present at the study sites during fruiting season. These flycatchers were also observed during the fruiting of *B. morelensis* in the Valley of Tehuacan in Puebla (Arizmendi & Ramos-Ordoñez, 2011), as well as the White-eyed Vireo (*Vireo griseus*), whose presence and abundance was correlated with the number of *B. simaruba* fruits in secondary growth forests in the Yucatan Peninsula (Greenberg, Foster & Márquez-Valdelamar, 1995).

The distribution of *Bursera* spp. and particularly *B. longipes* apparently coincides with that of the *Myiarchus* genus throughout the Neotropics, and in this study these flycatchers have proven to be its most effective seed dispersers (*sensu* Schupp, 1995). The distribution of both groups is characteristic of semi-arid environments, and both the birds and the plants diversified during the Miocene (Ohlson, Fjeldsa & Ericson, 2008; De-Nova et al., 2012). Both groups are also adaptable to anthropogenic disturbances throughout their range (Howell & Webb, 1995; Rzedowski, Medina & Calderón de Rzedowski, 2005), and this also has been a determinant factor of their recent success throughout Mesoamerican tropical forests.

Overall, the minimum retention time of seeds by frugivorous seed dispersers was greater than the time that they remain on *B. longipes* trees. This indicates they do not defecate immediately after feeding, and therefore seeds are transported and deposited to other sites far from the mother plant, such as under nurse plants (Schupp, 1995; Godínez-Alvarez & Valiente-Banuet, 1998; Padilla & Pugnaire, 2006).

Moreover, the germination rate of seeds that have passed through the digestive tract of *M. cinerascens*, *M. tyrannulus* and *M. chrysogenys* was significantly higher than seeds without pseudoarile (control group 2), although not in the case of *M. nuttingi* and *M. luteiventris*. While *Bursera* seeds responded to similar physiological treatments during endozoochory (Stevenson et al., 2002), germination differences between species can potentially be explained by time spent in the digestive system (Dominguez-Dominguez, Morales-Mávil & Alba-Landa, 2006), as *M. nuttingi* and *M. luteiventris* had a lower retention time (although the differences were not significant). *B. longipes* seeds are hard and possibly require a longer time in order to soften the endocarp. The fact that none of the seeds sown with pseudoaril germinated, highlights the importance of frugivorous birds in removing this tissue, as it may contain substances that inhibit the germination of seeds as found in *B. fagaroides* (Ortiz Pulido & Rico-Gray, 2006). Moreover, these bird species consume insects throughout much of the year, and their intestines are usually small and require additional enzymatic attack, contrary to strict frugivores whose digestive system is more long and simple (Jordano, 1986).

The probability that *B. longipes* seeds are deposited by flycatchers of the genus *Myiarchus,* in suitable sites for germination and the subsequent development of seedlings, confirms that these flycatchers are the most efficient seed dispersers across different stages of successional dry forest. These dispersers often select perches belonging to plants of the *Acacia* and *Mimosa genera*, which have been previously identified as nurse plants throughout the arid environments of Mexico (Valiente-Banuet et al., 1991; Godínez-Alvarez & Valiente-Banuet, 1998 Castillo & Valiente-Banuet, 2011). This demonstrates the importance of legumes in aiding seedling establishment as they foster nutrient recycling, accumulation of organic matter and a shadow effect, thereby creating more favorable temperatures that promote the development of native plants (Franco & Nobel, 1989; Bonanomi et al., 2007).

Other members of the Tyrannidae family, such as *T.verticalis* and *T. vociferans*, were also considered as dispersers in this study, since they remove fruits in large quantities, swallow whole seeds and typically perch on the top branches of *B. longipes* trees for long periods of time. However, the quality of dispersal by these species was low, as conspecific trees recruitment was not observed at our study sites (see also Godínez-Alvarez, Valiente-Banuet & Rojas-Martínez, 2002).

The observed number of recruited seedlings was lower in the early successional site with respect to the intermediate and mature sites. *Mimosa polyantha* was one of the most preferred nurse species by dispersers for perching, resulting in a higher recruitment of seeds and consequently, the number of seedlings was higher underneath this plant than expected by chance at all stages of succession. Similar results were obtained for other species of the same nurse genus (Castillo & Valiente-Banuet, 2011).

At the mature and intermediate sites, density of recruited seedlings increased due to seed rain from dispersers, but it is also likely influenced by the seed bank in the soil, which may be of lower density in earlier successional stages, as found for other DTF sites (Uhl, 1987; Hammond, 1995). The presence of a seed bank fosters a higher rate of germination at the advanced successional stages that along with a high number of disperser visits improve the microenvironmental conditions favoring seedling establishment (Valiente-Banuet et al., 1991 Godínez- Alvarez & Valiente-Banuet, 1998; Orozco-Almanza et al., 2003; Padilla & Pugnaire, 2006).

Although the number of frugivorous birds was lower in the earlier successional stages (Almazán-Núñez et al., 2015), the presence of dispersers that can tolerate disturbed sites ultimately contributes to the regeneration of these forests (Griscom et al., 2007). At a lesser density, the number of seedlings recruited underneath mother plants in the early site was greater. However, it is also likely that the process of germination and establishment at this stage is slower than for other stages of succession, mainly due to the more inhospitable conditions facing seeds once they are dispersed (Padilla & Pugnaire, 2006; Obeso et al., 2011). In this scenario, the increased presence of legumes at early successional stages, the preference of various dispersers to perch on these plants and the adaptability of some zoochorous plants to these new conditions generates greater chances of recovering these habitats. Regional or genetic studies to analyze the spatial variability of seed dispersal are necessary to further understand both the preferences and the movements of the frugivorous birds (Carlo, Aukema & Morales, 2007; Gonzalez-Varo et al., 2014), as well as differences they experience plants in different environments.

Conclusions

The study of sites with different levels of disturbance and local environmental variations can aid in the understanding of biotic seed dispersal at a regional level (Carlo, Aukema & Morales, 2007). It is also possible to analyze mutualistic interactions and local adaptations, where these may be considered to be active processes that have shaped co-evolutions in the geographic mosaic (Thompson, 2005; Kiers et al., 2010; Guimaraes et al., 2011).

In this study, the sites varied locally in their soil and climatic conditions and demonstrated differences in structure and species composition (Almazán-Núñez et al., 2012). Although the interaction of the genus *Myiarchus* spp. with the *B. longipes* fruits varied slightly between successional sites, these flycatcher species were the most efficient dispersers of its seeds, as has been previously reported for other species of *Bursera* (Ramos-Ordoñez & Arizmendi, 2011). This suggests that *Bursera* has co-evolved with Tyrannidae family, in particular with *Myiarchus* flycatchers, positioning both *Bursera* and *Myiarchus* as successful members of the arid environments in Mesoamerica.

Acknowledgements

We thank Hector Godinez, Pedro Luis Valverde and Maria Ramos for the critical review of this document, as well as two anonymous reviewers who improved this manuscript. We also appreciate the valuable support in the fieldwork of Roberto Bahena, Trinidad Cruz, Noemí González, Jeraldín González, Brenda Pérez, Pablo Sierra and Jaili Sánchez.

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Table 1. Relative abundance (individuals/hr-net), frequency of visits (visits/hr-observation), fruits and time spent per visit of birds that consumed *B. longipes* fruits in three successional stages of tropical dry forest in the Balsas basin of Guerrero. The values shown are as the mean ± standard error.

Table 1.

The species with a dash (-) were not collected (relative abundance) or observed visiting trees (frequency of visits).

Family	Species	Early succession				Intermediate succession				Mature succession			
		Rel.Ab.	Freq. Visit	Fruits/ visit	Time/ visit	Rel. Ab.	Freq. Visit	Fruits/ visit	Time/ visit	Rel.Ab.	Freq. Visit	Fruits/ visit	Time/ visit
Psittacidae	*Eupsittula canicularis*	-	-	-	-	-	-	-	-	-	0.029	11.00 ± 4.00	8.00 ± 4.00
Picidae	*Melanerpes chrysogenys*	0.0061	-	-	-	0.0074	0.057	2.25 ± 0.25	2.75 ± 0.48	0.0054	0.071	2.66 ± 0.56	2.83 ± 0.53
Tyrannidae	*Myiarchus tuberculifer*	-	-	-	-	-	0.043	2.00 ± 0.58	2.40 ± 0.83	-	0.086	1.83 ± 0.31	4.17 ± 0.65
	M. cinerascens	0.0067	0.086	2.50 ± 0.43	3.33 ± 0.99	0.0061	0.257	2.11 ± 0.42	2.56 ± 0.37	0.0135	0.243	2.52 ± 0.37	4.07 ± 0.34
	M. nuttingi	0.0013	-	-	-	0.0189	0.143	2.20 ± 0.53	4.00 ± 0.68	0.0135	0.1	2.77 ± 0.62	4.17 ± 0.76
	M. tyrannulus	0.0027	0.129	3.77 ± 0.52	5.00 ± 0.76	0.0047	0.143	2.40 ± 0.37	4.90 ± 1.22	0.0128	0.114	1.75 ± 0.49	2.00 ± 0.46
	Myiodynastes luteiventris	0.0054	0.029	3.50 ± 1.50	2.75 ± 0.25	0.0108	-	-	-	0.0054	0.071	4.33 ± 0.56	5.50 ± 0.99
	Tyrannus melancholichus	-	-	-	-	-	0.014	5	10	-	-	-	-
	T. vociferans	0.0013	-	1.50 ± 0.50	1.75 ± 0.25	0.002	0.3	3.00 ± 0.43	6.33 ± 1.13	0.0054	0.214	2.56 ± 0.52	4.41 ± 0.60
	T. verticalis	0.0027	0.129	4.11 ± 0.98	6.78 ± 1.30	0.002	0.3	3.52 ± 0.59	5.76 ± 1.02	0.0061	0.129	5.45 ± 0.76	6.31 ± 1.13
Corvidae	*Calocitta formosa*	0.0007	-	-	-	-	0.029	3.00 ± 1.00	2.50 ± 0.50	0.0013	-	-	-
Vireonidae	*Vireo gilvus*	-	-	-	-	0.0007	-	-	-	0.0013	0.029	1.00 ± 0.00	1.50 ± 0.50
Cardinalidae	*Passerina caerulea*	0.004	0.043	1.00 ± 0.00	1.83 ± 1.09	0.0013	0.029	1.50 ± 0.50	5.00 ± 2.00	-	-	-	-
	P. versicolor	0.004	0.029	1.00 ± 0.00	3.00 ± 2.00	0.0088	0.114	2.38 ± 0.46	4.31 ± 1.02	0.0067	-	-	-
	P. lechlacherii	0.0074	-	-	-	0.0141	0.029	2.00 ± 0.00	3.50 ± 0.50	0.0034	0.029	1.50 ± 0.50	5.00 ± 1.00
	Pheucticus melanocephalus	-	-	-	-	0.0007	-	-	-	0.0007	0.043	3.33 ± 1.86	6.83 ± 4.28
Emberizidae	*Haemorhous mexicanus*	0.0027	-	-	-	0.004	0.043	3.00 ± 0.00	3.67 ± 0.88	0.002	-	-	-
Icteridae	*Icterus wagleri*	-	0.029	2.00 ± 0.00	2.00 ± 0.00	-	0.029	2.50 ± 1.50	5.00 ± 2.00	-	0.029	5.00 ± 1.00	3.25 ± 1.75
	I. pustulatus	0.0088	0.086	3.83 ± 0.87	3.33 ± 0.80	0.0189	0.257	2.17 ± 0.26	3.27 ± 0.49	0.0135	0.086	4.83 ± 1.33	8.50 ± 1.72
Fringillidae	*Spinus psaltria*	0.0074	0.057	5.00 ± 1.58	4.25 ± 1.16	0.0007	0.071	4.40 ± 0.51	5.00 ± 0.89	0.0061	0.029	2.00 ± 0.58	2.83 ± 0.17

Table 2. Average seed retention time from point of seed consumption to defecation by individuals. S.E. = Standard error.

Statistics	Myicin	Myinut	Myityr	Myilut	Melchr
Average time (min)	104	60	129	69	80
Standar Error	11.3	5.8	23.0	8.2	11.0
Minimum	22	18	10	12	7
Maximum	225	179	230	155	155

Myilut (*Myiodynastes luteiventris*), Myinut (*Myiarchus nuttingi*), Melchr (*Melanerpes chrysogenys*), Myityr (*Myiarchus tyrannulus*).

Table 3. Standardized Residuals (StaRes) for the number of young *B. longipes* seedlings (<50 cm) according to observed (Obs) and expected (Exp) coverage under nurse plants. Residual values > 2 are significant at a 95% confidence level for a normal distribution.

		Early Succession			Intermediate Succession			Mature Succession		
Species	Family	Obs	Exp	StaRes	Obs	Exp	StaRes	Obs	Exp	StaRes
Tecoma stans	Bignoniaceae	1	0.1	**3**	1	0.3	1.3	0	0	-0.2
Cordia sp	Boraginaceae	1	1.9	-0.7	0	1.2	-1.1	1	0.8	0.3
Opuntia sp	Cactaceae	0	0.2	-0.4	1	0.2	1.6	0	0	0
Senna wislizeni	Caesalpinaceae	2	0.7	1.5	3	1.1	1.8	8	2.9	**3**
Senna skinneri	Caesalpinaceae	0	0	0	2	1.2	0.8	0	0.3	-0.5
Ipomoea pauciflora	Convolvulaceae	0	0.5	-0.7	0	2.7	-1.6	1	1.2	-0.1
Euphorbia schlechtendalii	Euphorbiaceae	0	0.1	-0.3	0	2.4	-1.6	1	0.7	0.4
Sebastiana pavoniana	Euphorbiaceae	0	0	0	0	0	0	1	0.2	**2.2**
Eysenhardtia polystachya	Fabaceae	0	0.5	-0.7	0	3.5	-1.9	2	0.2	**4.4**
Gliricidia sepium	Fabaceae	3	3.5	-0.3	0	3.3	-1.8	0	0.8	-0.9
Havardia acatlensis	Fabaceae	2	1.5	0.4	3	4.3	-0.6	1	2.7	-1
Pterocarpus acapulcensis	Fabaceae	0	0.3	-0.6	2	4.1	-1	3	8.5	-1.9
Plocosperma buxifolium	Loganiaceae	1	0.1	**3.1**	0	2.7	-1.6	1	0.6	0.5
Acacia cochliacantha	Mimosaceae	1	1.4	-0.3	2	0.7	1.5	9	3.1	**3.3**
Acacia subangulata	Mimosaceae	0	0.9	-1	3	6.1	-1.3	5	13.6	**-2.3**
Calliandra eryophylla	Mimosaceae	0	0	0	4	0.7	**4**	0	0	0
Desmanthus balsensis	Mimosaceae	0	0	0	0	0.7	-0.9	3	3.5	-0.2
Lysiloma tergemina	Mimosaceae	0	0.5	-0.7	5	2.5	1.5	2	2.2	-0.2
Mimosa polyantha	Mimosaceae	2	0.4	**2.3**	10	1.9	**5.9**	9	4.6	**2.1**
Ziziphus amole	Rhamnaceae	0	0	0	0	0	0	1	0.8	0.2
Randia sp	Rubiaceae	0	0	0	1	0.3	1.2	0	0	0
Cissus sp.	Vitaceae	1	1.3	-0.2	6	3	1.8	0	0.5	-0.7

Significant values of standardized residuals (StaRes) for each successional stage are highlighted in bold.

Table 4. Probability of seed deposition, contribution to the establishment of seedlings and effectiveness of *B. longipes* seed dispersal by frugivorous birds in a successional gradient of tropical dry forest in southwestern Mexico.

Species	Probability of *B. longipes* seed deposition in secure sites			Value of contribution to the establishment of *B. longipes* seedlings in secure sites			Seed dispersal effectiveness		
	Early	Intermediate	Mature	Early	Intermediate	Mature	Early	Intermediate	Mature
C. formosa	-	0.02	-	-	-	-	-	-	-
I. pustulatus	0.15	0.07	0.05	0.16	0.6	-	-	-	-
I. wagleri	0.05	0.01	0.02	-	0.2	-	-	-	-
M. chrysogenys	-	0.02	0.06	-	0.2	0.25	0	1.1 x 10^{-4}	4.2 x 10^{-4}
M. cinerascens	0.29	0.18	0.17	1	0.2	0.5	0.011	0.003	0.023
M. luteiventris	0.05	-	0.09	-	-	0.25	0	0	5.4 x 10^{-4}
M. nuttingi	-	0.18	0.09	-	1	1	0	0.016	0.007
M. tuberculifer	-	0.12	0.08	-	-	0.25	-	-	-
M. tyrannulus	0.20	0.14	0.08	-	0.4	0.25	0	0.002	0.001
T. melancholicus	-	0.02	-	-	-	-	-	-	-
T. verticalis	0.17	0.14	0.11	-	0.4	0.25	-	-	-
T. vociferans	0.10	0.08	0.25	-	-	0.50	-	-	-
V. gilvus	-	-	0.01	-	-	-	-	-	-

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Figure 1. Projection of the study area and distribution of *Bursera longipes* in the biotic province of the Balsas basin. Photograph of (a) the rainy season with presence of foliage and in (b) the dry season with the presence of ripe fruit.

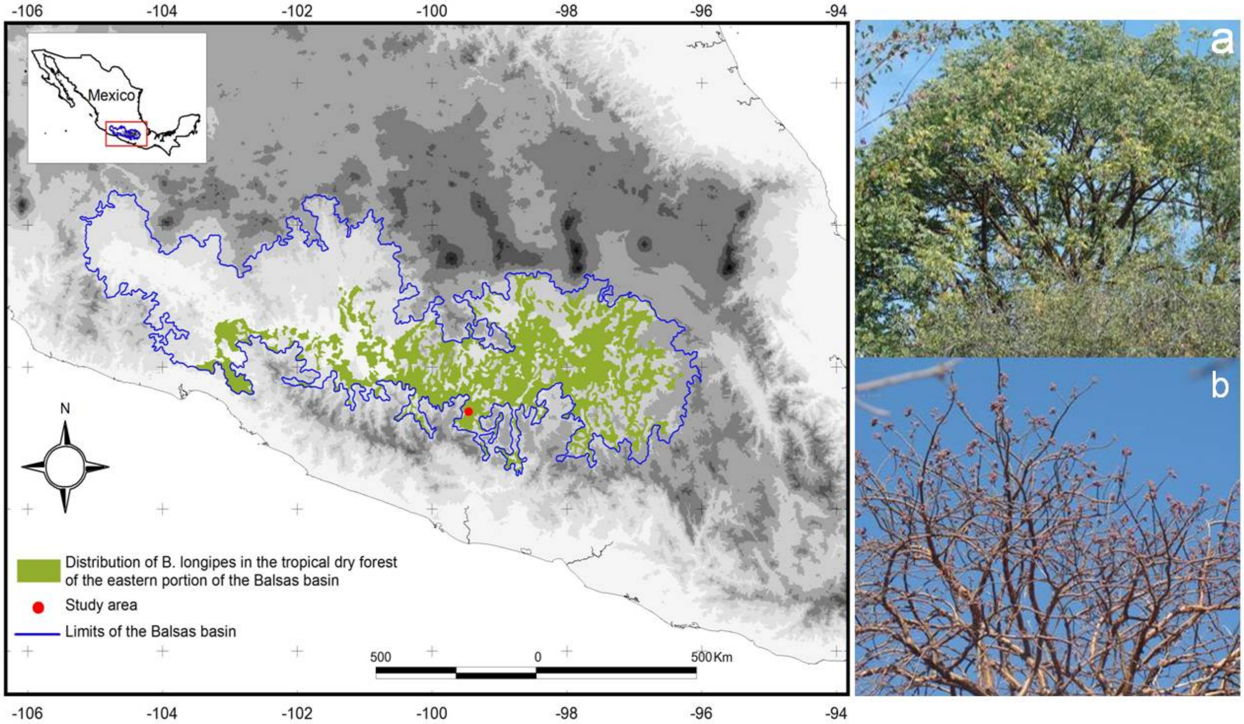

Figure 2. Seed germination of *B. longipes* after passing through the digestive system of birds and compared with control group 1 (seed with pseudoaril) and control group 2 (seeds without pseudoaril).

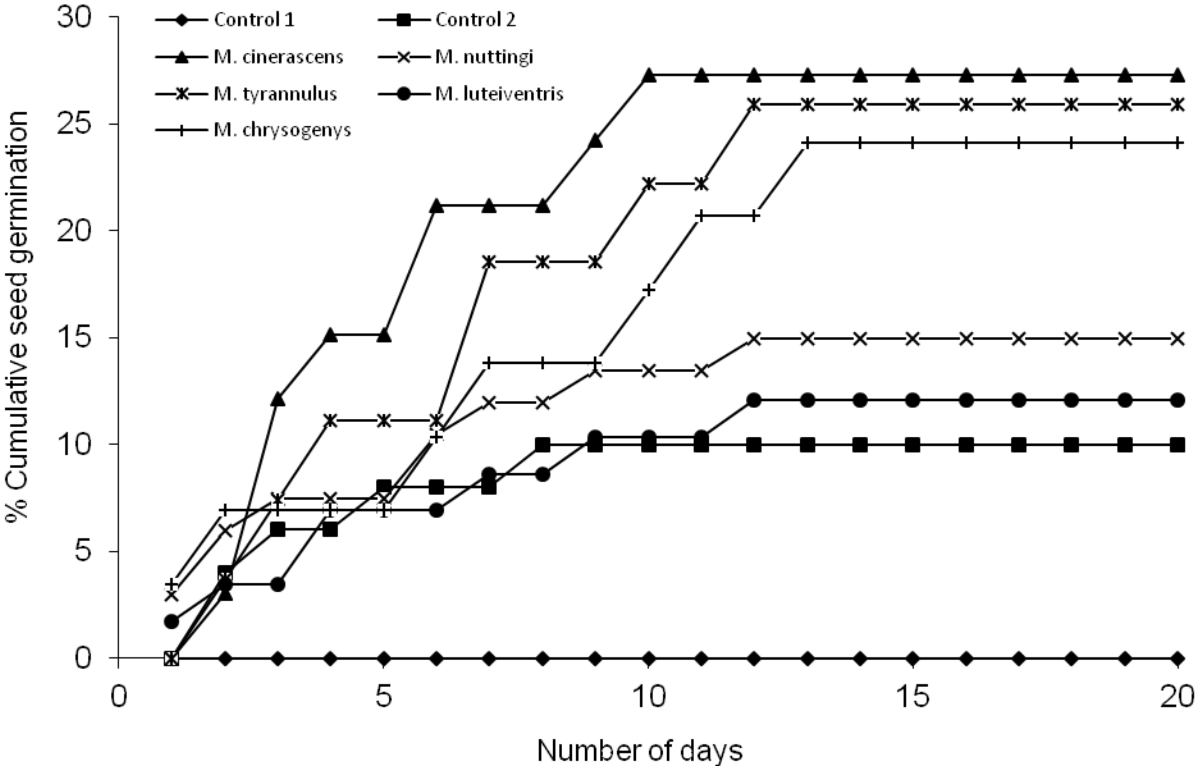

Figure 3. Proportion of seeds germinated after passing through the digestive system of birds. Different letters among treatments indicate significant differences (Tukey, $p < 0.05$).

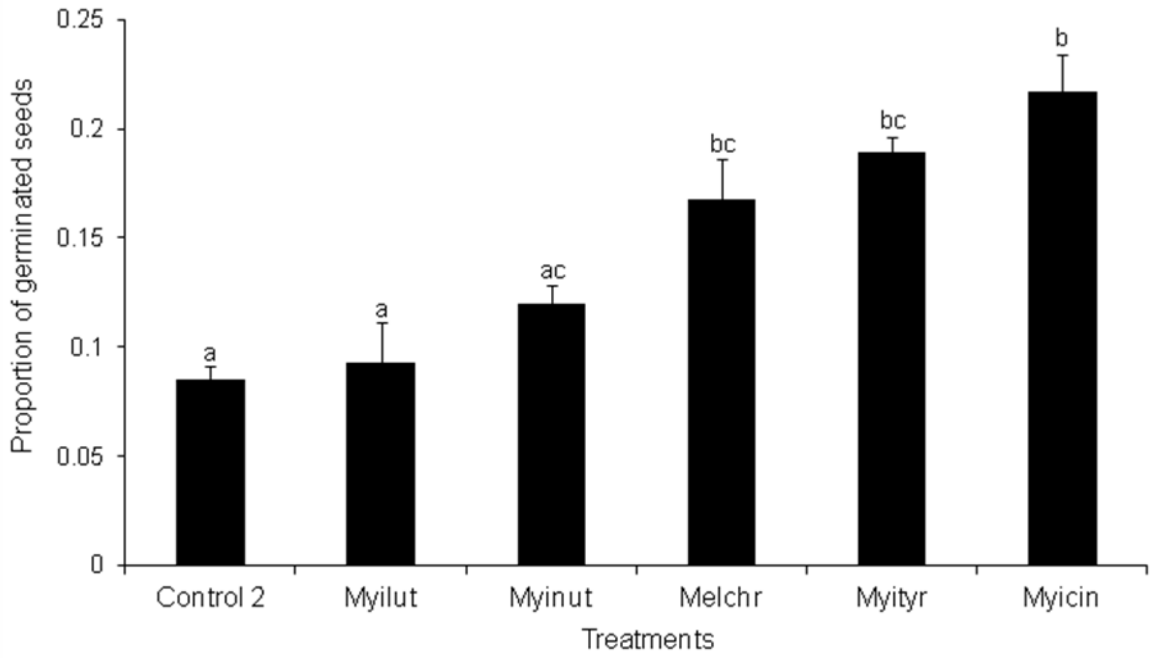

Figure 4. Residuals of a contingency table comparing perching sites for birds after consumption of *B. longipes* fruit in the three stages of succession: a) early, b) intermediate c) mature. Bars represent frequencies, and significant residuals indicate preference (positive residual) or rejection (negative residual). * $p < 0.05$, ** $p < 0.01$.

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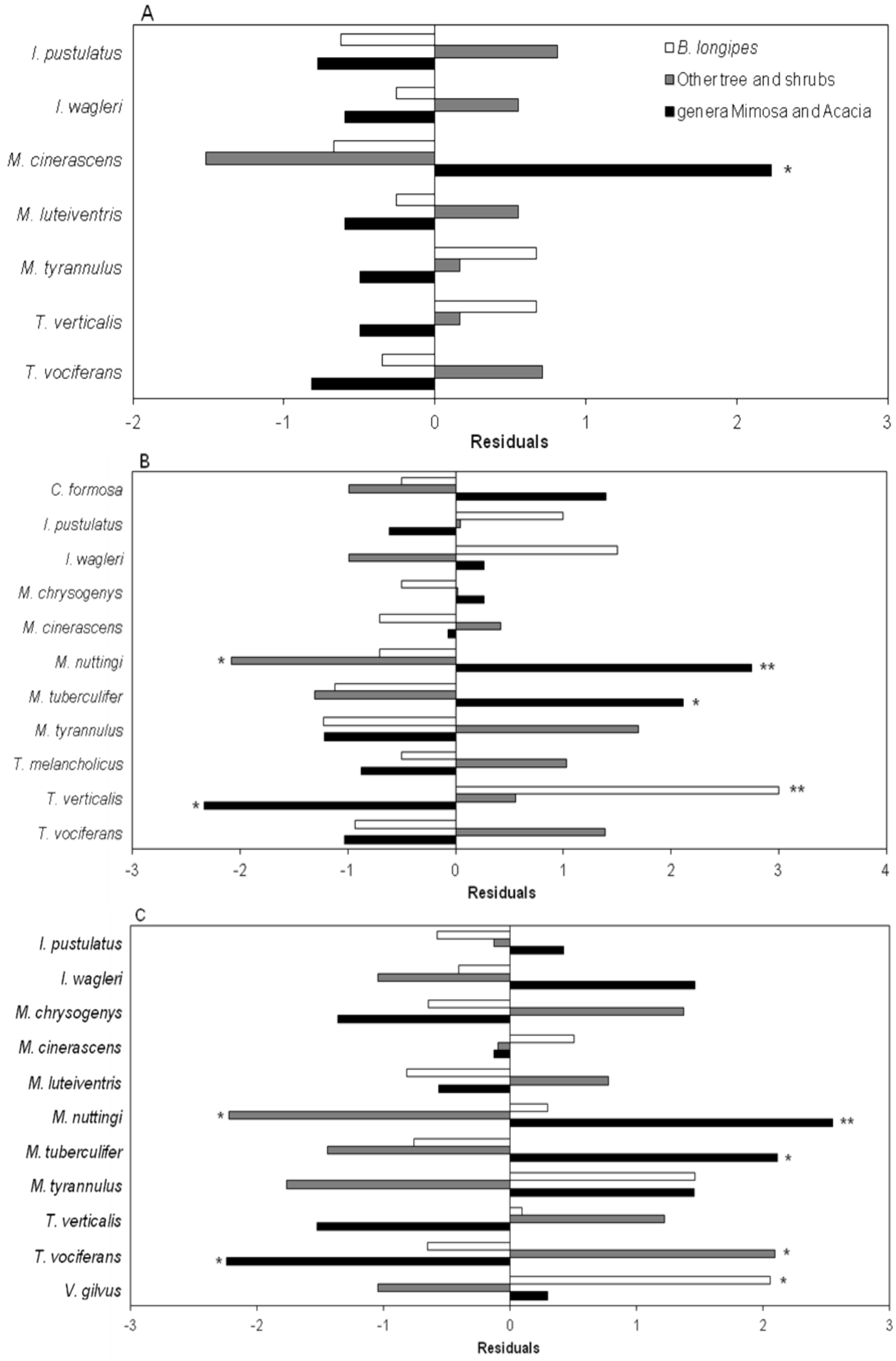
Figure 4.


A
I. pustulatus
I. wagleri
M. cinerascens
M. luteiventris
M. tyrannulus
T. verticalis
T. vociferans
□ B. longipes
▨ Other tree and shrubs
■ genera Mimosa and Acacia
*
-2
-1
0
1
2
3
Residuals
B
C. formosa
I. pustulatus
I. wagleri
M. chrysogenys
M. cinerascens
M. nuttingi
M. tuberculifer
M. tyrannulus
T. melancholicus
T. verticalis
T. vociferans
*
**
*
**
*
-3
-2
-1
0
1
2
3
4
Residuals
C
I. pustulatus
I. wagleri
M. chrysogenys
M. cinerascens
M. luteiventris
M. nuttingi
M. tuberculifer
M. tyrannulus
T. verticalis
T. vociferans
V. gilvus
*
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*
*
*
*
-3
-2
-1
0
1
2
3
Residuals