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**THE ADVANTAGE OF THE RARE: FIELD EXPERIMENTS ON DENSITY-
DEPENDENT SEED DISPERSAL BY AVIAN FRUGIVORES**

A Thesis in

Ecology

by

Benjamin Scott Vizzachero

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The thesis of Benjamin Scott Vizzachero was reviewed and approved* by the following:

Tomás A. Carlo

Associate Professor of Biology

Thesis Advisor

David A. W. Miller

Assistant Professor of Wildlife Population Ecology

Margaret C. Brittingham

Professor of Wildlife Resources

Jason Kaye

Professor of Soil Biogeochemistry

Chair of Ecology Intercollege Graduate Degree Program

*signatures are on file in the Graduate School

ABSTRACT

Frugivorous birds provide dispersal for a large portion of plant species, yet little research has explored how plant-frugivore mutualisms influence plant community diversity. Recent work in tropical forests demonstrates that many fruiting plant species which are rare in a particular time and place occupy a disproportionately high fraction of the diet of avian frugivores. This rare-biased or “anti-apostatic” pattern of frugivory is a previously unexplored mechanism promoting the maintenance of diverse plant communities. The present work entails the first attempt to determine experimentally if anti-apostatic frugivory is a general pattern among common frugivorous birds in multiple environments. Between September 2016 and October 2017, I performed field experiments in Argentina, Puerto Rico, and Pennsylvania in which I presented arrays of artificial fruit in contrast to a background of abundant real fruit. I varied the color and density of artificial fruit arrays and measured the interest of visiting birds with camera traps. I found that wild birds exhibited anti-apostatic selection in most, but not all circumstances. In four of five experiments, avian visitors were more interested in artificial fruit which appeared novel than those which resembled a common fruit in that environment. Avian visitors also made more visits-per-fruit in low-density arrays (10 fruit), compared to high-density arrays (100 fruit). This is the first experimental evidence for anti-apostatic frugivory, demonstrating that frugivorous birds may equalize seed dispersal in plant communities where abundances are imbalanced.

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INTRODUCTION

Mutualistic relationships between fruit-bearing plants and their avian dispersers are believed to be central to the structure and maintenance of plant diversity (Bascompte & Jordano 2007). Understanding the continued existence of diverse plant communities is a central topic almost as old as ecology itself; more than 100 hypotheses have been proposed to explain variation in species richness (Palmer 1994, Vellend 2010). Vertebrates provide dispersal for a large proportion of all plant species, and where plant diversity is greatest, the frequency of bird-dispersed plants is also greatest (**Table 1**, Herrera 2002). Of the extant frugivore groups, birds are the most dominant and likely the most ancient (Fleming & Kress 2011, Jordano 2000). Despite this, little research has explored how plants and frugivorous birds interact to create broad-scale patterns of frugivory and seed dispersal. Conspicuously absent from the slough of diversity maintenance mechanisms are those which concern mutualistic interactions such as frugivory – most deal with interference interactions such as competition, predation, and herbivory (Chesson 2000, Palmer 1994, Terborgh 2012, Wright 2002).

Table 1 – Frequency of bird-dispersed plant species is highest in tropical ecosystems. Estimates are presented for three areas of study, alongside the approximate global maximum.

Location	Percent of woody plant species with fleshy fruit
Bariloche, Argentina	60% (Amico & Aizen 2005)
State College, Pennsylvania	60% (Grinstead 2007)
Aguadilla, Puerto Rico	75% (Carlo <i>et al.</i> 2003)
Neotropical Rainforest (e.g. Ecuador)	90% (Fleming & Kress 2013)

Frugivory is a mutualistic interaction between plant and frugivore, and these two participants benefit differently. Fruiting plant species pursue various evolutionary strategies to achieve the most efficient dispersal of undamaged seeds to suitable habitats, while frugivorous

birds seek to obtain the greatest nutritional reward with minimal foraging effort (Jordano 2000). Foraging birds encounter these fruit resources that vary in abundance along with other visual characteristics (color, shape, size, etc.) and cryptic traits (nutritional content, secondary metabolites, seed volume) (Jordano 2000). Many factors inform how frugivores may interact with these dynamic resources. Birds are limited by the morphology, physiology, and phenology of both the fruit and themselves – a bird cannot consume a fruit which is larger than the gape of its mouth, or one which ripens after birds have migrated away (Jordano 2005, Oleson *et al.* 2011, González-Castro *et al.* 2015). The fruit of any one plant species does not comprise a nutritionally complete meal, so birds consume fruit in complement with live prey, seeds, or other fruit varieties (Levey & Del Rio 2001, Murphy 1994). Some fruit are toxic due to the presence of certain secondary metabolites, but birds can tolerate toxins through physiological or behavioral adaptations conferring resistance (Cipollini & Levey 1997, Levey & Del Rio 2001). Foraging birds seek to minimize search effort while maximizing the energy they consume, thus avian fruit choices are also influenced by the spatial layout of resources (Martin 1985).

Variation in abundance of individual plants and overall fruit availability is associated with evolutionary tradeoffs for that plant. Fruit present in great abundance are more likely to be encountered by foraging frugivores. Many studies have determined that abundance is a strong predictor of interaction probability (Jordano *et al.* 2003, Vazquez 2005), and that frugivorous birds track areas of high fruit density through space and time (Hampe 2008, Saracco *et al.* 2004). However, dense concentrations of resources may satiate vertebrate frugivore communities and be vulnerable to exploitation by non-dispersers (Jones & Comita 2010, Terborgh *et al.* 1993). This plays into a suite of negative density-dependent mechanisms known as Janzen-Connell Effects (Janzen 1970, Connell 1971, Terborgh 2012). Fruit present in low overall densities may suffer

less from density-responsive predators but must compete for the attention of dispersers.

Fortunately, plant species which present a smaller number of fruit can typically afford a greater energetic investment in each fruit (Howe 1993). More energy-rich pulp provides a greater nutritional reward to frugivores (Cazetta *et al.* 2008), and larger seeds contain larger energy reserves which aid seedling establishment (Venable 1992).

We consider three hypothetical functional responses that birds may exhibit in response to variation in abundance of fruit resources. The null hypothesis is that birds forage in a random manner (*sensu* Carlo & Morales 2016). This entails the expectation that the abundance of a fruit is proportional to its prevalence in the diet of frugivores (**Figure 1A**); in other words, the frequency of interactions-per-fruit is constant. One alternative hypothesis is that fruits present in high abundance are consumed at greater-than-random rates; this is described as apostatic or common-biased frugivory (**Figure 1B**). This may arise from optimal foraging, in that foraging birds concentrate on resources present in greatest abundance, which can be consumed most efficiently while minimizing the frugivore's search time and effort (Macarthur & Pianka 1966, White *et al.* 2005). Under this model, we expect that rare or less-preferred fruits are consumed when common or preferred species are not available in great numbers (Carlo *et al.* 2003), or when their dispersal is facilitated by proximity to preferred species (Levey *et al.* 1984). Agent-based simulation models show that apostatic plant-frugivore interactions would result in a loss of plant diversity over time (Morán-López *et al.* 2017).

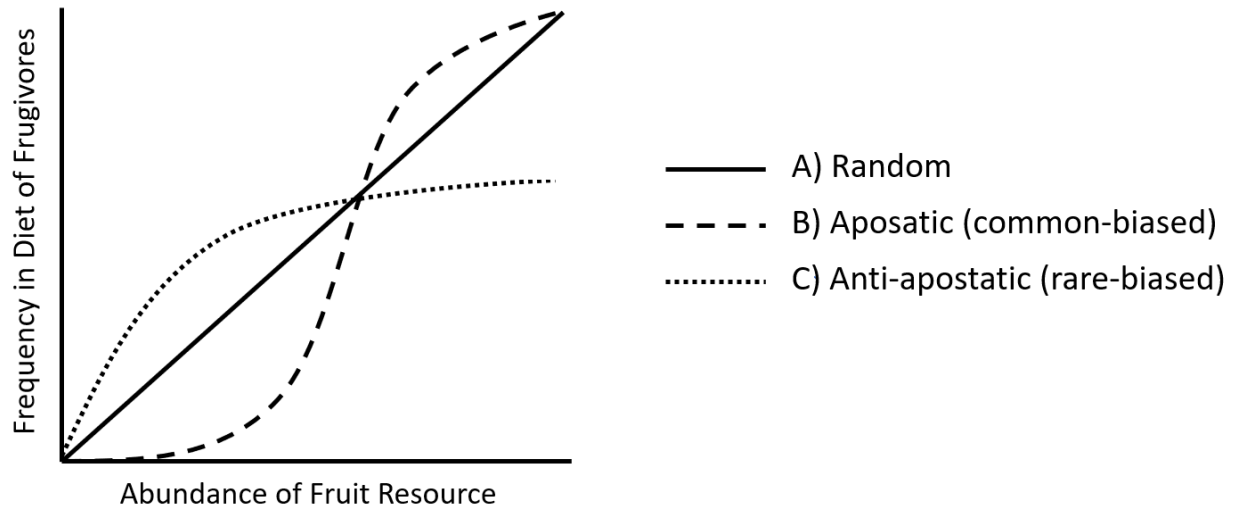


Figure 1 – Three hypothetical functional responses of frugivorous birds to variation in the abundance of a fruit resource. A) Birds forage in a complete random way. B) Birds tend to select fruit which are more common. C) Birds tend to select fruit which are more rare.

Anti-apostatic or rare-biased frugivory describes when rare fruits occupy a disproportionately large portion of bird diets, while common fruits are underrepresented (**Figure 1C**). This does not necessarily mean that common fruits are rarely consumed, merely that their use is less than we would expect under a random foraging model. Recently, Carlo & Morales (2016) proposed that frugivores bird communities generally exhibit anti-apostatic selection, resulting in equalized quantities of seeds dispersed among plants with drastically different fruit availability. Agent-based simulations demonstrate that this pattern may increase the diversity of the plant community and could arise from dietary complementation (Morán-López *et al.* 2017, 2018). Thus, anti-apostatic frugivory comprises a previously unexplored mechanism of plant diversity maintenance mediated by plant-frugivore mutualisms. However, it may work in concert with other negative density-dependent process that aid persistence of rare plants (Terborgh 2012, Wright 2002). Previous research has investigated anti-apostatic selection without regard to frugivory or the ecology of seed dispersal. This concept was originally explored through a series

of “cafeteria” experiments demonstrating that birds prefer rare colors of artificial baits (Allen & Anderson 1984, Allen *et al.* 1998); related work has also studied effects of neophilia or conspicuity from the background on avian foraging (Cooper & Allen 1994, Schaefer *et al.* 2006, Sol *et al.* 2011). Only Whelan *et al.* (1998) explored rare-biased frugivory as a consequence of nutritional complementarity and suggested it may increase dispersal efficiency by encouraging movement of foraging birds.

Since anti-apostatic frugivory presents a previously unexplored mechanism of diversity maintenance, there is a clear need to determine if it is a general pattern amongst avian frugivores worldwide. Here, I present an experimental approach comparing the interest of frugivorous birds between fruits which they perceive as being abundant or rare. This was achieved with artificial fruit, which allowed me to control all aspects of how fruit appeared without providing an exploitable food resource (Alves-Costa & Lopes 2001). I placed arrays of artificial in natural areas in close proximity to an abundant fruit resource. I simulated commonness by presenting artificial fruit which closely resembled the abundant fruit species, and simulated rareness by presenting artificial fruit which looked unlike any naturally occurring fruit in that habitat. I also presented artificial fruit in arrays of high- and low-density, to further explore how frugivores react to variation in fruit availability. I monitored the arrays with camera traps so that I could identify all visitors and determine how they interacted with the array. I completed this experiment in three locations (State College, PA, USA; Llao Llao, Rio Negra, Argentina; Aguadilla, Puerto Rico, USA) to determine if anti-apostatic frugivory is a general pattern observable in different ecosystems. I expected that birds would exhibit anti-apostatic functional responses to variation in perceived availability of artificial fruit. Concerning the two fruit types,

this entails that birds would make more overall visits to fruit which appear rare. Concerning the two densities, I expected that birds would make more visits-per-fruit to low-density arrays.

METHODS

Field Methods

In each study area, I began the experiment by selecting a species of fruiting tree or shrub (hereafter “focal fruit”) that met the dual criteria of being relatively abundant within the study region and being a regular food source for frugivorous birds, as determined by personal observation. I then selected experimental sites, individual locations where the selected species possessed at least several hundred ripe fruit (**Figure 3A**). The number of experimental sites was between 9 and 30, as determined by the availability of the selected fruiting species. Experimental sites were always separated by 25 meters, and usually separated by at least 50 meters.



Figure 2 –*Dumetella carolinensis* (Gray Catbird) is an abundant frugivore in eastern North America, seen here feeding on the fruit of *Phytolacca americana* (Pokeweed) on Penn State campus near experimental sites. © Tomás Carlo, 2017.

Each experimental site received an array of artificial fruit. Artificial fruit arrays varied by two factors: fruit type and fruit density (**Figure 4B**). Fruit type included three levels. “Imitation” fruits were painted or dyed to match the color of real fruit, either red or purplish-black (**Figure 3B**). “Novel” fruits were bright blue, representing a color of fruit that is not found naturally in any of the study areas (**Figure 3C**). “Real” fruits are real fresh fruit from other areas within the study area that were attached to the array with wire. Density included two levels: I presented artificial fruit in numbers of one-hundred or ten.



Figure 3 – Photos from the field experiment on fruit selection by birds. A) A “background” of abundant fruit. In each experimental site, an array of artificial fruit was placed adjacent a similar background. B) “Imitation” treatment, 100 artificial fruit which closely resemble abundant fruit present in the background. C) “Novel” treatment, 100 artificial fruit of unique bright blue color.

I constructed artificial fruit from children’s modeling clay, which is often used in field experiments on frugivory or predation due to the non-toxicity and availability in a variety of bright colors (Alves-costa & Lopes 2001, Madsen 1987, Valdivia & Simonetti 2006). During experiments with *Rhamnus cathartica*, *Aristotelia chilensis*, and *Maytenus boaria* I also painted the artificial fruit with non-toxic acrylics, though this was later deemed unnecessary. Other aspects of artificial fruit, such as size, shape, and luster, imitated the real fruit as closely as possible. I constructed artificial fruit arrays from a post of PVC or wood driven into the ground, with six 15-inch wooden rods inserted into holes along the length of the post. I impaled artificial

fruit onto wire spikes that were affixed to the wooden rods. I positioned artificial fruit arrays within 0.5 meters of the fruit-laden focal plant at heights between 1 and 2.5 meters (**Figure 4A**).

Each experimental site also received a motion-sensitive video camera (Bushnell Trophy Camera, models 119836 or 119636C) to monitor activity on that array. I attached the cameras to wooden posts exactly 1.5 meters from the array. I set the cameras to record 60-second videos when motion was detected, at maximum sensitivity.

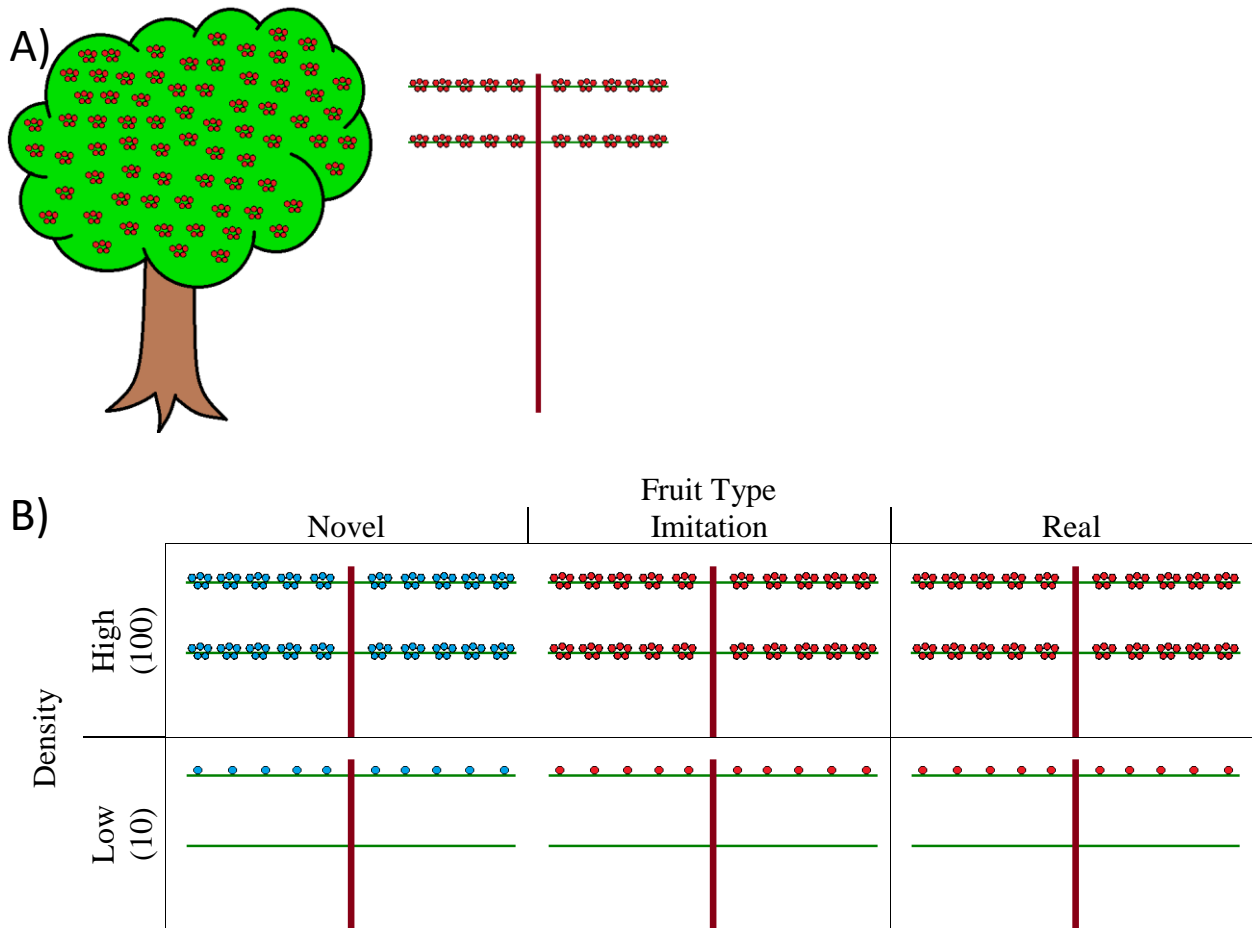


Figure 4 – A) Diagram of one experimental site, in which the array of artificial fruit is placed on a post immediately adjacent a background of the abundant focal fruit. Focal fruit were not always red in color but are depicted this way for ease of illustration. Camera is not depicted. This figure is not drawn to scale. B) Table of experimental design. Artificial fruit arrays varied by two factors, “fruit type” and “density.” Fruit type include levels “Novel” (bright blue artificial fruit), “Imitation” (artificial fruit closely imitated the focal fruit), and “Real” (real focal fruit were affixed to the array). Artificial fruit were presented in high-density arrays (100 fruit) and low-density arrays (10 fruit).

I completed this experiment with five different species of fruit in three study areas. During experiments with *Cestrum* and *Phytolacca* we used a randomized complete block design. Each experimental site received all six possible treatment combinations in a random order. The experiment with *Rhamnus* functioned as a pilot, and low-density treatments were not yet incorporated. Each site received all three fruit types in high-density arrays only. During experiments with *Maytenus* and *Aristotelia*, I did not have time to perform all treatment combinations at all sites, so I used a split-plot design. Half of all plots received only low-density treatments, and the rest only high-density. Each site received all three fruit types in the given density in random order. In all experiments, adjacent study sites never received the same treatment. Because of their proximity, I do not assume that each experimental site is independent of the next. However, any individual bird rarely encountered any two sites of the same treatment within the same day.

At the onset of each trial, I deployed the fruit array, turned on the camera, and then left the area until the trial was concluded. Each trial lasted for between 6 and 72 hours; this duration was consistent during experiments with each fruiting species. Trials with *Rhamnus* lasted 72 hours because I did not know how much time was required to collect useful results. Trials with *Cestrum* were restricted to approximately 6 hours (from dawn to early afternoon) due to heavy rainstorms occurring almost every afternoon. Trials with *Aristotelia*, *Maytenus*, and *Phytolacca* all lasted approximately 48 hours. At the conclusion of each trial, I collected the artificial fruit, noted the number of missing fruit or other evidence of avian visits, and shut off the camera. I rested each experimental site for a minimum of 18 hours before the next trial began.

Video Data

I first viewed all of the collected videos at two- or five-times actual speed to eliminate videos that did not contain avian visitors. I then determined if each video constitutes a “foraging interaction” in which a bird expresses interest in the fruit on the array, as if they are considering it as an exploitable resource. This includes any video in which a bird handles, pecks, or closely examines fruit from the array. I excluded videos in which birds visit the array without examining the artificial fruit. When two or more videos of one species of bird occurred in sequence less than 3 minutes apart, I inferred that this was not a unique visitor, and only counted the first video in the sequence as a foraging interaction. Individual birds which made repeat visits over longer time intervals could not be conclusively identified and were treated as unique visitors.

Analyses

I calculated the total number of avian foraging interactions for each treatment combination in each experimental site (hereafter described as the “interaction rate”). Experimental sites which received zero interactions for all treatment combinations were removed from analysis.

I then created a general linear mixed model with penalized quasi-likelihood (glmmPQL), because it allowed us to fit a quasipoisson distribution to our overdispersed dataset (Bolker *et al.* 2008). I modeled the interaction rate as the response. As fixed effects I used fruit type, density, the interaction of fruit type with plant species, and the interaction of fruit type with density. I used plant species as a random effect because it allowed us to control for variation in the duration of experiments and for differences in overall bird abundance. I also used experimental site, nested within plant species, as a random effect, because it accounted for differences in bird

abundance between experimental sites. I excluded the real fruit treatment from this analysis, because comparing visitation rates between a decoy and an exploitable resource is misleading. Birds repeatedly revisited real fruit arrays to consume fruits, whereas birds typically did not revisit artificial fruit arrays after discovering that the fruits were not palatable. I performed this analysis using R version 3.4.3.

I also calculated the “per-capita” interaction rate by taking the number of visits in a trial and dividing it by the number of fruit in that array. This represents the number of foraging visits per fruit in the array. I compared the per-capita interaction rate between low- and high-density arrays using a 2-sample t-test. I performed this analysis for the real fruit treatment only. This is because birds typically did not revisit artificial fruit arrays, so the per-capita interaction rate is not an accurate depiction of how birds interact with a real fruit resource. I performed this analysis in JMP Pro version 12.2.0.

STUDY AREAS

The Arboretum at Penn State – State College, Pennsylvania, USA

I first performed this experiment in September and October of 2016, then repeated it in September and October of 2017 on the Arboretum at Penn State (40° 48' N, 77° 52' W). The Pennsylvania State University manages this land for research, conservation, and recreation. The climate is temperate, with temperatures highest in July (22°C on average) and lowest in January (-2°C on average). The area receives about 100 cm of rainfall and 115 of snowfall per year; precipitation is dispersed throughout the year but peaks around April.

The Arboretum at Penn State contains over 300 acres of natural lands, in patches of forest, meadows, and agricultural land. This area contains approximately 60 species of trees, shrubs, and vines, of which 36 bare bird-dispersed fruit. Approximately one-third of these fruiting species are invasive (Grinstead 2007). Forest understories are dominated by invasive shrubs, most notably *Rhamnus cathartica* (European Buckthorn, hereafter “*Rhamnus*”), *Ligustrum obtusifolium* (Obtuse-leaved Privet), and *Lonicera* spp. (Honeysuckle). The meadows of the arboretum are occupied by numerous early-successional species, including fruiting species such as *Phytolacca americana* (Pokeweed, hereafter “*Phytolacca*”), *Solanum americanum* (American Black Nightshade), and *Rhus glabra* (Smooth Sumac) alongside the aforementioned shrubs and various other forbs and grasses.

I performed the experiment with *Rhamnus* and *Phytolacca*. *Rhamnus* is a shrub introduced from Europe sometime in the past century that commonly invades pastures and open woods. It bears large numbers of fleshy, glossy-black berries, 5mm in diameter, which are mildly toxic to mammals but readily consumed by birds (Gale 2000). *Phytolacca* is a perennial herb which produces many large racemes of 20-40 shiny, dark purple berries, approximately 6mm in

diameter. These fruits are highly toxic to all mammals but are voraciously consumed by many birds (Owen 1988). Fruit of both *Rhamnus* and *Phytolacca* are high in water and carbohydrates (Snow & Snow 1988, Whelan & Willson 1994).

This area hosts many migratory and resident fruit-eating birds, and our experiments occurred during the fall migration. *Dumetella carolinensis* (Gray Catbird, hereafter “*Dumetella*”) was the most conspicuous fruit-eater in this habitat. It is generally categorized as an insectivore, consuming 60% of its diet from invertebrates and the remainder in fruit (Wilman *et al.* 2014). However, during the fall, *Dumetella* may consume as much as 81% of its diet from fruit (Smith *et al.* 2011). Other conspicuous frugivores included *Sayornis phoebe* (Eastern Phoebe), which mainly eats insects but relies on fruit as an alternate food source when few invertebrates are available (Weeks Jr. 2011, Wilman *et al.* 2014), and *Turdus migratorius* (American Robin), an omnivore which is especially frugivorous in the fall and winter (Vanderhoff *et al.* 2016).

Parque Municipal de Llao Llao – San Carlos de Bariloche, Rio Negra, Argentina

I performed this experiment in February and March of 2017 in Parque Municipal de Llao Llao (41° 03' S, 71° 34' W). The climate here is temperate, cool, and windy. Out of 78 cm of average annual rainfall, the majority falls between May and August. Average temperatures are highest in January (15°C) and lowest in July (3°C) (Amico & Aizen 2005).

This park is situated on a large peninsula surrounded by vast alpine lakes and contains temperate primary forests. The overstory layer is characterized by a lack of diversity, primarily composed of *Nothofagus dombeyi*. These large trees are vulnerable to windfall, particularly on this wind-swept lakeside peninsula, thus this forest has an open canopy and many small

clearings. This allows for a diverse understory of at least 30 species of shrubs and small trees, about half of which produce fleshy, bird-dispersed fruits (Amico & Aizen 2005).

Here, I executed the experiment for two shrub species. *Aristotelia chilensis* (Maqui, hereafter “*Aristotelia*”) produces large numbers of round, shiny, purple-black fruit 5mm in diameter with wet, sugary pulp and 3-4 moderately small seeds (Brauch *et al.* 2016). Of focal fruits used in this experiment, *Aristotelia* is the only one commonly eaten by humans and other mammals (Brauch *et al.* 2016). *Maytenus boaria* (Mayten, hereafter “*Maytenus*”) produces small, oblong, bright red fruit, 5-7 mm in length, with lipid-rich pulp surrounding a single large seed (Reid & Armesto 2011a). These fruits are encased in pairs in a pale-yellow capsule which bursts open when ripe. *Maytenus* is consumed by common passerines of the region (Reid & Armesto 2011b) but was refused by a mammal in experimental trials (Amico *et al.* 2009). No other species reached landscape-scale abundance in the study area, although *Azara microphylla* (Box-leafed Azara) and various introduced *Rubus* species (Blackberry, Raspberry, etc.) were moderately abundant.

Despite the prevalence of fruit-bearing shrubs, this habitat is noted for the small assemblage of migratory passerines which function as dispersers (Armesto *et al.* 1987). A comprehensive study within Parque Municipal de Llao Llao named *Elaenia albiceps* (White-crested Elaenia, hereafter “*Elaenia*”) and *Turdus falklandii* (Austral Thrush) as being responsible for the vast majority of endozoochorous seed dispersal in this habitat; of these, the *Elaenia* is far more abundant (Amico & Aizen 2005). Overall, the *Elaenia* consumes half of its diet from fruit (Wilman *et al.* 2014), though evidence suggests they consume less while occupying their southerly breeding grounds (Cueto *et al.* 2016). Several other common passerines may occasionally consume fruit in spite of primarily insectivorous diets, including *Aphrastura*

spinicauda, *Anairetes parulus*, *Colorhamphus parvirostris*, and *Scelorchilus rubecula* (Carlo *et al.* in prep., Wilman *et al.* 2014).

La Finca Montaña – Aguadilla, Puerto Rico, USA

I conducted this experiment in June of 2017 in La Finca Montaña of Aguadilla, Puerto Rico (N 18° 28'; 67° 06' W). This area is managed for research and conservation by Universidad de Puerto Rico – Recinto Universitario de Mayagüez. This climate is warm and humid, receiving 100 cm of rainfall throughout the year, but more predominantly in the wet season from May to October. The average temperatures are warmest in July (27°C) and coolest in January (24°C) (Carlo & Morales 2016). This landscape is a patchwork of active cattle pastures and secondary subtropical moist forests. These forests and edges contain more than 40 bird-dispersed fruiting species, which vary widely in appearances, abundances, and nutritional contents.

Our experimental sites were located within cattle pastures while all livestock were absent. I selected *Cestrum diurnum* (Day-blooming Jasmine, hereafter “*Cestrum*”) as the focal fruit due to its outstanding dominance, long fruiting season, and accessible height. *Cestrum* is a medium shrub which favors early-successional habitats and produces large numbers of nearly-round black fruit approximately 8 mm in diameter. Like most plants in family Solanaceae, these fruit are high in water and carbohydrates, contain many small seeds, and may be toxic to mammals (Benitez de Rojas & D’Arcy 1998, Wheelright *et al.* 1984).

Puerto Rico hosts a diverse community of frugivores; the frugivorous birds are too numerous to list. These experiments occurred during June, when few migrants are present. The fruit-eating bird community was further restricted by the open habitats, as many of Puerto Rico’s most conspicuous frugivores are adapted to forested habitats. In our experimental sites, *Mimus*

polyglottos (Northern Mockingbird, henceforth “*Mimus*”) was the most conspicuous frugivore. Though the diet of *Mimus* is generally split between insects and fruit, evidence suggests the Puerto Rican population consumes nearly 70% of their diet from fruit (Wetmore 1916, Wilman *et al.* 2014). *Zenaida aurita* (Zenaida Dove, hereafter “*Zenaida*”) was another prevalent frugivore, although their diet is split between fruit, grains, and a small proportion of insects (Wetmore 1916, Wilman *et al.* 2014).

RESULTS

Of 87 experimental sites, 41 received one or more visits to any experimental unit (**Table 2**). Birds interacted with fruit arrays in various ways (**Table 3**). Overall, foraging interactions were evenly divided between birds handling the fruit, birds pecking at the fruit, and birds inspecting fruit. At low-density sites for novel and imitation fruit, a larger proportion of visitors only examined the fruit. Arrays of real fruit at high density saw a higher proportion of birds handling fruit, reflecting how many birds both handled and consumed the fresh fruit. Videos that did not constitute foraging interactions were mostly the result of birds perching on the array without expressing interest. However, arrays of real fruit at high density saw a higher proportion of visitors that lingered through numerous sequential videos. With focal fruits *Aristotelia*, *Cestrum*, and *Phytolacca*, real fruit treatment accounted for a large portion of total visits.

For experiments with *Cestrum*, *Maytenus*, *Phytolacca*, and *Rhamnus*, the interaction rate was twice as high for arrays of one hundred novel fruit, as compared to arrays of ten novel fruit or either density of imitation fruit (**Figure 5**). For these four experiments, the interaction rate was generally similar between one hundred imitation and both low-density treatments. For *Aristotelia*, both imitation treatments had a substantially higher interaction rate, and ten novel fruit was the only treatment receiving absolutely zero visits.

The analysis by glmmPQL revealed that fruit type is a significant predictor of the interaction rate, which justifies the observation that novel fruits saw a generally higher interaction rate. However, the interaction of fruit type with plant species had the largest effect size, indicating that the preferred fruit type varied between the different focal fruit. Density and the interaction of fruit type with density were both marginally significant, suggesting that

interaction rate was generally different between the two density levels, but this preference varied between fruit types.

Among all locations, visitors were mostly birds in the families Mimidae, Tyrannidae, or Turdidae. Within each location, one dominant frugivore accounted for the majority of observed interactions (**Table 5**). In Pennsylvania (experiments with *Phytolacca* and *Rhamnus*) this was *Dumetella*. In Argentina (experiments with *Aristotelia* and *Maytenus*) this was *Elaenia*. In Puerto Rico (experiments with *Cestrum*), this was *Mimus*.

Concerning the “per-capita” interaction rate, I found that there were significantly more visits-per-capita for low-density fruit (**Figure 6**), suggesting that a single fruit has a greater chance of being consumed when located alongside fewer similar fruit.

Table 2 – The number of study sites included for experiments with each focal fruit. “Full-factorial sites” refer to experimental sites which received all six treatment combinations. “Low-density only” and “High-density only” sites received all fruit types for just that given density. “Effective” number of study sites includes only sites which received one or more visits to at least one treatment combination. Sites with no visits to any treatment were excluded from analysis.

Focal Fruit	Full-factorial sites		Low-density only sites		High-density only sites	
	Total	Effective	Total	Effective	Total	Effective
<i>Aristotelia chilensis</i>	0	0	15	3	15	7
<i>Cestrum diurnum</i>	14	6	0	0	0	0
<i>Maytenus boaria</i>	0	0	12	3	12	7
<i>Phytolacca americana</i>	9	9	0	0	0	0
<i>Rhamnus cathartica</i>	0	0	0	0	10	6

Table 3 –The total number of videos in which birds approached the artificial fruit array, divided into videos that do and do not constitute foraging interactions. Foraging interactions are divided into three types, by percent: (i) bird inspects fruit in the array without pecking or handling them, (ii) bird pecks fruit in the array without handling them, and (iii) bird handles fruit in the array by picking it up with their bill. Non-interactions are divided into two types, by percent: (i) sequential videos (one of multiple videos of a single visitor taken in immediate succession), and (ii) videos where birds sat on the perch without expressing interest in the artificial fruit array.

Fruit Type	Density	Foraging Interactions (used in analysis)				Non-interactions (not used in analysis)		
		Total	Bird inspects fruit only	Bird pecks fruit, without holding	Bird holds fruit in beak	Total	Sequential visits	Disinterested visits
imitation	Low	13	54%	31%	15%	8	13%	88%
	High	30	33%	33%	33%	5	0%	100%
novel	Low	12	50%	33%	17%	4	0%	100%
	High	55	27%	38%	35%	13	15%	85%
real	Low	17	29%	35%	35%	10	0%	100%
	High	113	11%	17%	73%	38	42%	58%

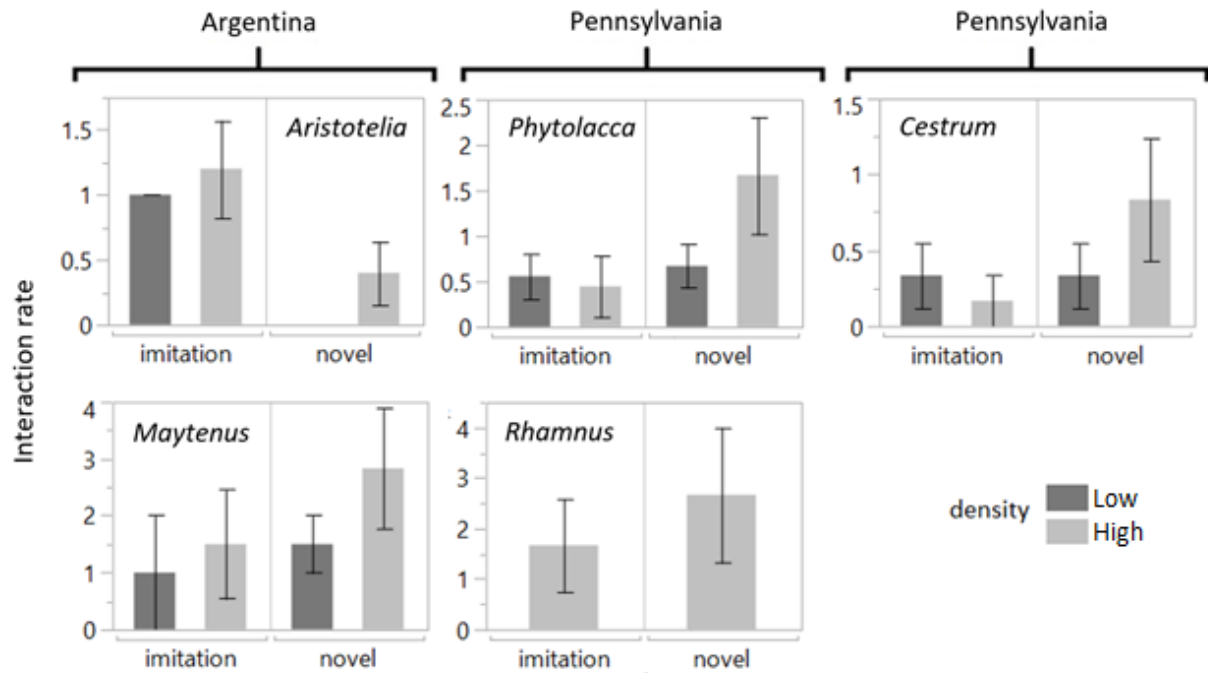


Figure 5 – Mean interaction rate for all treatment combinations (excluding real fruit treatment) for experiments with each of five focal fruit species. Error bars represent one standard error within the mean. The experiment with *Rhamnus* included only one density treatment.

Table 4 – Results of a general linear mixed model to predict the interaction rate for all treatment combinations in fruit selection experiments. Model used a quasipoisson distribution and penalized quasi-likelihood to accommodate overdispersion. Fixed effects are given below, and all are significant or marginally significant. Random effects include plant species and experimental site (not shown). *p<0.05; **p<0.01

Factor	χ^2	Degrees of Freedom	P-value
Density	3.53	1	0.060
Fruit Type	5.24	1	0.022*
(Fruit Type)*(Plant sp.)	23.91	8	0.002**
(Density)*(Fruit Type)	3.15	1	0.076

Table 5 – The identity of all visitors to each treatment combination during fruit selection experiments with each plant species. Within each focal fruit, one or two avian frugivores typically accounted for the majority of foraging interactions of any treatment.

Focal Fruit	Bird Species	Bird Family	Fruit Type		Imitation		Novel		Real	
			Density		Low	High	Low	High	Low	High
<i>Aristotelia chilensis</i>	<i>Elaenia albiceps</i>	Tyrannidae	3	5	0	4	0	16		
	<i>Turdus falklandii</i>	Turdidae	0	1	0	0	1	4		
<i>Cestrum diurnum</i>	<i>Mimus polyglottos</i>	Mimidae	1	1	1	4	2	3		
	<i>Zenaida aurita</i>	Columbidae	0	0	1	1	0	3		
	<i>Tiaris olivaceus</i>	Thraupidae	1	0	0	0	0	3		
	<i>Coereba flaveola</i>	Thraupidae	0	0	0	0	0	1		
	<i>Crotophaga ani</i>	Cuculidae	0	0	0	0	0	1		
	<i>Tiaris bicolor</i>	Thraupidae	0	0	0	0	1	0		
	<i>Zenaida asiatica</i>	Columbidae	0	0	0	0	0	1		
	<i>Maytenus boaria</i>	<i>Elaenia albiceps</i>	Tyrannidae	1	6	1	10	1	6	
<i>Colorhamphus parvirostris</i>		Tyrannidae	1	3	0	1	0	4		
<i>Anairetes parulus</i>		Tyrannidae	0	0	0	4	0	1		
<i>Aphrastura spinicauda</i>		Furnariidae	0	0	1	1	0	0		
<i>Phrygilus patagonicus</i>		Thraupidae	0	0	0	0	0	2		
<i>Scelorchilus rubecula</i>		Rhynocryptidae	0	0	0	1	0	0		
<i>Spinus barbatus</i>		Fringillidae	0	0	0	0	1	0		
<i>Xolmis pyrope</i>		Tyrannidae	0	0	1	0	0	0		
<i>Phytolacca americana</i>	<i>Dumetella carolinensis</i>	Mimidae	4	4	6	12	10	57		
	<i>Sayornis phoebe</i>	Tyrannidae	2	0	0	1	1	0		
	<i>Troglodytes aedon</i>	Troglodytidae	0	0	1	1	0	0		
	<i>Baeolophus bicolor</i>	Paridae	0	0	0	1	0	0		
<i>Rhamnus cathartica</i>	<i>Dumetella carolinensis</i>	Mimidae		9		12		11		
	<i>Sayornis phoebe</i>	Tyrannidae		1		2		1		
	<i>Turdus migratorius</i>	Turdidae		0		2		0		

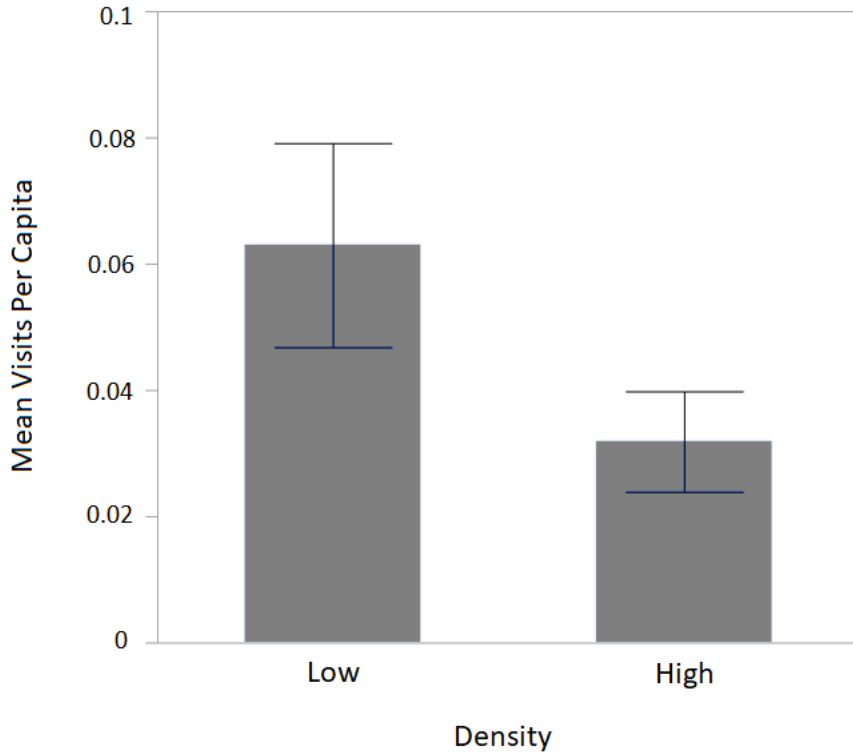


Figure 6 – The “per-capita” interaction rate, representing the number of visits per fruit in the array, for real fruit arrays, combined for all focal fruit excluding *Rhamnus*. It is significantly higher ($p = 0.046$) for low-density fruit. Error bars represent one standard error within the mean.

DISCUSSION

This experiment demonstrates that common avian frugivores in several ecosystems are biased towards interacting with less familiar fruit resources, and that fruits present in low densities receive significantly higher rates of interaction than those present in higher densities. This is the first experimental evidence for the hypothesis of anti-apostatic foraging in the context of frugivory, and part of a growing body of field- and simulation-based research on this topic (Carlo *et al.* in prep.; Carlo & Morales 2016; Morán-López *et al.* 2017, 2018). Anti-apostatic frugivory can have the effect of promoting dispersal for any species whose fruit appear rare in space or time, which may lead to increased plant diversity (Carlo & Morales 2016, Morán-López *et al.* 2017). This emphasizes the role of mutualistic interactions in the maintenance of diverse plant communities, an understanding which has traditionally been more so concerned with interference interactions such as competition, predation, and herbivory (Palmer 1994, Terborgh 2012, Wright 2002).

Anti-apostatic frugivory provides new context in understanding the evolution of fruit traits. Anti-apostatic frugivory entails that plants can achieve adequate dispersal without investing in large, conspicuous fruit crops. Freed from this energetic burden, small-cropped fruiting plant species can increase the energetic investment in both the fruit pulp and the seed, increasing their chance of dispersal and recruitment (Cazetta *et al.* 2008, Venable 1992). However, anti-apostatic frugivory is only detectable at the community-scale. Patches with low overall fruit availability are less frequently visited by avian frugivores (Hampe 2008, Saracco *et al.* 2004), so small-cropped fruiting species may depend on facilitation by nearby plants presenting larger numbers of fruit (Gleditsch & Carlo 2011).

Our results suggest that fruits with colors that contrast nearby abundant fruit are preferred by frugivorous birds. Though this experiment only tested two factors which may influence how birds perceive the rarity of a fruit (fruit type and density), it follows that that a similar anti-apostatic effect would exist for any fruit that is unique by way of any other visual factor such as shape, size, or infructescence type. This experiment provides an adequate framework to compare birds' interest between fruits with varying traits, and it would be beneficial to repeat it with a thorough assortment of color and density combinations, as did Allen & Anderson (1984) and Allen *et al.* (1998).

Though anti-apostatic patterns of frugivory are general, they are not universal. The experiment with *Aristotelia* in Argentina was the only one in which birds interacted more with imitation fruits. This pattern was driven by the *Elaenia*, and observational evidence confirms that *Elaenia* exhibited apostatic patterns of frugivory during the study period (Carlo *et al.* in prep.). However, this same species exhibited anti-apostatic patterns of use during our experiment with *Maytenus*, suggesting that the functional response is not inherent to the species. *Aristotelia*'s chemical properties may explain its unique results. While the rest of the focal fruits considered here are toxic in some degree, fruit of *Aristotelia* are safe for consumption by many vertebrates; it has even been touted as a new “superfruit” due to dense concentrations of pigments and antioxidants (Brauch *et al.* 2016). Although frugivorous birds have adapted some degree of resistance to toxic secondary metabolites in fruit, they may still experience detrimental effects if a large enough volume of fruit is consumed (Levey & Del Rio 2001, Cipollini & Levey 1997). When toxic compounds are absent, birds can safely consume large numbers of that fruit, and the anti-apostatic effect may be weakened or absent. Alternatively, our observations may relate to time of year and the age of visiting birds. Experiments with *Phytolacca*, *Rhamnus*, and *Maytenus*

occurred during fall migration, however our experiment with *Aristotelia* coincided with the *Elaenia*'s breeding season (Schulenberg 2009). During the fall, bird populations contain a higher proportion of juvenile birds than in prior seasons. It is possible that inexperienced juvenile birds are more interested in exploring unfamiliar resources, compared to adults with established preferences. Unfortunately, my methods did not allow me to confidently age visiting birds.

Anti-apostatic frugivory has far-reaching effects to many fruit-bearing plant species. Anti-apostatic effects apply temporally as well as spatially: fruit of a particular species may be consumed at less-than-random rates during times of peak abundance and consumed at greater-than-random rates when few ripe fruits are available (Carlo & Morales 2016). If individual plants with atypical phenology receive a disproportional amount of dispersal, and their atypical phenology is a heritable trait, then anti-apostatic frugivory might hasten plant populations' adaptation changing climates. This pattern may also offset the effect of density-responsive pre-dispersal seed predators. For instance, when the abundance of seed predators corresponds to the abundance of fruit, as is often the case (Janzen 1970, Jones & Comita 2010), early- or late-ripening fruits may thwart these attackers. Anti-apostatic frugivory may be especially beneficial to bird-dispersed parasitic plants that inhabit fruiting host plants, such as mistletoe (Caraballo-Ortíz *et al.* 2017, Carlo & Aukema 2005). By presenting a comparatively small number of fruits in direct contrast to a more abundant resource, mistletoes are consumed and dispersed despite offering exponentially fewer fruit.

Management Implications

Our results suggest that attracting dispersers is not necessarily a challenge for rare, bird-dispersed plants so long as they appear as distinct from common resources. Thus, managers of

declining fruiting plant species must consider other factors limiting plant populations. These may relate to the quality (rather than quantity) of dispersal events (Schupp 1993) or could involve anthropogenic disturbances like habitat fragmentation (Krauss *et al.* 2010) and population genetic processes such as inbreeding depression (Marden *et al.* 2017). In the case of rare plant reintroduction, managers can maximize the efficiency of dispersal by interspersing small patches within areas already populated by fruiting plants. Despite increased competition for light, space, and dispersal, this juxtaposition may facilitate the consumption of the rarer fruit, especially if these resources are nutritionally complementary. However, anti-apostatic effects are irrelevant if no suitable disperser exists. For example, large-seeded fruiting tree species are disappearing from remnant Brazilian forests where habitat fragmentation has excluded large-bodied frugivores (Emer *et al.* 2018).

Research on invasive species management has compared the efficiency of attacking core source populations or smaller satellite populations (Shea *et al.* 2002). Concerning invasive fruiting plants, the observation of greater fruit removal in densely concentrated areas has led researchers to believe dispersal increases sharply above a “critical abundance level” (Gosper 2005), implying management effort is best spent on core populations. Conversely, I predict that a lone invasive shrub surrounded by native fruiting plants would receive proportionally far greater dispersal than one surrounded by conspecifics. This dispersal may be of higher quality, as dispersal distances are often greater in areas of lower fruit availability (Carlo & Morales 2008, Herrera *et al.* 2011). Thus, these isolated “pioneers” have a disproportionate impact, hastening the pace of large-scale plant invasions. If trying to control species invasions, land managers efforts should include a patrol through uninvaded areas rich in fruit and frugivores, where new dispersal is most likely (Kwit *et al.* 2004, Wenny 2001). Techniques that attempt to reduce fruit

crop sizes without complete eradication, such as sublethal herbicide application (Scanlon & The Camphor Laurel Taskforce 2001), may unintentionally create an “advantage of the rare” for the species in question.

Conclusion

Anti-apostatic frugivory is an emerging concept with far-reaching implications. Of many negative density-dependent mechanisms of diversity maintenance, this one is the first that arises from mutualistic seed dispersal events driven by the cognitive processes of foraging frugivores. Future research should aim to survey if anti-apostatic frugivory is a ubiquitous pattern of frugivores around the world, and to determine the behavioral and physiological factors that drive it. Specifically, it is necessary to understand how broad variation in morphological and nutritional attributes of fruit influence functional responses of foraging birds, and to quantify the effects of anti-apostatic frugivory on plant community diversity. By learning what gives rare plant populations their ability to persist and grow, we come closer to comprehending the mechanistic underpinnings of plant community diversity.

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