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ORIGINAL ARTICLE

MASSIVE CONSUMPTION OF UNRIPE SLASH PINE (*PINUS ELLIOTTII*) SEEDS BY BLUE-AND-YELLOW MACAWS (*ARA ARARAUNA*)

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Abstract · This study reports the first case of wild Blue-and-yellow Macaws (*Ara ararauna*) feeding on a gymnosperm, specifically seed consumption in a slash pine (*Pinus elliottii*) stand in an urban area in Brazil. Flocks of up to 25 macaws spent long periods feeding on the pine cones and damaged up to 14% of the cones per plant. This massive granivory event lasted for at least a month, even in the presence of other food plants abundantly blooming and fruiting nearby. Seemingly, this foraging activity is a response of macaws to a concentrated food source. Slash pine unripe seeds appear to be valuable food sources for the wild Blue-and-yellow Macaws inhabiting this anthropogenic area. Moreover, seed consumption by macaws could potentially reduce the spreading of this invasive conifer.

Resumo · Consumo maciço de sementes imaturas em cones do pinho-americano (*Pinus elliottii*) pela Arara Canindé (*Ara ararauna*)
Este estudo relata o primeiro caso de Araras Canindé (*Ara ararauna*) selvagens se alimentando de uma gimnosperma, especificamente o consumo de sementes em uma plantação de *Pinus elliottii* em uma área urbana do Brasil. Bandos de até 25 araras passaram longos períodos se alimentando de sementes de pinhas e destruiram até 14% dos cones por planta. Este maciço evento de granivoria durou pelo menos um mês, mesmo na presença de outras plantas alimentícias abundantemente florescendo e frutificando. Aparentemente, esta atividade de forrageamento é uma resposta das araras a uma fonte concentrada de alimento. As sementes imaturas do pinho-americano parecem ser fontes alimentares valiosas para as Araras Canindé selvagens que habitam a área antropogênica. Além disso, o consumo de sementes pelas araras poderia potencialmente reduzir a disseminação desta conífera invasora.

Key words: Anthropogenic environment · *Ara ararauna* · Brazil · Exotic plant · Food patch · *Pinus elliottii* · Seed predation

INTRODUCTION

Granivory, i.e., seed consumption (*sensu* Lopes et al. 2016), is the main diet of macaws, the largest Neotropical parrots (Munn 1988, Lee et al. 2014). Due to a formidable beak, a fortified skull, and strong jaw muscles, they are able to breach the hard and thick pericarps of the fruits they exploit (Forshaw 1989, Norconk et al. 1997, Sick 1997). These effective adaptations to overcome the mechanical defenses of the fruits may allow macaws to prevent seed dispersal (Haugaasen 2008; but see Tella et al. 2015, Blanco et al 2016, Baños-Villalba et al. 2017). Macaws are, therefore, heavy-billed, pre-dispersal seed predators (Peres 1991, Haugaasen 2008, Gilardi & Toft 2012), suggesting that they could regulate plant populations (Janzen 1970, Silva 2005, Ragusa-Netto 2011).

The consumption of unripe seeds can be an important nutritional strategy, since they are softer, less toxic and are concentrated in the plant crown – i.e., they have not fallen or been dispersed (Janzen 1980). Most importantly, young seeds require a large amount of nutrients to complete their development (Janzen 1980). Hence, plants supply the unripe seeds with soluble nutrients rich in amino acids, providing a valuable source of nitrogen (White 2011). Due to their large body size and high mobility, macaws have a high protein demand to support their daily activities (Koutsos et al. 2009). It is no surprise, therefore, that the availability of immature fruits (i.e., unripe seeds), has a strong influence on the pattern of abundance and habitat use by macaws (Haugaasen & Peres 2007). Most notably, these phenomena are conspicuous when clusters of a single plant species concurrently bear fruits (Moegenburg & Levey 2003, Tubelis 2009a, Ragusa-Netto 2011).

The Blue-and-yellow Macaw (*Ara ararauna*) is one of the most abundant members of the genus *Ara* (Forshaw 1989). This generalist psittacid can exploit a variety of environments, and forage on a wide diversity of plants (ca. 110 plant species; Roth 1984, Munn 1988, Ragusa-Netto 2006, Faria et al. 2009, Tubelis 2009b, Ragusa-Netto 2011, Gilardi & Toft 2012, Silva 2013, Lee et al. 2014, Santos & Ragusa-Netto 2014, Silva et al. 2015). The Blue-and-yellow Macaw eats seeds of most of these species, all of them angiosperms. Yet, except for a naturalized population originated from escapees (Pranty et al. 2010), there are no records of gymnosperm seed consumption, such as cone-bearing plants of the genus *Pinus* (Pinaceae), by wild Blue-and-yellow Macaws.

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Figure 1. Study area in the municipality of Ilha Solteira, in the northwest of the State of São Paulo, Brazil. The dark green site at "A" is Mantiqueira Park. The red lines at "A" show the streets used to detect macaws feeding specifically on pine seeds. This same street and the other transects (B–H) were used to search for macaws feeding on a variety of plant species. Image adapted from Google Earth.

The slash pine (*Pinus elliottii*, Pinaceae) is a tree (c. 30 m tall) native to the southeastern United States (Farjon 2013). In Brazil, the introduction of this conifer occurred in the 1940s for silvicultural experiments near São Paulo (Baldanzi et al. 1974). Subsequently, they were planted throughout the state of São Paulo to meet the demand for timber, cellulose, and resin (Garrido et al. 1998, Kronka et al. 2005, Lorenzi et al. 2018). Currently, this pine species is cultivated in several Brazilian regions (Richardson et al. 2008, Lorenzi et al. 2018). Overall, the slash pine appears to have little value in maintaining biodiversity (*cf.* Abreu & Durigan 2011). Instead, the slash pine in Brazil is seen as one of the most aggressive invasive alien plants, and is usually considered a threat to native biodiversity (Richardson et al. 2008, Zenni & Ziller 2011).

Gymnosperm cones seem to be important seed sources for parrots (Juniper & Parr 1998, Tella et al. 2016), including where these plants are introduced (Kristosch & Marcondes-Machado 2001, Stock et al. 2013). Presumably, the seeds of the introduced slash pine may be an important food subsidy (*sensu* Rodrigues 2006). Here, I report a massive event of exploitation of slash pine seeds by wild Blue-and-yellow Macaws.

METHODS

Study area and Blue-and-yellow Macaw in the site. This study was performed in the municipality of Ilha Solteira (20° 25'S, 51°20'W, 380 m a.s.l.), in the northwest of the State of São Paulo, bordering the state of Mato Grosso do Sul, Brazil (see Silva & Melo 2013 for more details on the site). In Brazil, the use of urban spaces by wild populations of Blue-and-yellow Macaw has increased, especially in cities of the states of São Paulo and Mato Grosso do Sul (Silva 2013, Santos & Ragusa-Netto 2014, Silva et al. 2015). Before 2007, it was uncommon to find macaws in the urban area of Ilha Solteira. Currently, I estimate that there are at least 179 macaws inhabiting that city (unpubl. data). These birds are well adapted to the urban environment of the Ilha Solteira, particularly since the supply of roosting sites and dead palm trees (*Roystonea oleracea*, Arecaceae) for nesting are high. I have been collecting dietary data from Blue-and-yellow Macaw for the last 10 years in urban and suburban areas. They feed on multiple native and exotic cultivated plant species and incorporate novel plant species and unusual food items in their diets (Silva 2013, Silva et al. 2015).

Study site description. I observed foraging activity of Blue-and-yellow Macaws on slash pine cones in the Mantiqueira Park (20°25'47.84"S, 51°21'13.94"W, 376 m a.s.l.), a suburban-forested area of about 8 ha (Figure 1). About 80% of the park area is composed of a pure stand of slash pine planted in the late 1960s, which currently has a closed canopy 20–30 m tall. In the 1970s, the local government founded the park as public space for recreational purposes. Since then, this pine stand has not undergone any anthropogenic change in its physiognomy. The surrounding landscape is composed of small farms, orchards, gardened residences, wooded streets, and green spaces (Figure 1), all rich in native and exotic plant species.

Field procedures and analyses. My first observation of macaws feeding on the pine seeds in the park was made on 17 December 2016. Residents of the surrounding area witnessed intense movements of the macaws toward the park for at least a week, and reported that this phenomenon had never been observed before. Given the novelty, I developed a protocol to investigate this strong feeding association of macaws with slash pine trees. I used a single 1.5-km long continuous street around the stand (Figure 1A) to search for foraging macaws. Searches were made from 20 December 2016 to 20 January 2017. After this period, I noticed an abrupt decrease of macaws feeding in the pine stand, apparently due to the decline in the availability of unripe cones. Each week, on one day I walked the street once in the morning (06:30–09:30 h), and once in the afternoon (16:30–19:30 h). On each of the four sampling days I walked 12 km. When I detected a flock of macaws in the pine stand, I recorded the number of birds and foraging time (time from detection until the macaws flew away). A single detection, defined as a foraging bout, may include several flock members feeding simultaneously, which I called feeding flock. I obtained the handling time of cones (independent of seed intake) and details of the feeding behavior using 8 x 40 binoculars or by videotaping and photographing at least one macaw in the flock that exploited the cones. Behavioral data were obtained from about 20 m away, thus avoiding disturbance while the macaws fed.

In order to evaluate the potential damage to cones by Blue-and-yellow Macaws, I sampled the amount of female cones (Figure 2A) produced in 10 slash pine trees located along the edge of the park. Species of *Pinus* generally bear mature and immature female cones in the branches (Williams 2009). Distinguishing the level of female cone maturity is easy since they are green (up to ~ 1 year old) or light brown (~ 2 years old) (Williams 2009). When ripe, the cone becomes dark brown and the opened megasporophylls release the winged seeds. I focused on the unripe cones because Blue-and-yellow Macaws only exploited these cones. Unripe female cones of the slash pine are conspicuous (8–18 cm long), thus easily seen in the tree crown (Figure 2B). I counted the number of unripe female cones in branches representing 10% of a plant crown. Subsequently, I extrapolated the value obtained for the remainder of the crown (Chapman et al. 1992). I calculated the rate of cone damage by Blue-and-yellow Macaws as follows: mean feeding time/mean cone-handling time x mean of birds per foraging bout. The value obtained was divided by the average cone number per tree and multiplied by 100, resulting in the average percentage of cones a feeding flock could damage in a single foraging tree.

I used the mornings and afternoons of another two days of each week from 20 December 2016 to 20 January 2017 to sample the consumption of slash pine seeds and other food plants by the Blue-and-yellow Macaw. My aim was to evaluate the contribution of slash pine in the diet of macaws in relation to other food plants during the study period (one month). I used the proportion of foraging bouts on the slash pine and the total number of foraging macaws in each species to evaluate this. For this, I conducted foraging observations of flocks using the single 1.5-km long continuous street around the slash pine stand and seven other 500-m long transects in the surrounding landscape in areas known to be frequented by macaws (Figure 1B–H). Each week, on one day I walked the street and the transects in the morning (06:30–09:30 h). On the following day, the street and transects were walked in the afternoon (16:30–19:30 h). This way, I devoted eight days to detect macaws feeding on a variety of plant species, walking a total of 40 km (12 km around the park and 28 km in the surrounding landscape).

I used the different types of food plants as a factor and compared the sizes of feeding flocks associated with these plants. The comparison was made using one-way analyses of variance (ANOVA) of square root-transformed data, followed by a Tukey test, considering the feeding flock sizes detected in the first five foraging bouts in each plant species (Zar 1999). This was done to balance the samples, thereby reducing biased analyses. To ensure independence, I considered only the initial observation for each feeding flock of macaws (Hejl et al. 1990). This procedure also avoids biases in the analyses, as the initial observations assume that macaws are equally likely to be seen feeding on any conspicuous food source (Hejl et al. 1990). I estimated the abundance of flowers or fruits for 10 individuals of each food plant species, all located within a radius of 1 km of the pine stand. I expected that there would be a low or moderate production of flowers or fruits in other plant species that was driving the macaws to forage mainly in the slash pine trees (*sensu* Ragusa-Netto 2006). The flowering and fruiting estimate was based on the Fournier Intensity Percentage or Fournier Index (Fournier 1974), which consists of the assignment of values ranging from 0 (absence of flowers/fruits in the plant crown) to 4 (flowers/fruits in 76–100% of the plant crown). Then, the sum of all intensity categories given to each individual plant was divided by the maximum sum that could be attributed to the population (10 plants selected multiplied by four, the uppermost intensity category). The value obtained corresponds to a proportion, which is multiplied by 100, i.e., transformed into a percentage value.

The values presented correspond to the means ± standard deviations (SD).

RESULTS

During the sampling on the street around the park, I observed seven foraging bouts, during which 10 to 17 Blue-and-yellow Macaws (14.0 ± 2.0 birds) were feeding on female cones of slash pine (Figure 2B). Upon arrival to the pine stand, macaws spread among 2–5 nearby pine trees. Perched in the tree, all macaws harvested the cones with their beaks. Then, holding the cone with one foot, a macaw would pierce the cone with its beak (Figure 2C). Subsequently, seeds were removed one at a time with their tongues and beaks. The foraging bouts lasted 54.6 ± 37.7 min (range 8.2–114.1 min, n = 7), and the macaws spent 9.6 ± 2.8 min handling completely one cone (range 6.2–14.0 min, n = 6). The feeding flock of macaws stopped foraging activity on cones synchronously, and then left the slash pine stand. Some macaws left the stand carrying full or partial cones in their bills. On five occasions, I found 1–3 macaws handling cones while perched on trees 400–600 m away from the slash pine stand. As there are no pine trees planted outside the stand, these cones most likely came from the stand.

I estimated production of 109 ± 41 immature female cones per slash pine tree (n = 10), as well as damage of c. 80 unripe female cones by macaws per foraging bout. This means that based on a cones-per-tree basis, Blue-and-yellow Macaws potentially damage 73.3% of the female cone crop per foraging bout. As macaw flocks spread among 2–5 pine trees, I estimate that ~ 14–37% of a tree's cones

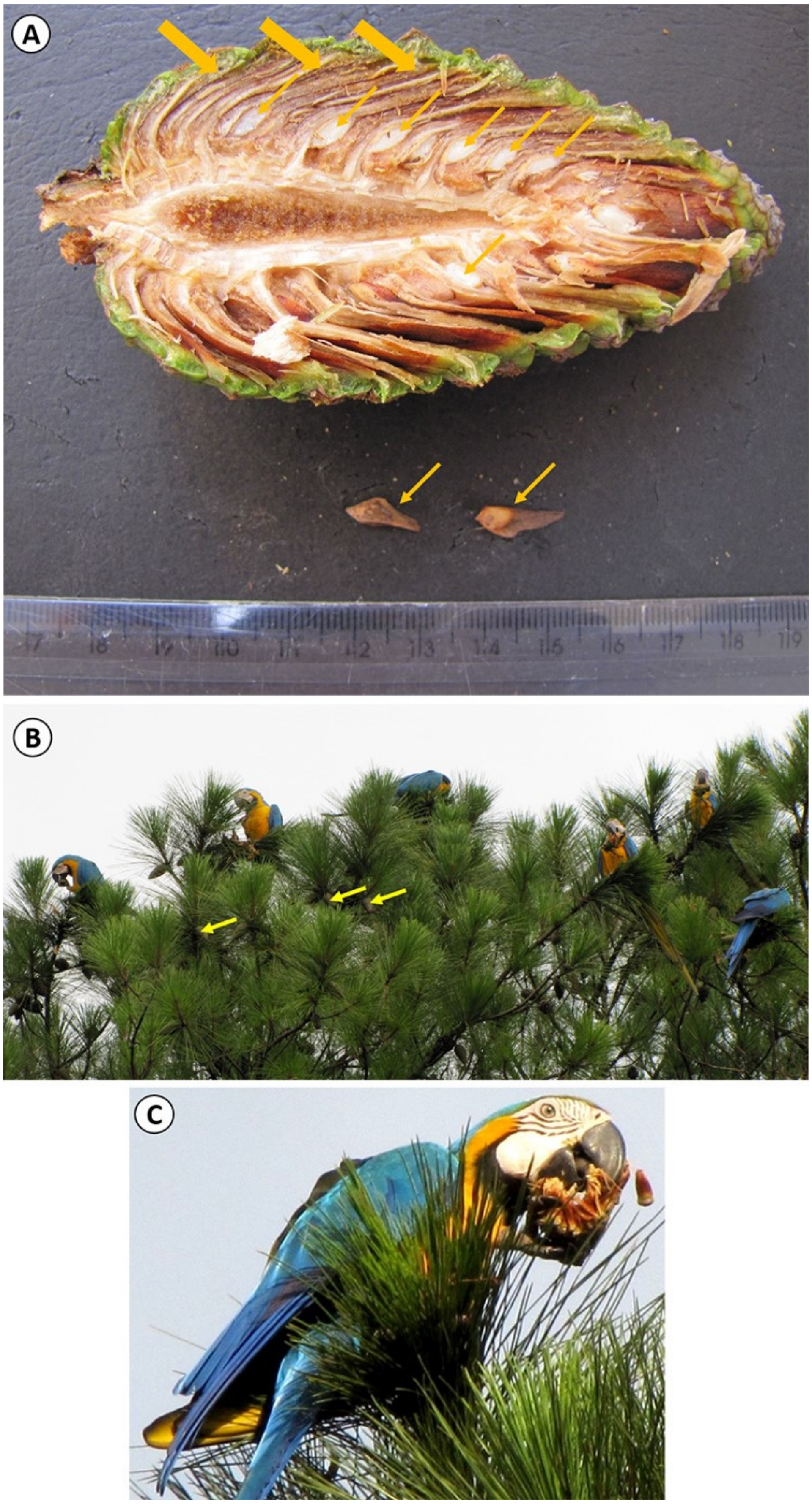

Figure 2. Foraging of Blue-and-yellow Macaws (*Ara ararauna*) at slash pines (*Pinus elliotti*) at Ilha Solteira, São Paulo, Brazil. A) A female pine cone showing the small seeds (narrow arrows) and tightly joined fibrous megasporophyll (wide arrows) protecting the seeds. B) Feeding flock exploiting the pine cones (the arrows indicate immature female cones in the plant crown). C) Details of a Blue-and-yellow Macaw handling an unripe female cone (note the intense damage). Photographs by Paulo Antonio Silva.

may be damaged in a single foraging bout by a flock of macaws.

During the sampling on the street around the park and transects in the surrounding landscape, I observed 66

Table 1. Plant species used as food resource by Blue-and-yellow Macaws (*Ara ararauna*) in urban environments of Ilha Solteira, São Paulo, Brazil, from 20 December 2016 to 20 January 2017. Foraging bouts were recorded during 40 km of surveys, 12 km around the park and 28 km in the surrounding landscapes. Asterisks indicate exotic species.

Family — species	Foraging bouts	Total of macaws detected feeding	Food item
Anacardiaceae — *Mangifera indica**	7	13	ripe pulp
Arecaceae — *Acrocomia aculeata*	6	15	ripe pulp
Arecaceae — *Cocos nucifera**	1	17	liquid endosperm
Arecaceae — *Roystonea oleracea**	6	20	unripe seeds
Arecaceae — *Syagrus romanzoffiana*	1	5	ripe pulp
Bignoniaceae — *Jacaranda cuspidifolia*	1	4	unripe seeds
Bignoniaceae — *Spathodea campanulata**	6	11	calyx-water
Combretaceae — *Terminalia catappa**	7	31	unripe seeds
Fabaceae — *Albizia niopoides*	2	12	flowers
Fabaceae — *Anadenanthera colubrina*	1	2	unripe seeds
Fabaceae — *Delonix regia**	1	2	flowers
Fabaceae — *Hymenaea courbaril*	6	13	nectar
Meliaceae — *Melia azedarach**	7	17	unripe seeds
Myrtaceae — *Corymbia citriodora**	5	16	unripe seeds
Pinaceae — *Pinus elliottii**	9	127	unripe seeds

foraging bouts, which included 305 Blue-and-yellow Macaws. Macaws foraged on 15 plant species from eight families, most of them exotic (Table 1). The slash pine was the most used plant of these 15 species (9 of 66 bouts were on pines, Table 1). I analyzed the abundance of flowers and fruits on all species with a minimum of five foraging bouts (n = 9 species). These data showed that three other food plants, *Mangifera indica* (Anacardiaceae), *Corymbia citriodora* (Myrtaceae), and *Roystonea oleracea* fruited abundantly, while *Hymaenea courbaril* (Fabaceae) was just in flower and two other ones, *Acrocomia aculeata* (Arecaceae) and *Melia azedarach* (Meliaceae), fruited moderately (Figure 3A). The feeding-flock sizes of macaws associated with slash pines (16.8 ± 5.3 macaws) was significantly higher than the flock sizes associated to the other eight plant species (2–5 macaws on average, Tukey post-hoc test after One-way ANOVA of square root-transformed data: $F_{8;36} = 10.489$, $P < 0.0001$; Figure 3B).

DISCUSSION

I report for the first time wild Blue-and-yellow Macaws feeding on the unripe seeds of a gymnosperm, the slash pine. As this pine species is exotic and its cones do not resemble angiosperm fruits, pine cone seeds are not a familiar food to Blue -and-yellow Macaws. The foraging reported here is, therefore, a typical case of dietary innovation in the Blue-and-yellow Macaw (*sensu* Overington et al. 2009). The likelihood of diet innovation is high in this macaw species as it exploits multiple habitats (Sick 1997), where it is likely to encounter many new food items over time (Ducatez et al. 2014). The opportunity for innovation is enhanced in anthropic landscapes, as they are rich in exotic plants providing many new foraging opportunities (Muñoz et al. 2007, *cf.* Silva et al. 2015; see also Table 1). This has important conservation implications in the Anthropocene, since the incorporation of exotic plants as food may positively influence Blue-and-yellow Macaws' persistence in human-modified environments (Matuzak et al. 2008).

Tightly joined fibrous megasporophylls of female unripe slash pine cones (Figure 2A) inhibit many pre-dispersal seed predators. I observed small parrots, such as White-eyed Parakeet (*Psittacara leucophthalmus*), Golden-capped Parakeet (*Aratinga auricapillus*), and Blue-winged Parrotlet (*Forpus xanthopterygius*) ignoring unripe cones, but eating seeds from ripe slash pine cones. In contrast, the large and strong beak of the Blue-and-yellow Macaw allowed them to easily open unripe cones (Figure 2C). As a result, Blue-and-yellow Macaws caused moderate cone damage in the slash pine trees, ~ 14% of cones lost per plant per foraging bout. This rate is similar to the damage caused by macaws in *Bertholletia excelsa* (Lecythidaceae, 10% of loss; Trivedi et al. 2004) and *Melia azedarach* (12% of loss; Silva 2005). However, is less than the damage inflicted by ma-caws to *Couratari guianensis* (Lecythidaceae, 99% of loss; Haugaasen 2008), *Caryocar brasiliense* (Caryocaraceae), and *Terminalia catappa* (Combretaceae) fruits (50% of loss for both; Ragusa-Netto 2011, Henn et al. 2014). Although being moderate, this rate of cones loss is relevant since it suggests that Blue-and-yellow Macaws potentially decrease the likelihood of spreading of the exotic invasive slash pine.

Recently, researchers have proposed that many psittacines can have positive impacts on plants, mostly through seed dispersal (Tella et al. 2015, 2016; Baños-Villalba et al. 2017). However, this is not likely the case in this system because 1) the birds completely crushed and consumed the seeds that they ate, and 2) because the cones that they did disperse away from the parent tree contained only very immature seeds (cf. Figure 2A) that had little or no chance of successful germination. As a result, there is little or no chance of positive impact of these macaws on the slash pines studied here.

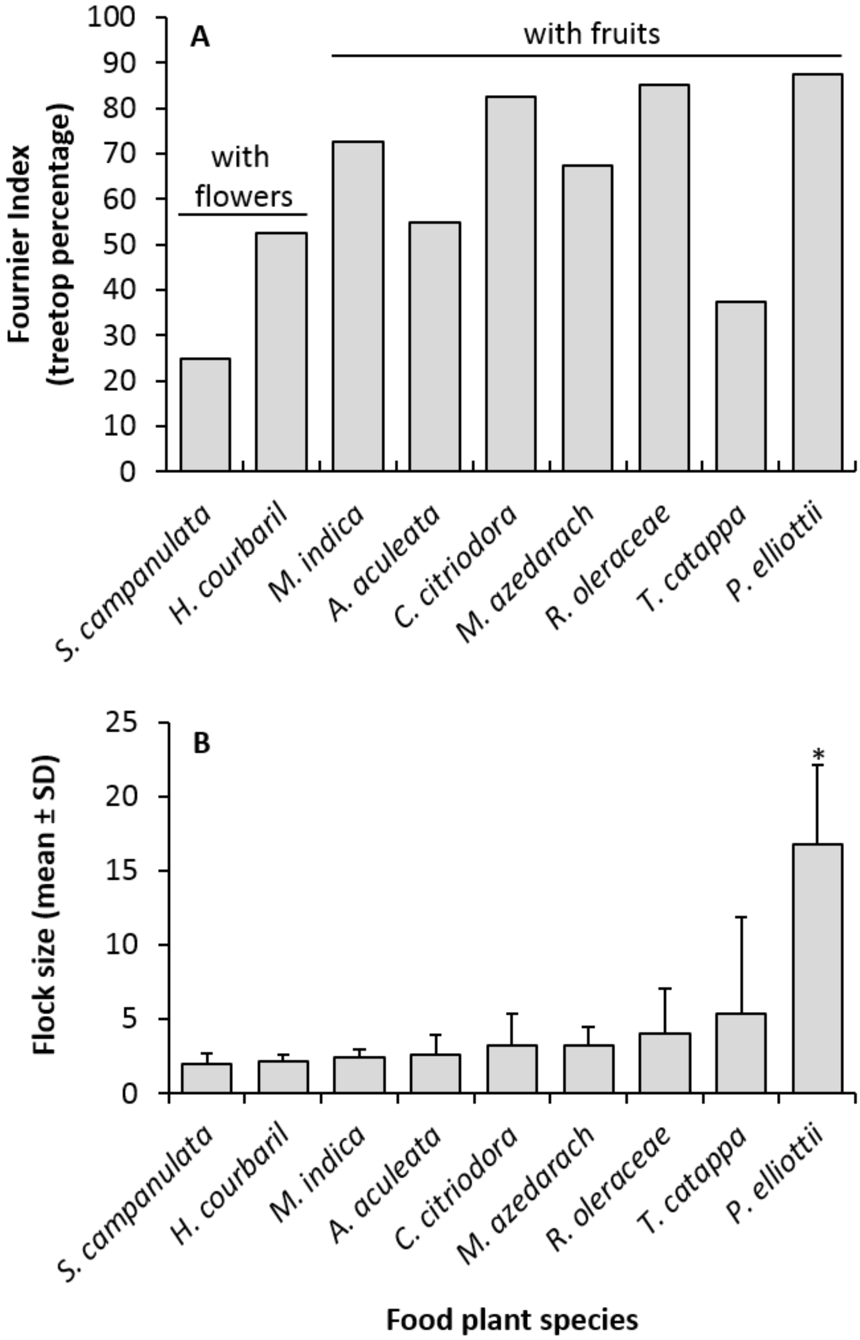

Figure 3. A) Flower and fruit production in the nine plant species (measurements made on 10 individuals of each species) consumed by Blue-and-yellow Macaws (*Ara ararauna*) at Ilha Solteira, São Paulo, Brazil, during the study period from 20 December 2016 to 20 January 2017. The other food plants recorded during this study (Table 1) were excluded due to insufficient foraging bouts (< 5 bouts). B) Mean (± SD) of feeding flocks size of Blue-and-yellow Macaws associated with each food plant species. Asterisk indicates a significantly higher mean compared to the other food plants (Tukey test, $P < 0.0001$).

Despite the presence of other food plant species bearing abundant flowers and fruits in the area (*cf.* Figure 3A), flocks of up to 25 Blue-and-yellow Macaws focused their feeding activities upon slash pine cones (*cf.* Figure 3B, see also Table 1) for long periods of time (up to 114.1 min). Clumps of fruiting slash pines provide a concentrated source of unripe seeds, thus a valuable source of amino acids, in addition to lipids, carbohydrates, moisture, fibers, and minerals (Koutsos et al. 2009, White 2011, Gilardi & Toft 2012). In addition, clumped fruiting plants can help macaws maximize foraging efficiency (*sensu* MacArthur & Pianka 1966). Such facts are extremely important to these large macaws, which have high metabolic demands due to large body size and long daily trips between feeding sites (Koutsos et al. 2009, Ragusa-Netto 2011).

This short-term study led me to conclude the following: i) unripe seeds of the exotic slash pine cones constitute a novel food item for the Blue-and-yellow Macaw; ii) macaws inflict moderate seed mortality, which potentially decrease the likelihood of spreading of this invasive conifer; iii) macaws were abundantly attracted by a highly concentrated source of unripe seeds in the pine stand, probably maximizing their efficiency in foraging; iv) although exotic, the slash pine is a food subsidy for wild Blue-and-yellow Macaws inhabiting a anthropic landscape.

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