



Spatiotemporal variation in the diet of Hooded Berryeater (*Carpornis cucullata*) in the southernmost section of the Atlantic Forest ecoregion

Variación espaciotemporal de la dieta del Cotinga Encapuchado (*Carpornis cucullata*) en la sección más austral de la ecorregión del Bosque Atlántico

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ABSTRACT. The endemic Hooded Berryeater (*Carpornis cucullata*) is an important seed disperser in the Atlantic Forest which is arguably a critical player for endemic large-seeded trees to cope with climate change, yet the diet and its spatiotemporal variations remain poorly understood. Here we compiled a comprehensive list of plant species consumed by this bird across its entire range, compared the diversity of plants consumed in two areas of southern Brazil, and assessed the temporal variation in frugivory. Our compilation resulted in 111 plant species on its diet, distributed in 39 families. In 1098 hours of sampling, we identified 53 species consumed in southern Brazil. At the southernmost of its range, the Hooded Berryeater consumes and disperses seeds of 47.7% of its known diet, most of them being trees endemic to the Atlantic Forest. Despite high temporal variation in plant consumption, the bird remained consistently frugivorous year-round, with minimal arthropod consumption at both sites. Fruit consumption peaked during summer and spring but at least five species were consumed during Winter in each area, underscoring its year-round importance for seed dispersal. The high diversity of plants whose fruits are consumed by the Hooded Berryeater suggests it is a keystone seed disperser in the southern portion of Atlantic Forest and that it may have an important role in helping endemic plants cope with climate change by tracking suitable habitats. Furthermore, our study shows that the levels of diversity and interaction complexity of the Atlantic Forest are retained in latitudes as high as 32° South.

RESUMEN. El endémico Cotinga Encapuchado (*Carpornis cucullata*) es un importante dispersor de semillas en el Bosque Atlántico, el cual podría decirse que es un actor fundamental para que los árboles endémicos de semillas grandes puedan hacer frente al cambio climático, sin embargo, la dieta y sus variaciones espaciotemporales siguen siendo poco conocidas. Aquí recopilamos una lista completa de especies de plantas consumidas por esta ave en toda su área de distribución, comparamos la diversidad de plantas consumidas en dos áreas del sur de Brasil y evaluamos la variación temporal de la frugivoría. Nuestra recopilación resultó en 111 especies de plantas en su dieta, distribuidas en 39 familias. Durante 1098 horas de muestreo, identificamos 53 especies consumidas en el sur de Brasil. En el extremo sur de su área de distribución, el Cotinga Encapuchado consume y dispersa semillas del 47.7% de su dieta conocida, siendo la mayoría de ellas árboles endémicos del Bosque Atlántico. A pesar de la alta variación temporal en el consumo de plantas, el ave se mantuvo consistentemente frugívora durante todo el año, con un consumo mínimo de artrópodos en ambos sitios. El consumo de frutos alcanzó su punto máximo durante el verano y la primavera, pero al menos cinco especies fueron consumidas durante el invierno en cada área, resaltando su importancia durante todo el año para la dispersión de semillas. La alta diversidad de plantas cuyos frutos son consumidos por el Cotinga Encapuchado sugiere que es un dispersor de semillas clave en la porción sur del Bosque Atlántico y que puede tener un rol importante a la hora de ayudar a las plantas endémicas a hacer frente al cambio climático a través de la búsqueda de hábitats adecuados. Además, nuestro estudio muestra que los niveles de diversidad y complejidad de interacción del Bosque Atlántico se mantienen en latitudes tan altas como 32° sur.

Key Words: *Pampa biome; climate change; Corocoxó; frugivory; ornithocory; seed dispersal*

INTRODUCTION

The cotingas (Cotingidae) comprise a diverse clade of birds endemic to the neotropics, most species being tropical forest dwellers (Snow 1982). This passerine family is iconic for the variety of sizes, plumages, and behavioral features observed among its 24 genera and 65 species (Snow 1982, Berv and Prum 2014, Winkler et al. 2020). Cotingas are remarkable frugivores well-known for their role in ecosystem maintenance through seed dispersal services (Winkler et al. 2020, Carlo et al. 2022). Thus, it is particularly concerning that over one-third of the cotinga

species are globally threatened by habitat loss (Winkler et al. 2020). In the Neotropical region, the Atlantic Forest of eastern Brazil is one of the most diverse ecoregions in terms of cotinga species, harboring 12 of the 65 recognized species (Snow 1982), including the only two species of *Carpornis*, the only endemic genus of cotingas of the Atlantic Forest (Snow 1982).

The Hooded Berryeater (*Carpornis cucullata*), in particular, has been identified as one of the most important avian frugivores in the Atlantic Forest of southeastern Brazil, dispersing seeds of several plant species (Pizo et al. 2002, Silva et al. 2002). Studies

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of plant-frugivore networks in the central part of the Atlantic Forest, which corresponds to the center of this bird's range, identified the Hooded Berryeater as the bird species with the greatest contribution to the structure of the seed dispersal network (Silva et al. 2002, Vidal et al. 2014). However, no study outside the central part of the Atlantic Forest has yet aimed at identifying the diet of this important frugivore and which plants rely upon it for seed dispersal. Furthermore, it remains unknown how its diet varies over time, which may be particularly important to understanding this species' subsistence over the year in more seasonal areas such as the southern portion of the Atlantic Forest.

As the Hooded Berryeater is a forest-dependent species and its southernmost distribution coincides with the southernmost limit of the Atlantic Rainforest where this ecoregion meets the open landscapes of the Pampas (Winkler et al. 2020), it is plausible that the limit of this ecoregion constrains the distribution of this bird species. In turn, it is also possible that the distribution of several large-seeded tree species endemic to the Atlantic Forest is, at least in part, constrained by the range of this important seed disperser. In fact, among the frugivores in the region (Belton 1994), it is one of the few species capable of consuming and dispersing fruits and seeds as large as 23.3 mm (Pizo et al. 2002, Maurício et al. 2024) owing to its large bill gape. Importantly, propagules of medium to large-seeded trees form the bulk of the arboreal strata of tropical forests, and the loss of large-bodied frugivores may affect plant range size, the likelihood of extinction, and the regeneration of tropical forests itself (e.g., Naniwadekar et al. 2015, Petrocelli et al. 2024). The lack of data about which plants are consumed and dispersed by animals capable of dispersing large-seeded plants at the southernmost limit of the Atlantic Forest, however, limits the evaluation of such hypotheses.

Such a gap becomes particularly important in the context of global warming (Pizo and Galetti 2010), as seed dispersal by animals is a critical process for plant populations to keep pace with environmental change by colonizing new areas with suitable climates (i.e., a process called niche tracking, González-Varo et al. 2021, Fricke et al. 2022, Nuñez et al. 2023). In fact, around 80% of woody plant species rely on animals to disperse their seeds in tropical forests and, therefore, losing dispersers may affect a large proportion of the plant species (Jordano 2000, Fricke et al. 2022) and their ability to move toward cooler climates (González-Varo et al. 2021).

In this context, we investigate the diet of the Hooded Berryeater and its spatiotemporal variation in the southernmost range of the species. Specifically, we (1) compiled a list of plant species whose fruits are consumed by this species throughout its entire range and compared it with the diet in our study sites. We also (2) compared the taxonomic diversity of plants consumed between two areas and (3) evaluated the temporal variation in the plants consumed throughout the year in each area.

MATERIALS AND METHODS

Compilation of the plants consumed

To compile a comprehensive list of the plants consumed by the Hooded Berryeater we carried out a systematic literature review. First, we filtered out the list of plants compiled by Bello et al. (2017) and double-checked the original references they used. For all publications found, we used the feature "cited by" of Google

Scholar and revised all articles detected in search of records of additional plants consumed. We also checked all references retrieved from Google Scholar searches that combined the terms *Carpornis cucullata*, Hooded Berryeater, *corocoxó*, frugivory and seed dispersal, both in Portuguese and English. We also revised classic books on neotropical ornithology (Sick 1997; Kirwan and Green 2011).

We added to this list all plants observed being consumed by this bird at our study sites. Plant nomenclature follows Flora e Funga do Brasil (2024).

Study sites

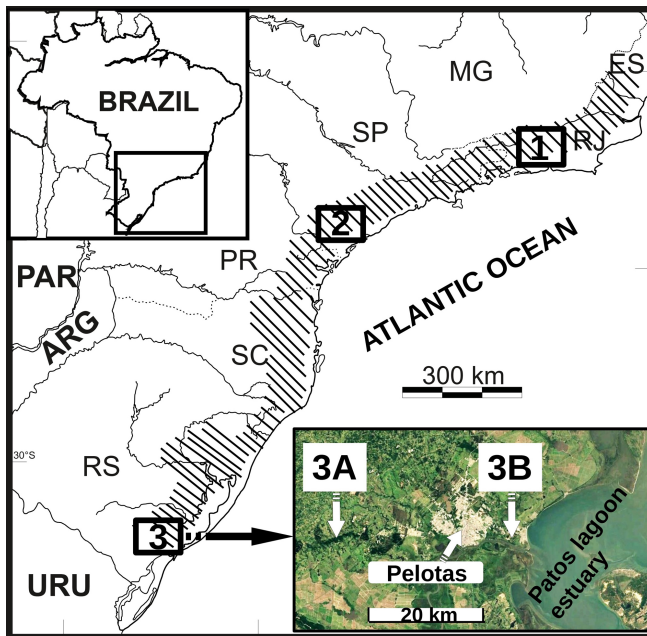
We studied the diet of Hooded Berryeaters at two localities 28 km apart in the species' southernmost distributional limit (Fig. 1): Cerro da Almas (31°46'S, 52°34'W) in the municipality of Capão do Leão, and Pontal da Barra (31°46'S, 52°14'W) in the municipality of Pelotas, both in Rio Grande do Sul state, Brazil. Cerro das Almas is a small chain of granitic hills varying between 100 and 260 m a.s.l. immersed in a matrix of open grasslands. The southeast-facing slopes are covered with about 500 ha of well-preserved forest, with the canopy ranging from 15 to 25 m tall in most of the area. Taller patches of forest occur in the bottom of small valleys while lower-stature patches occur in the hilltops. The other site, Pontal da Barra, is located near the Laranjal beach town and lies around sea level within the large coastal plain of the Patos lagoon estuary. Here we studied the diet of the Hooded Berryeater at a 40 ha forest patch that covers ancient dunes and the edge of an adjacent peat marsh (altitudinal range 5–25 m a.s.l.), with forest no taller than 18 m. In both areas, forest communities have the most abundant and conspicuous trees or understory treelets being plant species such as *Ilex dumosa*, *Syagrus romanzoffiana*, *Cordia ecalyculata*, *Diospyros inconstans*, *Vitex megapotamica*, *Aiouea saligna*, *Nectandra megapotamica*, *Ocotea pulchella*, *Trichilia clausenii*, *T. elegans*, *Ficus cestrifolia*, *F. luschnathiana*, *Sorocea bonplandii*, *Eugenia uruguayensis*, *Myrcia palustris*, *Psidium cattleyanum*, *Guapira opposita*, *Myrsine* spp., *Faramea montevidensis*, *Psychotria brachyceras*, *Banara parviflora*, *Casearia decandra*, *Casearia sylvestris*, *Xylosma pseudosalzmannii*, *Allophylus edulis*, *Cupania vernalis*, *Chrysophyllum gonocarpum*, *C. marginatum*, *Styrax leprosus*, *Symplocos uniflora*, and *Citharexylum myrianthum*. Species exclusive to Cerro das Almas include *Annona sylvatica*, *Didymopanax calvus*, *Dasyphyllum spinescens*, *Cordia americana*, *Trema micrantha*, *Sloanea hirsuta*, *Alchornea triplinervia*, *Miconia pusilliflora*, *Cabralea canjerana*, *Campomanesia xanthocarpa*, *Eugenia involucrata*, *E. rostrifolia*, *E. uniflora*, *Myrcia glabra*, *Pisonia ambigua*, *Chionanthus trichotomus*, *Urera baccifera*, and *Citharexylum montevidense*. Species exclusive to Pontal da Barra include *Annona maritima*, *Geonoma schottiana*, *Ocotea acutifolia*, *Myrcia multiflora*, and *Sideroxylon obtusifolium*. Forests of both sites have substantial epiphytic load, including *Tillandsia* spp., *Vriesea gigantea*, *Vriesea friburgensis*, *Rhipsalis teres*, *Lepismium* spp., and several orchids.

The climate in the region is humid subtropical (Rosa 1985) and four seasons can be recognized (description to follow).

Data collection

Our sampling effort summed 1098 hours of observations (Appendix 1: Table ESM 1). At Cerro das Almas, observations were conducted monthly from July 1997 to May 1999, and from November 1999 to April 2000, in an estimated total of 815 hours of fieldwork. We visited the site once or twice a month for about one day and a half,

Fig. 1. Map showing the distribution (hatched) of the Hooded Berryeater (*Carpornis cucullata*) and the location of the main areas (1 and 2) from where data on the diet of this species was compiled and from our study sites in southern Brazil (3). (1) Serra dos Órgãos, in Rio de Janeiro state (Parrini et al. 2017) and (2) at Parque Estadual Intervales, in São Paulo state (Pizo et al. 2002, Bello et al. 2017) and our study sites (3A) Cerro das Almas and (3B) Pontal da Barra. Abbreviations: ARG, Argentina, PAR, Paraguay; URU, Uruguay. Brazilian states: MG, Minas Gerais; ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; PR, Paraná; SC, Santa Catarina, and RS, Rio Grande do Sul.

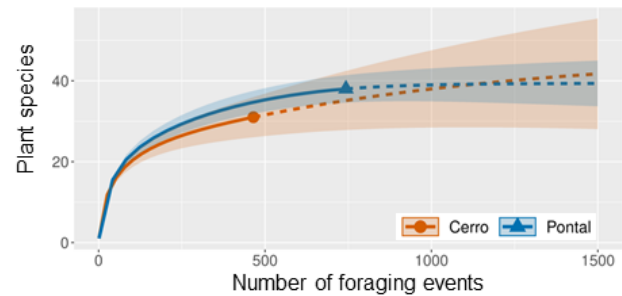


sampling at least one day from sunrise to sunset. At Pontal da Barra, observations took place from July 2022 to June 2024 (24 consecutive months), in an estimated total of 280h. The site was visited two to three times a week and included at least a sampling from sunrise until 10a.m. and a sampling from 4p.m. to sunset. Despite the differences in observation efforts, sampling completeness was high and similar across the two areas (Fig. 2). The distribution of the sampling effort per month was approximately 68 ± 28 h (30–118h) at Cerro das Almas and 23 ± 6 h (12–33h) at Pontal da Barra (mean \pm S.D, range; Appendix 1: Table ESM 1).

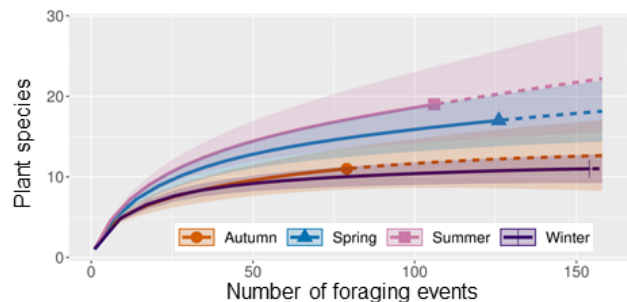
In addition, in June and July 1997, we detected a female Hooded Berryeater in the Horto Botânico Irmão Teodoro Luis ($31^{\circ}48'48''$ S; $52^{\circ}26'00''$ W), a forest patch of 23ha located 14km east of Cerro das Almas. We carried out 14h of opportunistic observation at this site until the individual was no longer found. Since 1997 this locality has been regularly visited by ornithologists (including the authors) and, more recently, by birdwatchers, but the Hooded Berryeater has not been detected, which suggests our records refer to a dispersing individual or a frustrated attempt of colonization. We kept these records here because they include the only known record of consumption of *Myrcia glabra* (one foraging event

Fig. 2. Rarefaction (interpolation-extrapolation) curves of the plant species consumed by the Hooded Berryeater (*Carpornis cucullata*) with the accumulation of foraging events observed throughout the study (A) and across seasons at Cerro das Almas (B) and Pontal da Barra (A): 95% confidence intervals based on 1000 bootstraps

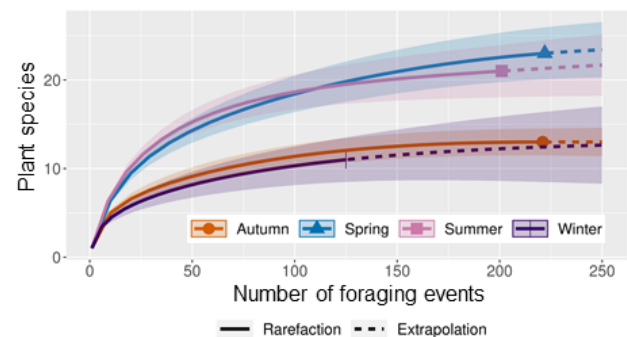
A – Cerro das Almas & Pontal da Barra



B – Cerro das Almas (seasons)



C – Pontal da Barra (seasons)



observed in each month), which is a species endemic to the Atlantic Forest (Results). We also considered the record of consumption of *Guettarda uruguensis* fruits, opportunistically recorded in a field expedition to forests along the margin of the Turucu river, municipality of Turucu, in 4 February 1999.

To locate and study the birds' diet, we followed singing males, as they tend to sing regularly throughout the day during the entire year. Following singing males was also the method used to locate individuals and study the reproductive behavior, being effective in finding nests of the species (Maurício 2013). At Cerro das

Almas, we followed presumably six distinct territorial males, four of which were paired with a female. Although we did not band birds to distinguish between individuals, we combined information on the location of their territories, differences in the pitch of their songs, and to a lesser extent, plumage, to estimate an approximate number of males monitored. For instance, a male that occupied a central territory had a yellow feather within the black part of the chest, making it unmistakable, and their neighbors had higher or lower-pitched songs. In the breeding season, our observations also included fledglings and juveniles, often observed accompanying the singing parent male. In sum, an approximate total of 12 individual birds were studied at Cerro das Almas. At Pontal da Barra, in turn, only a paired male and female and, eventually, their fledgling, were studied. This area has been regularly visited by the first author since 1987 and these individuals were first detected in 2011, since then they have been regularly detected at the same territory, thus, presumably consisting of the same individuals observed recurrently.

Females of this species rarely vocalize which makes our detection of feeding events biased toward males. However, paired individuals were often detected and females were always seen consuming fruits known to be consumed by males which lead us to believe there is no difference in the diet between sexes.

Sampling of frugivory interactions

In the field, once an individual bird was detected, we followed it and observed its behavior until we lost sight of the bird. During this period, we identified the items consumed. Each uninterrupted sequence of foraging maneuvers on the same plant was considered a single foraging event, regardless of how many fruits were collected. However, if the bird paused at the same perch after foraging maneuvers and items were expelled (defecated and/or regurgitated), the next foraging sequence was counted as a new foraging event, even if occurring on the same plant.

At Pontal da Barra, we used an additional and complementary method to identify the plants consumed. The method consisted of placing between one and four pieces of cloth (around 1 m² each) under the exact point where a Hooded Berryeater was perched. We used up to four pieces of non-woven cloth (TNT fabric) at once. After a few minutes, birds usually regurgitated seeds which fell on the cloth, preventing them from getting lost or mixed with the litter. After ingesting several fruits, individuals of this species usually remain on the same perch between the middle stratum and the canopy (personal observation), for long periods (usually up to 30 minutes) facilitating interception of the material expelled. Seeds were then collected, labeled and later identified by comparing with a reference collection of the local seeds (details in Maurício et al. 2024).

Data analysis

To assess whether sampling was sufficient to detect most plants in the diet of the species, we ran an adapted version of the individual-based rarefaction, using iNEXT (Chao et al. 2016). We created rarefaction curves of detected plant species consumed and confidence intervals (95%) built based on 1000 iterations (bootstraps) of the data. We replaced “species abundance” by the “number of foraging events” recorded on each plant species consumed, similar to Vizentin-Bugoni et al. (2019). Besides evaluating sampling completeness, the rarefaction allows to

testing the existence of differences in the plant richness on the diet between datasets across areas. Species richness may be considered statistically different when the 95% confidence intervals do not overlap.

To evaluate temporal variation in the diet, we grouped sets of three months within seasons: summer (January to March), autumn (April to June), winter (July to September), and spring (October to December). The forest vegetation is semideciduous and presents seasonality following changes in temperature and rainfall. Data from 1971 to 2000 shows that the annual average temperature is 17.8 °C, with rainfall evenly distributed over the year (average accumulated rainfall per season: summer = 333.5 mm, autumn = 289.7, winter = 356.3, and spring = 286.1) and amounting to 1366 mm per year (Station located at 31°52'00"S; 52°21'24" W; altitude of 13.24 m a.s.l.; EAP, 2024). The average mean, minimum and maximum temperatures, respectively, vary across seasons as follows: summer (mean = 22.9 °C, min = 18.9 °C and max = 27.8 °C), autumn (16.4, 12.4–21.9 °C), winter (13.2, 9.3–18.3 °C), and spring (19.0, 14.8–23.8 °C). During the winter frost events are common (14.3 days per winter; EAP 2024) but snowfall is rare and never accumulates beyond a few hours. Although some plants lose completely their leaves in the winter, most species retain leaves over the year and go through pronounced sprouting in the spring. As above, a rarefaction was used to test sampling sufficiency within each season and test whether plant richness in the diet varied among seasons for each study site separately.

RESULTS

Diet compilation

Considering the literature and our records, 111 species of fruits have been reported to be consumed by *Carpornis cucullata* to date, encompassing 39 plant families (Table 1).

Diet at the study sites

In the communities studied in southern Brazil, we detected consumption of 53 species belonging to 29 plant families, including an unidentified vine, an unidentified Solanaceae, and both opportunistic records of *Myrcia glabra* and *Guettarda uruguensis* (Data Collection). Of these, 16 species and two families had not yet been reported to be consumed by this bird (Table 1).

Of the 51 species (two unidentified morphotypes excluded) consumed in the study sites, eighteen (35.3%) were consumed in both areas, with 14 species (27.5%) consumed exclusively at Cerro das Almas and 19 (37.3%) consumed exclusively at Pontal da Barra (Table 1; Fig. 3). There was no difference in the total number of species consumed between areas and the asymptotic trend of the rarefaction curves indicates that most species consumed in both areas were detected (Fig. 2). In fact, the sample coverage was 0.98 for Cerro das Almas and 0.99 for Pontal da Barra, however, the upper limit of the 95% confidence interval obtained with the rarefaction (Fig. 2A) suggests that, considering the number of foraging events observed in each site, around 45 species at Pontal da Barra and 42 species at Cerro das Almas are expected to be consumed.

At Cerro das Almas, we observed a total of 465 feeding events by the Hooded Berryeater involving fruits of 32 species, of which 30 were trees and two were vines (*Hyperbaena domingensis* and an

Table 1. Plants consumed by the Hooded Berryeater (*Carpornis cucullata*) throughout its range including literature reports and records at two sites (Cerro das Almas and Pontal da Barra) in southern Brazil. † Introduced species; ‡ opportunistic record at the Horto Botânico Irmão Teodoro Luis; § opportunistic record at the margin of Turucu river. Parentheses include names used in the original publications.

Family / Species	This study		Literature
	Cerro das Almas	Pontal da Barra	
Anacardiaceae			
<i>Schinus terebinthifolia</i>		X	
Apocynaceae			Emer et al. (2019)
<i>Tabernaemontana catharinensis</i>			
Aquifoliaceae			
<i>Ilex microdonta</i>			Bello et al. (2017), Emer et al. (2019)
<i>Ilex dumosa</i>	X	X	Mauricio et al. (2024)
Araliaceae			
<i>Didymopanax angustissimum</i> (<i>Schefflera angustissima</i>)			Bello et al. (2017), Parrini et al. (2017), Emer et al. (2019)
<i>Didymopanax calvus</i>	X		
Arecaceae			
<i>Euterpe edulis</i>			Bello et al. (2017), Parrini et al. (2017), Emer et al. (2019)
<i>Geonoma gamiova</i>			Bello et al. (2017), Emer et al. (2019)
<i>Geonoma pauciflora</i>			Bello et al. (2017), Emer et al. (2019)
<i>Geonoma schottiana</i>		X	Parrini et al. (2017), Mauricio et al. (2024)
<i>Syagrus romanzoffiana</i>		X	Mauricio et al. (2024)
Boraginaceae			
<i>Cordia ecalyculata</i>	X	X	Bencke (1996), Mauricio et al. (2024)
Cactaceae			
<i>Rhipsalis teres</i>		X	Bello et al. (2017), Emer et al. (2019), Mauricio et al. (2024)
Cannabaceae			
<i>Trema micranthum</i>			Emer et al. (2019)
Cardiopteridaceae			
<i>Citronella gongonha</i>		X	Mauricio et al. (2024)
Celastraceae			
<i>Monteverdia tetragona</i> (<i>Maytenus gonoclada</i>)			Bello et al. (2017), Emer et al. (2019)
Chloranthaceae			
<i>Hedyosmum brasiliense</i>			Bello et al. (2017)
Ebenaceae			
<i>Diospyros inconstans</i>	X	X	Mauricio et al. (2024)
Ephedraceae			
<i>Ephedra tweediana</i>		X	Mauricio et al. (2024)
Erythroxylaceae			
<i>Erythroxylum ambiguum</i>			Bello et al. (2017)
<i>Erythroxylum argentinum</i>		X	Mauricio et al. (2024)
Euphorbiaceae			
<i>Alchornea triplinervia</i>	X		Bello et al. (2017), Emer et al. (2019)
<i>Sebastiania brasiliensis</i>		X	Mauricio et al. (2024)
Lamiaceae			
<i>Vitex megapotamica</i>	X	X	Mauricio et al. (2024)
Lauraceae			
<i>Aiouea saligna</i>	X	X	Mauricio et al. (2024)
<i>Nectandra cuspidata</i>			Bello et al. (2017), Emer et al. (2019)
<i>Nectandra megapotamica</i>	X		Bello et al. (2017), Emer et al. (2019)
<i>Ocotea aciphylla</i>			Bello et al. (2017)
<i>Ocotea acutifolia</i>		X	
<i>Ocotea catharinensis</i>			Montagna et al. (2018)
<i>Ocotea odorifera</i>			Bello et al. (2017), Emer et al. (2019)
<i>Ocotea pulchella</i>	X	X	Bello et al. (2017), Emer et al. (2019), Mauricio et al. (2024)
<i>Ocotea spixiana</i>			Bello et al. (2017), Emer et al. (2019)
<i>Ocotea teleiandra</i>			Bello et al. (2017), Emer et al. (2019)
<i>Persea willdenovii</i> (<i>Persea pyrifolia</i>)			Bello et al. (2017), Emer et al. (2019)
Loranthaceae			
<i>Psittacanthus</i> sp.			Emer et al. (2019)
Melastomataceae			
<i>Leandra australis</i>			Bello et al. (2017), Emer et al. (2019)
<i>Leandra brackenridgei</i> (<i>Leandra pilonensis</i>)			Bello et al. (2017), Emer et al. (2019)

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<i>Leandra regnellii</i>			Bello et al. (2017), Emer et al. (2019)
<i>Leandra variabilis</i>			Bello et al. (2017), Emer et al. (2019)
<i>Miconia buddlejoides</i>			Bello et al. (2017), Parrini et al. (2017), Emer et al. (2019)
<i>Miconia cubatanensis</i>			Bello et al. (2017), Emer et al. (2019)
<i>Miconia flammea</i> (<i>Miconia chartacea</i>)			Bello et al. (2017), Emer et al. (2019)
<i>Miconia formosa</i> (<i>Miconia altissima</i>)			Parrini et al. (2017)
<i>Miconia pusilliflora</i>	X		Bello et al. (2017), Emer et al. (2019)
<i>Miconia sellowiana</i>			Bello et al. (2017), Parrini et al. (2017), Emer et al. (2019)
<i>Miconia valtheri</i>			Bello et al. (2017), Emer et al. (2019)
<i>Pleiochiton blepharodes</i>			Parrini et al. (2017)
Meliaceae			
<i>Cabralea canjerana</i>			Bello et al. (2017), Emer et al. (2019)
<i>Trichilia claussoni</i>	X		
<i>Trichilia elegans</i>	X		
Menispermaceae			
<i>Hyperbaena domingensis</i>	X		
Monimiaceae			
<i>Mollinedia</i> cf <i>widgrenii</i>			Bencke (1996)
Moraceae			
<i>Ficus cestrifolia</i>	X	X	Parrini et al. (2017), Mauricio et al. (2024)
<i>Ficus luschnathiana</i>	X	X	Bello et al. (2017), Emer et al. (2019), Mauricio et al. (2024)
<i>Morus nigra</i> †			Bello et al. (2017)
<i>Sorocea bonplandii</i>	X	X	Mauricio et al. (2024)
Myrtaceae			
<i>Eugenia involucrata</i>	X		
<i>Eugenia melanogyna</i>			Bello et al. (2017), Emer et al. (2019)
<i>Eugenia mosenii</i>			Bello et al. (2017), Emer et al. (2019)
<i>Eugenia rostrifolia</i>	X		Bencke (1996)
<i>Eugenia uniflora</i>	X		
<i>Eugenia uruguayensis</i>	X	X	Mauricio et al. (2024)
<i>Myrcia anacardiifolia</i>			Bello et al. (2017), Emer et al. (2019)
<i>Myrcia glabra</i> ‡			
<i>Myrcia hebeptala</i> (<i>Gomidesia affinis</i>)			Bello et al. (2017), Emer et al. (2019), Pizo et al. (2002)
<i>Myrcia multiflora</i>		X	Mauricio et al. (2024)
<i>Myrcia palustris</i>	X	X	
<i>Myrcia pubipetala</i>			Bello et al. (2017), Emer et al. (2019)
<i>Myrcia spectabilis</i>			Bello et al. (2017), Parrini et al. (2017), Emer et al. (2019)
<i>Myrcia splendens</i> (<i>Myrcia rufula</i>)			Bello et al. (2017), Emer et al. (2019), Pizo et al. (2002)
<i>Myrcianthes gigantea</i>	X		
<i>Neomitranthes glomerata</i>			Bello et al. (2017), Emer et al. (2019)
<i>Psidium cattleianum</i>	X	X	Mauricio et al. (2024)
<i>Siphoneugena densiflora</i>			Bello et al. (2017), Emer et al. (2019)
Nyctaginaceae			
<i>Guapira opposita</i>	X	X	Bello et al. (2017), Parrini et al. (2017), Emer et al. (2019), Mauricio et al. (2024)
Onagraceae			
<i>Fuchsia regia</i>			Bello et al. (2017), Emer et al. (2019)
Primulaceae			
<i>Myrsine coriacea</i>			Bello et al. (2017), Emer et al. (2019)
<i>Myrsine lancifolia</i>			Emer et al. (2019)
<i>Myrsine umbellata</i> (<i>Rapanea acuminata</i>)	X	X	Bello et al. (2017), Parrini et al. (2017), Emer et al. (2019), Pineschi (1990), Mauricio et al. (2024)
<i>Myrsine venosa</i>			Bello et al. (2017), Emer et al. (2019)
<i>Myrsine villosissima</i> (<i>Rapanea villosissima</i>)			Pineschi (1990)
Rosaceae			
<i>Rubus urticifolius</i> (<i>Rubus urticaefolius</i>)			Bello et al. (2017), Emer et al. (2019)
Rubiaceae			
<i>Faramea montevidensis</i>	X	X	Mauricio et al. (2024)
<i>Guettarda uruguensis</i>			
<i>Ixora gardneriana</i>			Bello et al. (2017), Emer et al. (2019)
<i>Palicourea sessilis</i> (<i>Psychotria vellosiana</i> ; <i>Psychotria longipes</i>)			Bello et al. (2017), Emer et al. (2019)
<i>Psychotria brachyceras</i>		X	Mauricio et al. (2024)
<i>Psychotria nuda</i>			Parrini et al. (2017)
<i>Psychotria suterella</i>			Parrini et al. (2017)
<i>Rudgea jasminoides</i>			Bello et al. (2017), Emer et al. (2019)
Salicaceae			
<i>Xylosma pseudosalzmannii</i>	X		
<i>Banara parviflora</i>		X	Mauricio et al. (2024)
<i>Casearia decandra</i>		X	Mauricio et al. (2024)
Sapindaceae			

(con'd)

<i>Allophylus edulis</i>	X	X	Mauricio et al. (2024)
<i>Cupania vernalis</i>	X	X	Mauricio et al. (2024)
<i>Paullinia</i> sp.			Emer et al. (2019)
Sapotaceae			
<i>Chrysophyllum gonocarpa</i>		X	Mauricio et al. (2024)
<i>Chrysophyllum marginatum</i>		X	Mauricio et al. (2024)
<i>Sideroxylon obtusifolium</i>		X	Mauricio et al. (2024)
Solanaceae			
<i>Solanum laxum</i>		X	Mauricio et al. (2024)
Unidentified Solanaceae		X	
Smilacaceae			
<i>Smilax elastica</i>			Bello et al. (2017), Emer et al. (2019)
Styracaceae			
<i>Styrax leprosus</i>		X	Mauricio et al. (2024)
Symplocaceae			
<i>Symplocos estrellensis</i>			Bello et al. (2017), Emer et al. (2019), Pizo et al. (2002)
<i>(Symplocos variabilis)</i>			
<i>Symplocos</i>			Bello et al. (2017), Emer et al. (2019)
<i>glandulosomarginata</i>			
<i>Symplocos tetrandra</i>			Bello et al. (2017), Emer et al. (2019)
<i>Symplocos uniflora</i>	X		
Thymelaeaceae			
<i>Daphnopsis fasciculata</i>			Mendonça-Lima et al. (2001)
Verbenaceae			
<i>Citharexylum myrianthum</i>		X	Mauricio et al. (2024)
Winteraceae			
<i>Drimys brasiliensis</i>			Bello et al. (2017), Emer et al. (2019)
<i>(Drimys winteri)</i>			
Other / Unknown			
Unidentified vine	X		

unidentified species). Botanic families most represented in the diet were Myrtaceae (eight species), Lauraceae (three species) and Moraceae (three species) (Appendix 1: Table ESM 2). Seven species accounted together for 74% of the foraging events observed: *Didymopanax calvus* (81 events; 17% of the total), *Ficus cestrifolia* (65; 14%), *Fareamea montevidensis* (62; 13%), *Miconia pusilliflora* (52; 11%), *Cordia ecalyculata* (34; 7%), *Eugenia rostrifolia* (26; 6%) and *Ficus luschnathiana* (23; 6%). All remaining species corresponded to 3% or less of the foraging events observed.

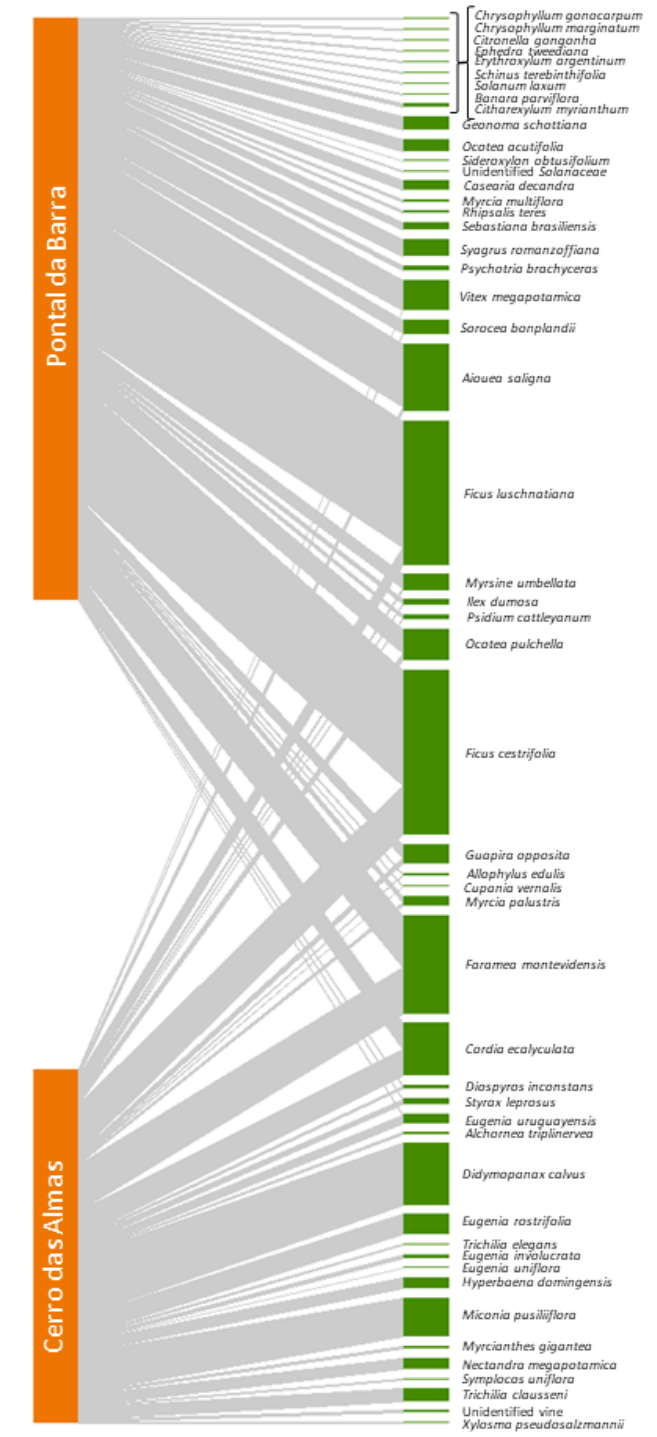
At Pontal da Barra, we observed a total of 804 feeding events involving fruits of 37 species, of which 32 were trees, a treelet (*Psychotria brachyceras*), a supporting bush (*Ephedra tweediana*), an epiphyte (*Rhipsalis teres*), and a vine (*Solanum laxum*; Appendix 1: Table ESM 3). Botanic families most represented in the diet were Myrtaceae (four species), Lauraceae, Moraceae and Sapotaceae (three species each). Similar to the other site, few species (seven) accounted together for 76% of the foraging events observed: *Ficus luschnathiana* and *Ficus cestrifolia* (354 events together; 44% of the total), *Aiouea saligna* (82; 10%), *Fareamea montevidensis* (68; 8%), *Vitex megapotamica* (39; 5%), *Ocotea pulchella* (32; 4%), and *Cordia ecalyculata* (35; 5%). All other species correspond to 3% or less of the foraging events observed.

Regarding the animal component of the diet of the Hooded Berryeater, we observed the consumption of 19 caterpillars (Lepidoptera) and one stick-insect (Phasmatodea) at Cerro das Almas and six records of consumption of caterpillars at Pontal da Barra. In addition, we recorded a stick-insect and several cicadas (Cicadoidea) being delivered to fledglings at the Pontal da Barra site, prior to the present study (unpublished data).

Intra-annual variation in the diet

Our sampling coverage estimation indicates that sampling was sufficient to detect most plants consumed in each season in both areas, with the sampling coverage 0.93 or higher (Table 2,

Fig. 3. Bipartite plot indicating the 51 plants (right) consumed by the Hooded Berryeater (*Carpornis cucullata*) at each site (left) in southern Brazil. The thickness of the gray bars indicates the frequency of the foraging events observed. For reference, the thickest gray bar (*Ficus luschnathiana* at Pontal) corresponds to 167 events.



At Pontal da Barra, only eight species (*Ficus cestrifolia*, *Ficus luschnathiana*, *Faramea montevidensis*, *Myrsine umbellata*, *Aiouea saligna*, *Ocotea pulchella*, *Geonoma schottiana*, and *Syagrus romanzoffiana*) were consumed along three or four seasons, whereas the remaining species were consumed in one or two seasons (Appendix 1: Table ESM 2; Fig. 4B, Fig. 5B, Appendix 1: Fig. ESM 2B). The number of species was higher in the summer (21 species) and spring (23) than in the winter (11) and autumn (11) (Table 2; Fig. 5B; Fig. 2C). However, there was no difference in the number of plant species between summer and spring nor winter and autumn (Fig. 2C).

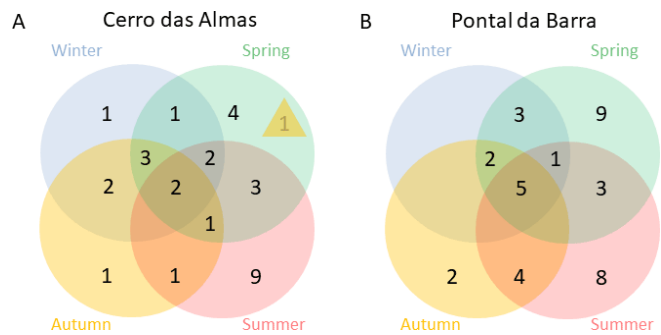
DISCUSSION

Regarding plant families consumed by Hooded Berryeater, our findings are similar to results from four sites at the Atlantic Forest in southeastern Brazil (at Parque Estadual Intervales) where the most represented plant families were Myrtaceae (with 10 species), Lauraceae (9), and Melastomataceae (7): Pizo et al., 2002, Bello et al. 2017, Emer et al. 2019). In fact, these plant families were, in the same order, the most well-represented (high species richness) in the diet of Hooded Berryeater in our study sites. Myrtaceae being the most species-rich is not surprising given that the high

Table 2. Seasonal variation in the number of foraging events, number of plants consumed, and sampling coverage of the diet of the Hooded Berryeater (*Carpornis cucullata*) in Cerro das Almas and Pontal da Barra.

	Winter	Spring	Summer	Autumn
Cerro das Almas				
N foraging events	154	126	106	79
N plants consumed	11	17	19	11
Sampling coverage	0.99	0.96	0.93	0.96
Pontal da Barra				
N foraging events	125	222	201	221
N plants consumed	11	23	21	13
Sampling coverage	0.98	0.98	0.99	1.00

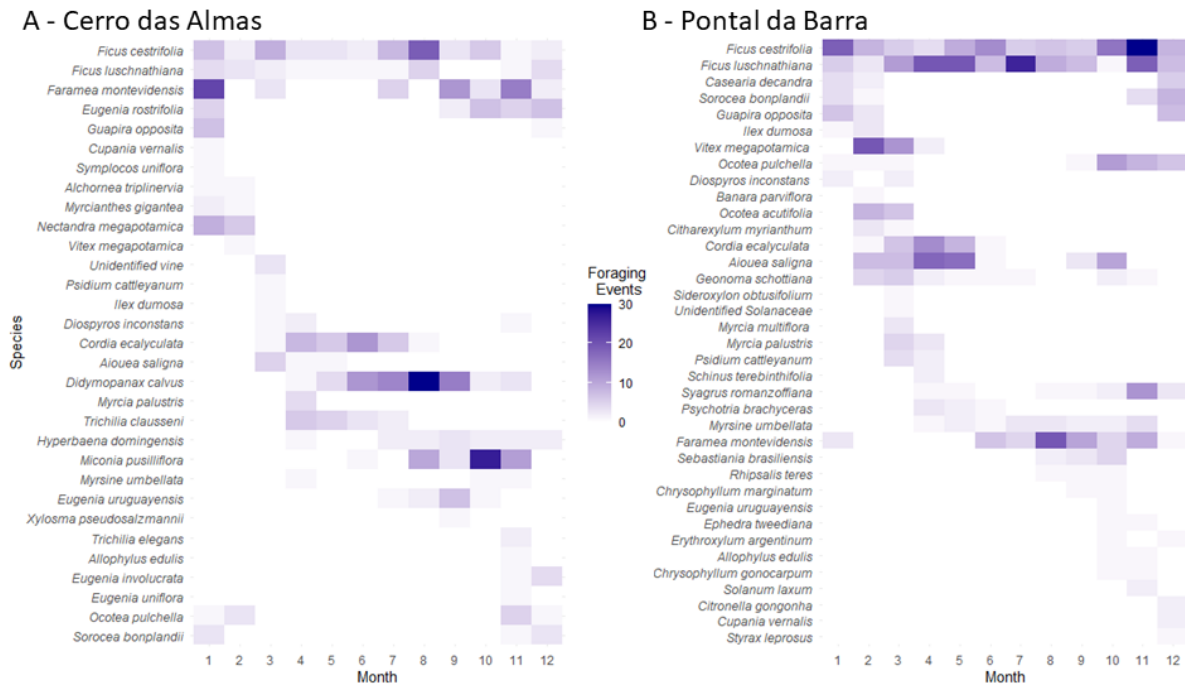
Fig. 4. Number of plant species shared by seasons in the diet of the Hooded Berryeater (*Carpornis cucullata*) in Cerro das Almas (A) and Pontal da Barra (B). The triangle in A shows a case of shared species between non-adjacent seasons (i.e., *Myrsine umbellata* was consumed in Spring and Autumn).



species richness of the family is a pervasive characteristic of low-elevation areas of the Atlantic Forest, being the dominant woody family in several sections of this ecoregion (Mori et al. 1983; Landrum and Kawasaki 1997, Oliveira-Filho and Fontes 2000, Guilherme et al. 2004), including on the region studied here (Venzke 2012, Venzke et al. 2012). However, in terms of the total number of foraging events observed, Myrtaceae ranked only as the fourth family at Cerro das Almas (53 events) and the seventh at Pontal da Barra (18 events). This scenario may be related to the abundance and phenology of the Myrtaceae species, as most species are rare trees, have aggregated spatial distributions and/or have short fruiting periods (personal observation), resulting in fruit production (and consequently frugivory opportunities) concentrated in time or space. This indicates that despite of its important role as a seed disperser for Myrtaceae species, the Hooded Berrvater relies more on plants of other families.

In fact, the leading plant families in terms of the total number of foraging events were Moraceae (95 events), Araliaceae (81) and Rubiaceae (62) at Cerro das Almas, and Moraceae (291), Lauraceae (114), and Rubiaceae (69) at Pontal da Barra, despite only one to three species of these families having been consumed. Most species of these families are abundant and produce fruits year-round or over most seasons. The consumption of *Ficus cestrifolia* and *Ficus luschnathiana* (Moraceae) is particularly

Fig. 5. Frequency of frugivory events by the Hooded Berryeater (*Carpornis cucullata*) per month at Cerro das Almas (A) and Pontal da Barra (B). In the x-axis, Summer (1, 2, and 3), Autumn (4, 5, and 6), Winter (7, 8, and 9) and Spring (10, 11, and 12).



remarkable both for the consistency throughout the year and the frequency of interactions (Fig. 6). Such species are particularly important in the colder period (austral autumn and winter) when fewer plants produce fruits in these areas. During this period, however, other species gain importance in the diet in both sites, especially *Cordia ecalyculata*, *Faramea montevidensis*, and *Aiouea saligna*, and also *Didymopanax calvus* which only occur at Cerro das Almas. Together, this set of species may be considered the main food resources that maintain the Hooded Berryeater populations at the studied sites in the southernmost of its distribution. Fruits of the remaining plant species are complementary in the diet being consumed at low frequencies or have episodic importance such as *Vitex megapotamica* at Pontal da Barra and *Miconia pusillifolia* at Cerro das Almas.

The high diversity of plants (53 species) consumed by the Hooded Berryeater in our two study sites in southern Brazil is remarkable and comparable to findings for the central portion of its distribution in southeastern Brazil, where fruits of 45 species were consumed across four areas with a much larger elevation gradient, from 100 to 800m a.s.l. (compared to 5 to 260m a.s.l. of our sites; Pizo et al. 2002). As at those areas in the core of the Atlantic Forest this bird is considered a key seed disperser (Vidal et al. 2014, Pizo et al. 2002), our findings suggest not only its high importance as a key seed disperser in the southernmost of its range but reveal the high diversity and ecological complexity of the Atlantic Forest in this region (around latitude 31°S). The region has been traditionally classified as part of the Pampas (or “*Campos Sulinos*”) ecoregion by governmental agencies (IBGE 2004), but also considered as belonging to the Atlantic Forest by other authors (e.g., Ihering 1891, Ribeiro et al. 2009) or, more

Fig. 6. Hooded Berryeater (*Carpornis cucullata*) consuming a fruit of *Ficus luschnathiana* (Moraceae), one of the most important plants in its diet in southern Brazil. Photography by Jefferson Silva.



recently, Coastal Subtropical forest (Hasenack et al. 2023). Our data support that the region we studied is part of the southern limit of the Atlantic Forest, where several tree species endemic to the Atlantic Forest meet their austral limit of distribution, such

as *Ficus cestrifolia*, *Fareamea montevidensis*, *Psychotria brachyceras*, *Geonoma schottiana*, *Miconia pusilliflora*, *Eugenia rostrifolia*, and *Psidium cattleyanum* (Forzza et al. 2010). We also show that their fruits are regularly consumed by the Hooded Berryeater, which is also an endemic organism restricted to the coastal belt of the Atlantic Forest. This scenario suggests that a fundamental ecological relationship so characteristic of the Atlantic Forest, that is, a strong linkage between the endemic flora and its endemic key seed dispersers, is maintained in the southern limit of this ecoregion.

Our data collection at Cerro das Almas occurred from 1997 to 2000, over two decades ago. Despite some changes in plant and bird communities that may have occurred over this time, we expect only a minor influence on the current diet of the Hooded Berryeater compared to the one reported here. The most important potential changes observed are related to the invasion of *Asparagus setaceus* and *Pittosporum undulatum* whose diaspores are consumed and dispersed by birds and have become widespread plants across forests in the region, affecting the native vegetation (Freitas et al. 2024) and potentially interfering with plant-disperser interaction involving native species (personal observation).

Altogether, our findings indicate that the Hooded Berryeater is a key seed disperser species in the southern limit of the Atlantic Forest and illustrates that the diversity and complexity of the forest at this ecoregion is retained in latitudes as high as 32° South. We suggest that this bird has the potential to play a critical role in the success of several plants in carrying out niche tracking and coping with climate change, as climatically suitable areas move southward. To properly test such prediction, further studies should consider evaluating movement data of this bird as well as how other factors such as introduced species, habitat loss, and fragmentation affect this species and the plants it relies on.

Author Contributions:

GNM collected and organized the data. CAS and LRS identified the plants consumed. GNM and JVB analyzed the data and wrote the manuscript. All authors revised and approved the last version of the manuscript.

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Data Availability:

All data is presented within the manuscript or as appendices.

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APPENDIX 1

Spatiotemporal variation in the diet of Hooded Berryeater (*Carpornis cucullata*) in the southernmost section of the Atlantic Forest ecoregion

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Figure ESM 1. Sampling coverage (interpolation-extrapolation) curves of the plant species consumed by the Hooded Berryeater (*Carpornis cucullata*) with the accumulation of foraging events observed throughout the study (A) and across seasons at Cerro das Almas (B) and Pontal da Barra (A). 95% confidence intervals based on 1000 bootstraps.

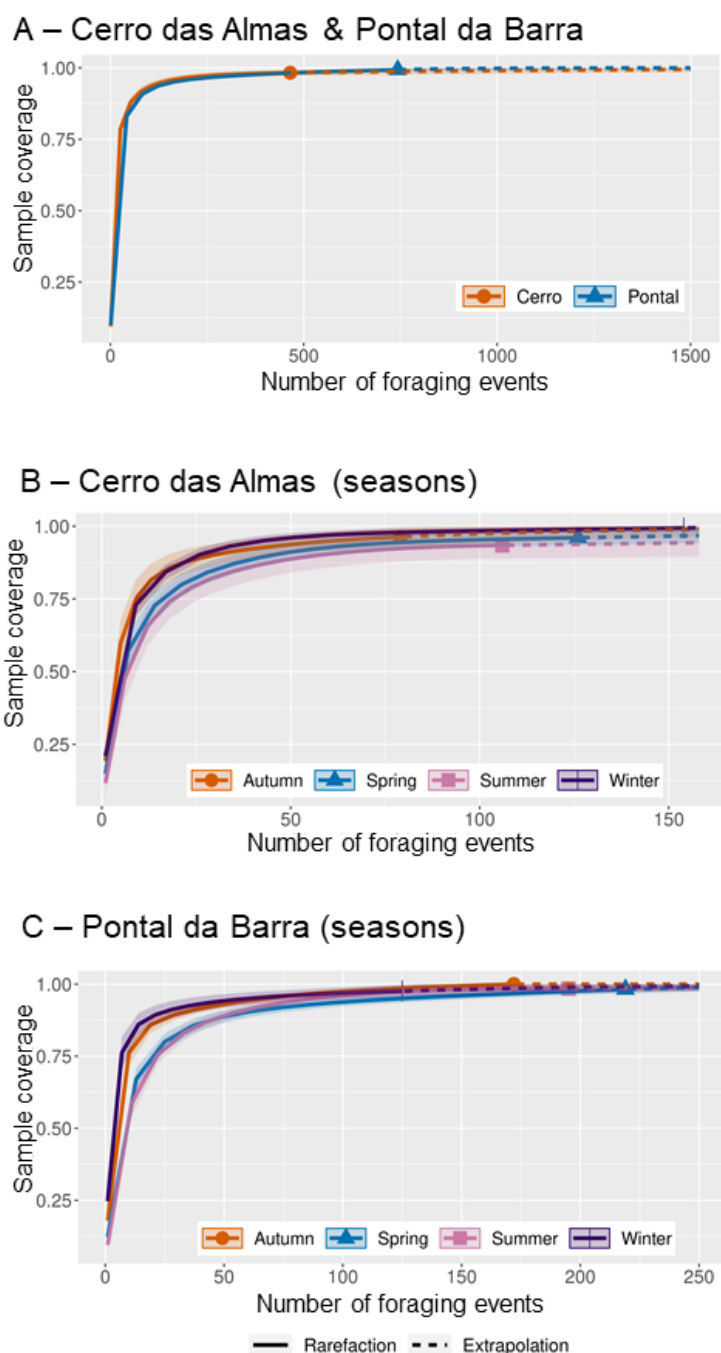


Figure ESM2. Frequency of frugivory events by the Hooded Berryeater (*Carponis cucullata*) per season at Cerro das Almas (A) and Pontal da Barra (B).

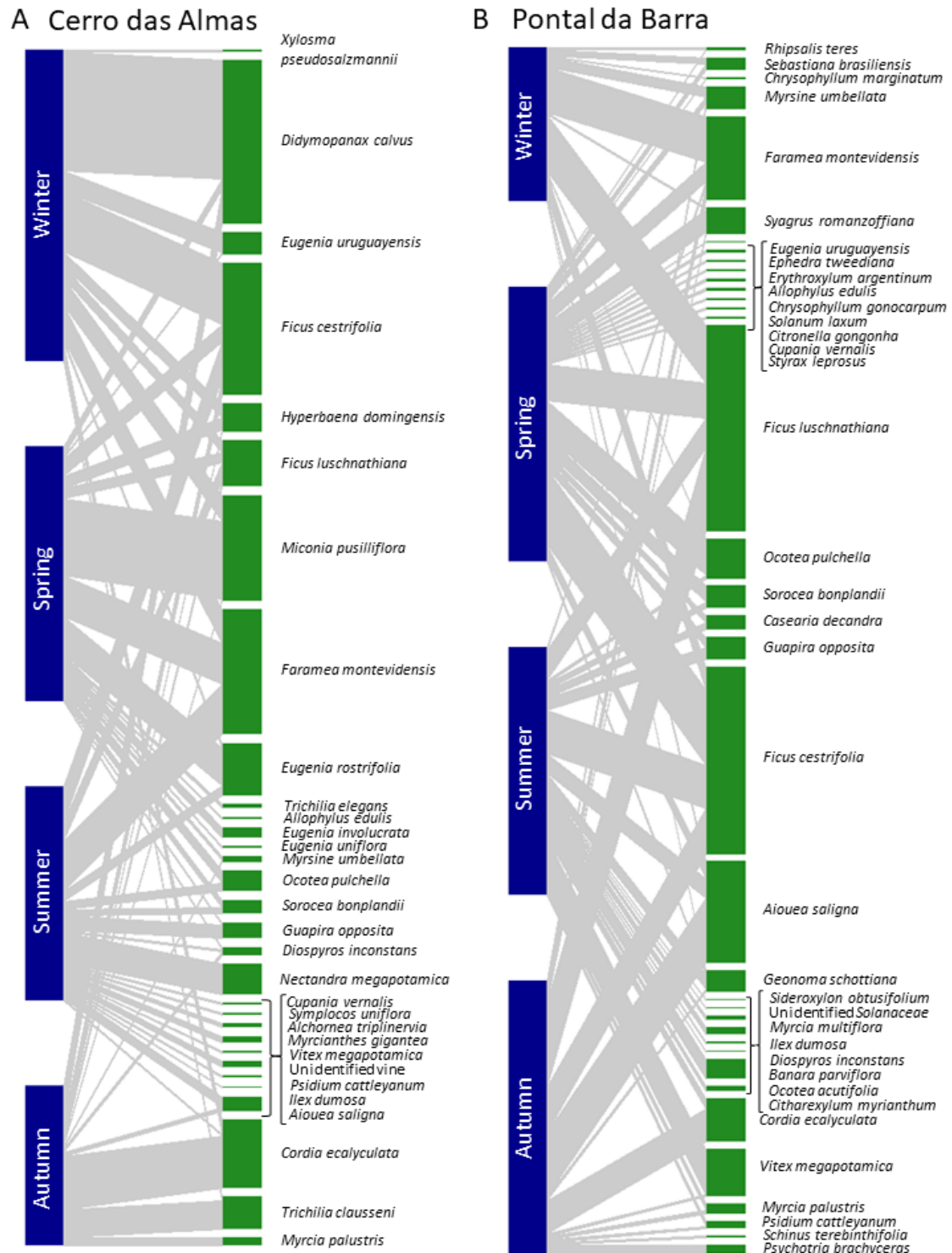


Table ESM 1. Sampling effort (in hours) per month in each area.

Cerro das Almas			Pontal da Barra (year 1)			Pontal da Barra (year 2)			Pontal da Barra (both years)		
Month	Year	Effort (h)	Month	Year	Effort (h)	Month	Year	Effort (h)	Month	Year	Effort (h)
Jan	multiple	118h	Jul	2022	7h20	Jul	2023	9h	Jul	both	16h20
Feb	multiple	59h	Aug	2022	8h20	Aug	2023	11h	Aug	both	19h20
Mar	multiple	64h	Sep	2022	7h	Sep	2023	5h	Sep	both	12h20
Apr	multiple	82h	Oct	2022	5h	Oct	2023	14h	Oct	both	19h
May	multiple	30h	Nov	2022	5h30	Nov	2023	19h	Nov	both	24h30
Jun	multiple	36h	Dec	2022	8h	Dec	2023	14h	Dec	both	22h
Jul	multiple	38h	Jan	2023	11h	Jan	2024	12h	Jan	both	23h
Aug	multiple	55h	Feb	2023	14h20	Feb	2024	16h	Feb	both	30h20
Sep	multiple	64h	Mar	2023	14h	Mar	2024	14h30	Mar	both	28h30
Oct	multiple	60h	Apr	2023	17h	Apr	2024	14h30	Apr	both	32h
Nov	multiple	109h	May	2023	12h	May	2024	12h	May	both	24h
Dec	multiple	100h	Jun	2023	17h	Jun	2024	16h	Jun	both	33h
Total		815h	Total		126h30	Total		157h	Total		284h

Table ESM 2. Number of foraging events per plant species consumed by the Hooded Berryeater (*Carpornis cucullata*) throughout the year at Cerro das Almas. Data includes all records during the study period.

Species	Summer			Autumn			Winter			Spring			Total
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Ficus cestrifolia</i>	7	2	9	3	3	2	8	19	3	6	1	2	65
<i>Ficus luschnathiana</i>	4	3	2	1	1	1	1	5			1	4	23
<i>Faramea montevidensis</i>	22		3				5		12	3	15	2	62
<i>Eugenia rostrifolia</i>	5								2	7	5	7	26
<i>Guapira opposita</i>	7											1	8
<i>Cupania vernalis</i>	1												1
<i>Symplocos uniflora</i>	1												1
<i>Alchornea triplinervia</i>	1	1											2
<i>Myrcianthes gigantea</i>	2	1											3
<i>Nectandra megapotamica</i>	9	6											15
<i>Vitex megapotamica</i>		1											1
Unidentified vine			3										3
<i>Psidium cattleyanum</i>			1										1
<i>Ilex dumosa</i>			1										1
<i>Diospyros inconstans</i>			1	2							1		4
<i>Cordia ecalyculata</i>			1	8	6	12	6	1					34
<i>Aiouea saligna</i>			5	1	1								7
<i>Didymopanax calvus</i>				1	4	12	14	30	15	2	3		81
<i>Myrcia palustris</i>				4									4
<i>Trichilia clauseni</i>				6	5	3	2						16
<i>Hyperbaena domingensis</i>				1			2	2	3	2	2	2	14
<i>Miconia pusiliiflora</i>						1		10	3	27	11		52
<i>Myrsine umbellata</i>				1						1	1		3
<i>Eugenia uruguayensis</i>							1	2	7	1			11
<i>Xylosma pseudosalzmannii</i>									1				1
<i>Trichilia elegans</i>											2		2
<i>Allophylus edulis</i>											1		1
<i>Eugenia involucrata</i>											1	4	5
<i>Eugenia uniflora</i>											1		1
<i>Ocotea pulchella</i>	1	3									5	1	10
<i>Sorocea bonplandii</i>	3										1	3	7
Arthropods	1	0	0	0	0	0	3	5	5	4	1	1	20
N species consumed/month	12	7	9	10	6	6	8	7	8	8	15	9	
N foraging events/month	63	17	26	28	20	31	39	69	46	49	51	26	

Table ESM 3. Number of foraging events per plant species consumed by the Hooded Berryeater (*Carpornis cucullata*) throughout the year at Pontal da Barra. Data includes all records during the study period.

Species	Summer			Autumn			Winter			Spring			Total
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Ficus cestrifolia</i>	20	9	6	4	13	20	6	7	6	17	32	12	152
<i>Ficus luschnathiana</i>	6	6	12	21	21	26	28	10	8	1	20	8	167
<i>Ficus cestrifolia/luschnathiana</i>	7	3	2	11	3	3					1	5	35
<i>Casearia decandra</i>	4	2										6	12
<i>Sorocea bonplandii</i>	4	1									4	9	18
<i>Guapira opposita</i>	7	3										8	18
<i>Ilex dumosa</i>	3	3											6
<i>Vitex megapotamica</i>	3	21	13	2									39
<i>Ocotea pulchella</i>	1	1	1						1	12	9	7	32
<i>Diospyros inconstans</i>	1		1										2
<i>Banara parviflora</i>		1											1
<i>Ocotea acutifolia</i>		9	7										16
<i>Citharexylum myrianthum</i>		3	1										4
<i>Cordia ecalyculata</i>		1	7	14	11	2							35
<i>Aiouea saligna</i>		8	8	19	19	14			3	11			82
<i>Geonoma schottiana</i>		5	6	1	1	1	1			2	1		18
<i>Sideroxylon obtusifolium</i>			1										1
Unidentified Solanaceae			1										1
<i>Myrcia multiflora</i>			3										3
<i>Myrcia palustris</i>			5	3									8
<i>Psidium cattleianum</i>			4	2									6
<i>Schinus terebinthifolia</i>				1	1								2
<i>Syagrus romanzoffiana</i>				1	1			1	1	2	13	3	22
<i>Psychotria brachyceras</i>				3	3	1							7
<i>Myrsine umbellata</i>				1	2	1	3	3	2	2	4		18
<i>Faramea montevidensis</i>	3					12	5	21	11	5	10	1	68
<i>Sebastiania brasiliensis</i>								2	3	5			10
<i>Rhipsalis teres</i>								1	1	1			3
<i>Chrysophyllum marginatum</i>									1	1			2
<i>Eugenia uruguayensis</i>										1			1
<i>Ephedra tweediana</i>										1	1		2
<i>Erythroxylum argentinum</i>										1		1	2
<i>Allophylus edulis</i>										1	1		2
<i>Chrysophyllum gonocarpum</i>										1	1		2
<i>Solanum laxum</i>											2		2
<i>Citronella gongonha</i>												2	2
<i>Cupania vernalis</i>												2	2
<i>Styrax leprosus</i>												1	1
Arthropods	0	1	0	2	3	0	0	0	0	1	0	0	7
N species consumed/month	11	15	16	13	10	9	5	7	10	16	13	13	
N foraging events/month	59	76	78	83	75	80	43	45	37	64	99	65	