



## RESEARCH ARTICLE

# Fruit resource provisioning for avian frugivores: The overlooked side of effectiveness in seed dispersal mutualisms

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**Funding information**

Agencia Estatal de Investigación, Spain, Grant/Award Number: CGL2017-82847-P; "la Caixa" Foundation, Grant/Award Number: LCF/BQ/DE18/11670007; European Commission; Junta de Andalucía Excellence, Grant/Award Number: RNM-5731; Ministerio de Ciencia, Innovación y Universidades; Fondo Europeo de Desarrollo Regional; CNPq

**Handling Editor:** Yvonne Buckley

**Abstract**

1. Mutualistic interactions between frugivorous birds and fleshy-fruited plants are key processes for both natural plant regeneration and the maintenance of birds relying on fruit resources. However, seed dispersal effectiveness (SDE) has been frequently studied only from the plant's perspective, that is the contribution of animals to plant fitness.
2. Using a sample of Atlantic rainforest avian frugivores, this study presents a first comparative, empirical study of fruit effectiveness as a nutritional food resource for seed-dispersing birds through the use of resource-provisioning effectiveness (RPE) models. RPE is the product of the amount of fruits a frugivore can consume (quantity component) and the quality of the ingesta in terms of energy and nutrients obtained (quality component).
3. Our results show wide variation in RPE among fleshy-fruited plant species. Energy-rich fruits consistently show a smaller quantity component, while energetically poor fruits are consistently the most consumed, with fruit species spanning a gradient from these two extremes.
4. The specific RPE<sub>i</sub> resulting from a pairwise fruit–frugivore interaction is positively correlated with the total RPE (RPE<sub>T</sub>) that a given fruit species has for the whole frugivore assemblage. RPE therefore appears to be a characteristic feature of the fruit species, rather than of the specific frugivore partner.
5. Only the fruit's specific energy content showed a significant phylogenetic signal, suggesting potential constraints for free covariation between RPE and SDE of fruits and frugivores.
6. *Synthesis.* We analyse variation in the effectiveness of fleshy-fruit food provisioning to avian frugivores by explicitly redefining RPE within the SDE framework. We found ample variation in RPE among plant species, showing differences in both quantity and quality components of fruit resources rewards for the frugivores. Our findings help unravel how seed-dispersing birds may discriminate among alternative fruit resources and to understand the configuration of mutual dependencies among mutualistic partners.

**KEYWORDS**

Atlantic rainforest, digestibility, effectiveness landscape, frugivory, mutualistic interactions, quantity and quality components, resource-provisioning effectiveness (RPE), tropical

# 1 | INTRODUCTION

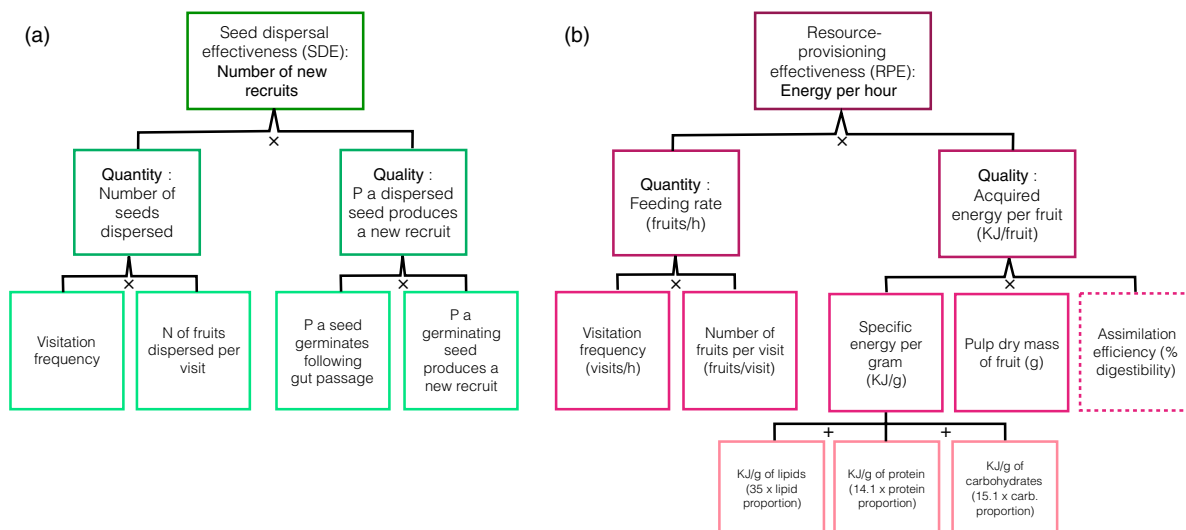
Seed dispersal processes exemplify the widespread animal–plant mutualisms present in nature (Janzen, 1983). Plants provide their fruits as a food resource, while animals are the transport vector for their seeds to get dispersed in conditions adequate for their establishment, with both partners attaining in the end a reciprocal benefit. However, all plant–frugivore interactions are not equally effective, and a major challenge has been to identify which elements are key determinants of their effectiveness for both animal and plant partners. The mutual dependence between partners in plant–frugivore interactions thus pivots on these aspects of effectiveness: how effective frugivores are for the plants, and how effective plants are as resource providers to the animals.

As a way to measure mutualistic interactions, early studies tried to quantify and compare how effective are different seed dispersal services. However, a persistent challenge has been obtaining effectiveness estimates that could be compared across studies and different forms of mutualisms, given the variety of approaches, measures and methods used. Seed dispersal effectiveness (SDE) arose as a novel framework with the aim of unifying, standardizing and comparing across studies (Schupp, 1993). SDE uses quantity and quality components as proxies to quantify the contribution of different frugivore species to plant fitness (Figure 1a). The quantity component measures the frequency of the interaction through visitation rate and the probability of seeds being removed and dispersed; while the quality component depends on the treatment of seeds in the animal's gut (for endozoochorous dispersal systems) and the deposition patterns. Quantity and quality components are multiplicative and together give a total effect (Vazquez, Morris, & Jordano,

2005) to the interaction. Effectiveness landscapes help visualizing variation in quantity and quality components across species and their contribution to the total effectiveness. They are two-dimensional representations of the possible combinations of the quantity and the quality components with elevational contours representing isoclines of SDE (Schupp, Jordano, & Gómez, 2010, 2017).

Recently, the SDE framework has been proposed to be applied to other plant–animal interactions, and extended to other perspectives (Schupp, Jordano, & Gómez, 2017). Most studies on SDE are focused on the ‘phyto-centric’ perspective, that is, the effect that dispersers have on the plant fitness—a plant’s perspective (Godínez-Álvarez, Valiente-Banuet, & Rojas-Martínez, 2002; Jordano & Schupp, 2000; Loayza & Rios, 2014; Loiselle & Blake, 1999; Rother, Pizo, & Jordano, 2016; Spiegel & Nathan, 2007). Yet, few or no studies look at the other side of the picture, that is the contribution of different fleshy-fruited plants for disperser fitness, or how plants vary in their resource-provisioning effectiveness (RPE) to frugivores—the frugivores’ perspective (Albrecht, Hagge, Schabo, Schaefer, & Farwig, 2018; Schupp et al., 2017).

Here we aim to assess and characterize variation in the effect that fruits have on avian frugivores in terms of energy intake, using the RPE framework initially suggested by Schupp et al. (2017). The RPE framework adapts SDE quality and quantity components for the disperser perspective. The quantity component is described as the feeding rate attained by the frugivore while feeding on the plant, while the quality component is defined as the energy that the frugivore is able to obtain from the fruit food (see Herrera, 1981). The multiplication of these two components yields the ultimate effect that fruit resources provisioned by a plant species have on the fitness of the frugivore consuming them (Schupp et al., 2017). We might expect



**FIGURE 1** (a) Seed dispersal effectiveness (SDE) and (b) resource-provisioning effectiveness (RPE) conceptual schemes. Both models are used as a framework to measure the effectiveness of mutualistic interactions; model (a) for the plant perspective and (b) for the frugivore perspective. All components are either multiplicative or additive (indicated by mathematical sign above) and ordered in hierarchical levels. The pink-dashed border (b) indicates a subcomponent of digestibility measures used to refine the quality estimates (see Figure S5). *N*, number; *p*, probability. See Schupp et al. (2017) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

ample variation in RPE among plant species, given not just variation in fruit morphology and nutrient content (Herrera, 1981; Jordano, 1995) but also in fruit availability, accessibility or any other characteristic that determines how rewarding a fruit resource is for the frugivore.

Understanding the variation in energy provisioning across plant taxa is thus fundamental to understand the drivers of frugivore foraging preferences and the evolutionary strategies of plants regarding fruit displays and dispersal ability. To the best of our knowledge, no previous study has attempted such a 'zoocentric' analysis of seed dispersal mutualism by addressing variation in RPE. As an example of this approach, consider a frugivorous bird consuming fruits to store fat for migration by consuming different fruit species. RPE in this case would be measured as the energy accumulated when feeding on different fruit species. From the frugivore perspective, variation in resource provisioning across plant species is expected to depend on differences in fruit traits determining quantity (e.g. fruit crop size, fruit accessibility, local density) and quality (e.g. per fruit content of nutrients and energy and assimilation efficiency) aspects of the use of this fruit resource by the frugivore (RPE; Figure 1b).

Many of the trees and shrubs present in tropical forests rely on frugivores for the dispersal of their seeds, and ultimately the successful establishment of new individuals (Howe & Smallwood, 1982; Jordano, 2013; Loiselle & Blake, 1999). For our comparative study of RPE patterns we use neotropical bird-plant interactions occurring in the Atlantic rainforest of Southeastern Brazil. The Atlantic rainforest is an extensive biome that has undergone a severe fragmentation retaining c. 11.4%–16% of its original cover (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009), yet being one of the world's biodiversity-hotspot areas (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000).

Specifically we asked the following questions: (a) which are the main patterns of variation and covariation of RPE components across fruit species that interact with a diverse frugivore avifauna?; (b) is the specific RPE of a given pairwise fruit-frugivore interaction ( $RPE_{ij}$ ) correlated with the average RPE of the fruit species across interactions ( $RPE_T$ )? In other words, are the overall  $RPE_T$  values of fruit species predictable from pairwise interactions?; (c) how does refining the quality component with measures of digestibility alter  $RPE_{ij}$ ?; and (d) does phylogenetic relatedness across the studied plant species explain a significant part of the variation in RPE?

Potential causes that modulate the configuration of each fruit's RPE are looked into in detail. Additionally, we explore the influence that fruits phylogenetic relatedness may have, assuming some effect in RPE or its components during the adaptive radiations of seed dispersal mutualisms, especially for the qualitative component. Finally, we propose new applications and further developments of the RPE framework here described.

## 2 | MATERIALS AND METHODS

The rationale for our study includes four steps: (a) selecting a representative sample of frugivore species illustrating both the full

range of body mass and phylogenetic diversity of the Brazilian Southeastern Atlantic forest frugivores, (b) compiling a literature dataset on fruit foraging and usage data for these frugivore species, (c) analysing variation in RPE across selected plant species by building effectiveness landscapes from the frugivore's perspective, and (d) experimentally assessing RPE subcomponents (i.e. fruit pulp digestibility) that refine the estimates of RPE variation among plant species.

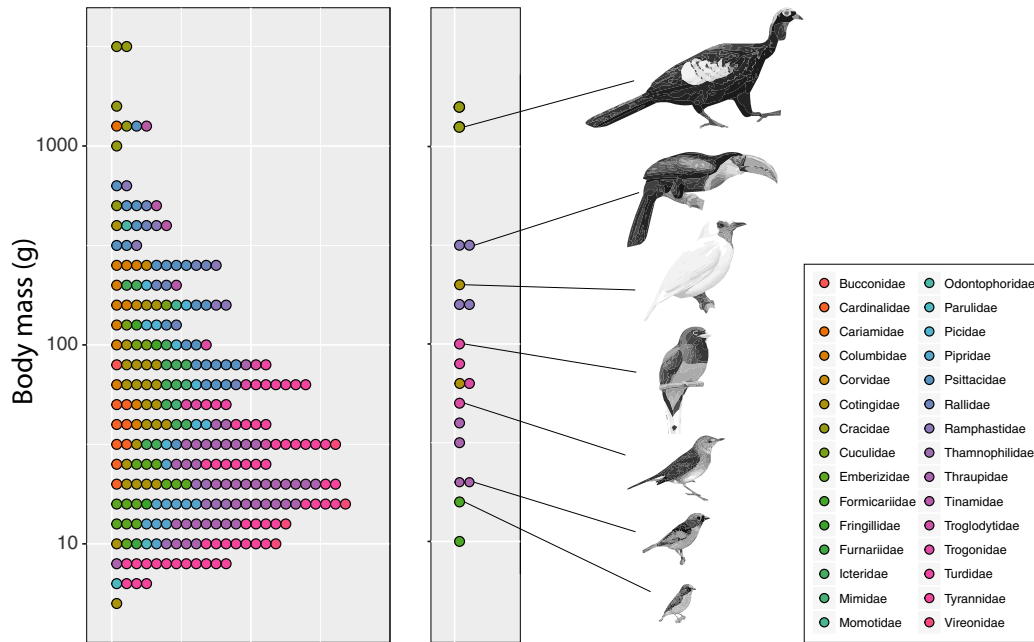
### 2.1 | Species selection

A total of eight different bird families have been selected: Cracidae, Ramphastidae, Trogonidae, Cotingidae, Tityridae, Turdidae, Thraupidae and Fringillidae. Within each family we selected two or more replicate species (we grouped *Tityra cayana* and *Procnias nudicollis*) which were relatively common and had enough information available in published studies. Because the scope of the study was to explore how effective different fruits are for their animal dispersers, we have not considered seed predators such as the Psittacidae family (however see: Blanco et al., 2016; Blanco, Hiraldo, Rojas, Dénes, & Tella, 2015). The resulting 18 species selected for evaluation in this study are located in assorted positions of the whole range of avian body masses present in Brazilian Atlantic rainforest (Figure 2; Table S1). Selected species show a homogenous distribution in terms of body size, higher order taxonomic categories, fruit handling behaviour (e.g. gulping, mashing; Levey, 1987) and seed treatment (ingestion vs. regurgitation).

Fruit species were selected a posteriori, based on the available information for feeding frequency and fruit energy, also looking to exemplify major endozoochorous plant taxa.

### 2.2 | Model details

To estimate the RPE for fruit species consumed by each frugivore species we have defined its two components (Figure 1b): the rate at which the fruits are ingested/handled by the animal (feeding rate) as the quantity component and the energy gained from eating the fruit (fruit energy) as the quality component. The feeding rate is calculated by multiplying the bird visitation frequency to the plant by the number of fruits consumed in each visit; from a frugivore perspective these subcomponents of RPE quantity illustrate potential encounter rates with the fruit resource (visitation) and potential handling/ingestion rates once the fruits are encountered (fruits/visit). Fruit pulp energy yield is assessed using the specific energy (kJ/g) multiplied by the fruit pulp dry mass. Since the nutrient proportional contents of the fruit pulp are calculated based on its dry mass, we use this value as the profitable fruit mass per fruit (Herrera, 1981). Specific energy was quantified using the following energy conversion factors for fruits (FAO, 2002): 14.1 kJ/g for proteins, 35 kJ/g for lipids and 15.1 kJ/g for carbohydrates. Ultimately, by multiplying the two components we



**FIGURE 2** Variation in body mass (g) across the frugivore bird species included in this study. Dots in the left rectangle correspond to all the avian frugivore species present in the Atlantic rainforest; dots in the right rectangle correspond to the 18 selected avian species for analysis of fruit resource-provisioning effectiveness (RPE) of their main fruit-food species. The colours of the dots indicate the family to which the species belongs. The bird pictures illustrate some of the frugivore species selected [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

obtained the total effect value for each specific interaction (RPE; Schupp, 1993; Schupp et al., 2017):

$$RPE_{[g \text{ energy assimilated}]} = \frac{\text{no fruits consumed}}{\text{obs time (hr)}} \times \frac{g \text{ energy accumulated}}{\text{fruit consumed}} \quad (1)$$

Note that the RPE estimate for a given fruit species is specific for its interaction with a frugivore, so we used the average RPE values of a given fruit of all the frugivore species it provides food, to characterize its overall or total effectiveness (RPE<sub>T</sub>):

$$RPE_T = \frac{\sum_{i=1}^N RPE_i}{N} \quad (2)$$

where, for a given focal fruit species, *N* is the number of pairwise interactions with RPE data available and RPE<sub>*i*</sub> is the RPE value for a specific pairwise interaction *i*. Thus, RPE<sub>T</sub> is fruit species-specific, while each pairwise interaction has a specific RPE value (RPE<sub>*i*</sub>) depending on the identity of the specific frugivore partner.

### 2.3 | Data collection

#### 2.3.1 | RPE quantity component

Most of the data used to calculate the quantitative component have been obtained from available bibliographic sources. Data compilation comes from a total of 51 studies and four databases for frugivore-plant interactions from the Brazilian Atlantic Forest (see Data Sources section for a list of data sources used and Figure S1 for a

map of study locations). Variables collected from the bibliography were as follows: number of visits, observation time and number of fruits consumed per visit. To reduce bias we divided the total number of visits to the plants by observation time to control for the different duration of each study. The fruit mass ingested per visit was positively correlated with frugivore body mass (Pearson's correlation  $r = .588, p < .001, n = 541$  distinct pairwise interactions; Figure S2). Fruit mass-body mass correlation allowed the estimation of the number of fruits consumed per visit for avian species with no data on fruit consumption rates available; this was done for special cases when avian species had limited number of records in most studies ( $n = 7$  fruit species for *Aburria jacutinga*,  $n = 2$  fruit species for *Penelope obscura*,  $n = 3$  fruit species for *Procnias nudicollis*).

We have referred to a fruit as all the dispersing and consequently ingested units (i.e. diaspora). Diaspora and fruit are often the same thing; however, in some cases such as *Cabralea canjerana* or *Virola* spp., an aril (i.e. a fleshy covering in some seeds) acts as a diaspore, being smaller than the actual fruit. Therefore, when the diaspore was actually different from the fruit, the energy in the qualitative component has been measured accordingly. In other cases frugivores may peck pieces and ingest just a part of the whole fruit or infructescence (e.g. catkins of *Cecropia* spp. or syconia from *Ficus* spp.). For those large infructescences that birds do not consume whole, we used the number of pecks and assessed the percentage of a single fruit actually consumed, corresponding to a given number of pecks and the beak size of the frugivore. Data on each species' gape size and fruit length (obtained from Bello et al., 2017 and Galetti et al., 2013) allowed us to estimate the total number of pecks needed to consume an infructescence (Table S1).

**TABLE 1** Fruit species mean values for overall quantity component, quality component, RPET and RPE values for frugivore species-specific interactions which include: *Penelope obscura*, *Aburria jacutinga*, *Ramphastos vitellinus*, *Ramphastos dicolorus*, *Selenidera maculirostris*, *Bailloni bailloni*, *Trogon surrucura*, *Trogon viridis*, *Procnias nudicollis*, *Tityra cayana*, *Turdus rufiventris*, *Turdus albicollis*, *Thraupis palmarum*, *Thraupis sayaca*, *Tangara cyanocephala*, *Tangara seledon*, *Euphonia chlorotica* and *Euphonia violacea*

Plant species	Family	n	Quantity C	Quality C	RPE <sub>T</sub>	Cracidae		Ramphastidae			
						<i>P. obs</i>	<i>A. jac</i>	<i>R. vit</i>	<i>R. dic</i>	<i>S. mac</i>	<i>B. bal</i>
<i>Acnistus arborescens</i>	Solanaceae	2	0.83 ± 0.22	0.25	0.16						
<i>Alchornea glandulosa</i>	Euphorbiaceae	12	3.67 ± 1.31	0.50 ± 0.16	1.57						
<i>Alchornea triplinervia</i>	Euphorbiaceae	3	0.54 ± 0.24	1.44	0.76						
<i>Cabralea canjerana</i>	Meliaceae	11	1.53 ± 0.78	10.02 ± 1.02	11.41			31.30	19.97		5.27
<i>Cecropia glaziovii</i>	Urticaceae	24	0.04 ± 0.02	5.08 ± 0.60	0.16		0.09		0.11	0.22	
<i>Cecropia pachystachya</i>	Urticaceae	5	0.01 ± 0.00	5.39 ± 0.62	0.03						
<i>Citharexylum myrianthum</i>	Verbenaceae	7	0.58 ± 0.19	2.08	1.04						
<i>Copaifera langsdorffii</i>	Fabaceae	6	0.38 ± 0.20	1.4 ± 0.46	0.76						
<i>Cupania oblongifolia</i>	Sapindaceae	6	1.78 ± 1.34	3.59 ± 1.08	4.09						
<i>Erythroxylum ambiguum</i>	Erythroxylaceae	5	0.53 ± 0.27	4.29	2.10				0.23		
<i>Eugenia umbelliflora</i>	Myrtaceae	5	0.88 ± 0.45	0.79	0.69						
<i>Eugenia uniflora</i>	Myrtaceae	5	1.81 ± 1.20	6.49 ± 1.28	6.72				0.21		
<i>Euterpe edulis</i>	Arecaceae	84	0.16 ± 0.04	5.18 ± 1.15	0.82	0.40	3.24	0.54	0.22	2.08	1.21
<i>Ficus benamina</i>	Moraceae	2	4.81 ± 3.64	1.19	5.74						
<i>Magnolia ovata</i>	Magnoliaceae	3	1.64 ± 0.51	5.45 ± 0.66	11.08						
<i>Miconia prasina</i>	Melastomataceae	3	2.89 ± 2.76	1.12	2.89						
<i>Miconia pusilliflora</i>	Melastomataceae	1	0.12	0.47	0.06						
<i>Myrsine coriacea</i>	Primulaceae	26	3.05 ± 0.94	0.25 ± 0.07	0.54				0.27		
<i>Myrsine gardneria</i>	Primulaceae	3	0.07 ± 0.04	0.17 ± 0.03	0.02						
<i>Myrsine umbellata</i>	Primulaceae	6	4.74 ± 3.84	0.03 ± 0.01	0.18						
<i>Nectandra megapotamica</i>	Lauraceae	4	3.18 ± 1.97	1.93 ± 0.53	6.13						
<i>Ocotea pulchella</i>	Lauraceae	1	1.91	1.63 ± 0.97	3.11						
<i>Phoradendron affine</i>	Santalaceae	2	36.0 ± 0.32	0.15 ± 0.08	5.53						
<i>Phoradendron crassifolium</i>	Santalaceae	1	3.81	0.15 ± 0.08	0.59						
<i>Phoradendron piperoides</i>	Santalaceae	2	3.60 ± 1.20	0.15 ± 0.08	0.55						
<i>Protium heptaphyllum</i>	Burseraceae	13	1.17 ± 0.34	4.2 ± 1.73	4.33			0.66			
<i>Schefflera morototoni</i>	Araliaceae	7	0.49 ± 0.13	1.88 ± 0.20	1.05			0.88			
<i>Schinus terebinthifolius</i>	Anacardiaceae	13	4.13 ± 1.41	0.02 ± 0.01	0.07						
<i>Sloanea guianensis</i>	Elaeocarpaceae	6	0.24 ± 0.06	2.75 ± 1.31	0.75					0.98	
<i>Sorocea ilicifolia</i>	Moraceae	1	0.40	4.48	1.79						
<i>Tapirira guianensis</i>	Anacardiaceae	7	1.08 ± 0.47	9.44	10.95						
<i>Trema micrantha</i>	Cannabaceae	8	3.42 ± 1.39	0.11 ± 0.03	0.47						
<i>Virola bicuhyba</i>	Myristicaceae	7	0.09 ± 0.04	14.72 ± 0.69	1.31		1.13	0.19		1.15	
<i>Virola oleifera</i>	Myristicaceae	5	0.01 ± 0.00	11.04 ± 0.50	0.09				0.17	0.04	0.08
<i>Virola sebifera</i>	Myristicaceae	5	0.33 ± 0.17	2.54 ± 0.42	0.96						
<i>Vitex polygama</i>	Lamiaceae	1	10.20	0.66	6.71				6.71		

Note: The n column indicates the number of recorded pairwise interactions for each plant species found in literature and used for the calculations.

Trogonidae		Cotingidae	Tityridae	Turdidae		Thraupidae				Fringilidae	
<i>T. sur</i>	<i>T. vir</i>	<i>P. nud</i>	<i>T. cay</i>	<i>T. ruf</i>	<i>T. alb</i>	<i>T. pal</i>	<i>T. say</i>	<i>T. cya</i>	<i>T. sel</i>	<i>E. chl</i>	<i>E. vio</i>
								0.16			
				2.49	1.55	0.73	3.76	0.42	0.49		
0.97				1.19	0.11						
1.37				5.30	5.23						
0.01	0.01		0.02	0.01		0.30	1.34	0.00	0.02	0.01	0.01
						0.03	0.04				
				1.08	1.04		1.61				0.42
				0.35	0.04		1.89				
				17.87	2.05	0.22	0.22			0.06	
				0.72	3.02		4.44				
		0.20		0.66	0.41	0.13	2.04				
				0.65			19.29				
	1.52	0.49	0.03	0.29	0.48			0.04	0.06		
						1.40	10.09				
				8.11			14.06				
						0.13	0.13				8.40
				0.06							
			0.18	2.32	0.44	0.04	0.25	0.68	0.17		
						0.02	0.01				
				0.07	0.61		0.00	0.04			
0.22			0.17	8.09	16.05						
				3.11							
										5.53	
											0.59
										0.74	0.37
		3.47		1.88	0.13	10.86	5.17			6.77	5.67
				0.07	1.68	1.14	1.48				
				0.04	0.07	0.05	0.18	0.01			
			0.20					0.79	0.69		
	1.79										
						8.06	30.01			3.88	1.85
				1.27		0.15	0.31	0.17			
	4.95			0.38	0.96	0.38					
	0.12	0.06									
			0.37	0.86	0.08	2.54					

### 2.3.2 | RPE quality component

All fruit pulp dry masses and nutrient proportions were obtained from available databases (Bello et al., 2017; Jordano, 1995, 2007; M.A. Pizo, unpubl. data). In a few cases, pulp dry mass values were missing; these were estimated using additional species-specific data such as pulp fresh mass or water proportion (six species records imputed in this way; see Table S2). However, when species-specific data were unavailable, we estimated the specific values by averaging the data available for congeneric species. This type of data imputation was done for a few cases and only when essential to retain a given species in the dataset (nine species records were imputed this way; see Table S3).

When calculating specific energy, we preferably used the non-structural carbohydrate content for the carbohydrate value; however, when this information was not available total carbohydrate content or total sugar content was used (see Table S4).

Due to the diverse origin of nutritional data, variation in the techniques and devices used for their analyses is likely. This variation in methods together with the use of different carbohydrate content variables have limitations when comparing energetic values among fruits. We therefore want to highlight these possible limitations and advise to take results cautiously. While the quality component gives us an approximate idea of the nutritional value of each fruit it does not offer a detailed ranking.

A total of 315 different fruit species were reported to be eaten by the frugivore species considered in this study, of which 36 fruits had enough data to calculate the quantity and quality component.

### 2.4 | Model refinement

With the aim of giving a higher resolution to the model, we additionally included bird's fruit pulp digestibility as a subcomponent to the quality component. This gives us additional information on potential nutrient absorption and so energy acquisition, thus refining the estimate of RPE for a given plant species. Unfortunately, very scant information and experimental data are available. To fill this knowledge gap and improve the RPE dataset, we performed feeding experiments with some bird species, and re-calculated the effectiveness for a small subsample of the plant–frugivore interactions (see Supporting Information Supplement 1).

### 2.5 | Data analysis

The data analysis was done using the R statistical environment (R Development Core Team, 2017). All the species nomenclature was checked and corrected with `TAXIZE` R package (Chamberlain et al., 2016) in order to have updated and consistent taxonomic information. Effectiveness landscapes were plotted using the R package `effect.landscape` (Jordano, 2017). The graphs were built for each frugivore species and grouped by family when possible to facilitate

comparisons between similar or congeneric species. A common effectiveness landscape was created using fruit-specific  $RPE_T$  as a general overview of RPE variation for the frugivore assembly.

In order to see if the  $RPE_T$  values of the different fruit species were consistent with  $RPE_i$  (interaction-specific RPE values), we plotted all specific interactions with two or more frugivores species consuming the same fruit ( $RPE_i$ ) against  $RPE_T$ . These excluded six plant species that have data for only one frugivore consuming it. The data were transformed logarithmically to improve normality. To visualize the relationship, we used local polynomial regression and calculated the correlation coefficient as a measure of the strength of the relationship.

Finally, we tested for plant phylogenetic signal in RPE and its components. Phylogenetic signal is the tendency of related species to resemble each other more than randomly selected species from the same phylogenetic tree (Münkemüller et al., 2012). To do this, we calculated three different statistics using the `phylosignal` R package (Keck, Rimet, Bouchez, & Franc, 2016). Abouheif's  $C$ , Blomberg's  $K$  and Pagel's  $\lambda$  are three different indexes used to estimate the phylogenetic signal. While both Blomberg's  $K$  and Pagel's  $\lambda$  assume a Brownian motion to model the evolution (i.e. random drift in speciation), Abouheif's  $C$  is not based in any evolutionary model but in autocorrelation (Münkemüller et al., 2012). Pagel's  $\lambda$  ranges from 0 to 1 and Blomberg's  $K$  from 0 to  $\gg 1$ . In both cases, 0 corresponds to independent trait evolution. For Pagel's  $\lambda$ , 1 indicates trait evolution according to Brownian motion along the phylogeny branches; in the case of Blomberg's  $K$ ,  $K > 1$  indicates higher phylogenetic signal than expected by Brownian motion, while  $K < 1$  suggests less phylogenetic signal than expected from Brownian motion. Abouheif's  $C$ , an autocorrelation index, ranges from 0 to 1, where deviation from zero indicates higher resemblance between traits and the phylogeny. Plant phylogeny was obtained with the web version of package `PhyloMatic` (v. 3.0; Webb & Donoghue, 2005), and branch length computation was done through Grafen method, which is based in simple node distances but not evolutionary time (Grafen, 1989), with R package `PICANTE` (Kembel et al., 2010).

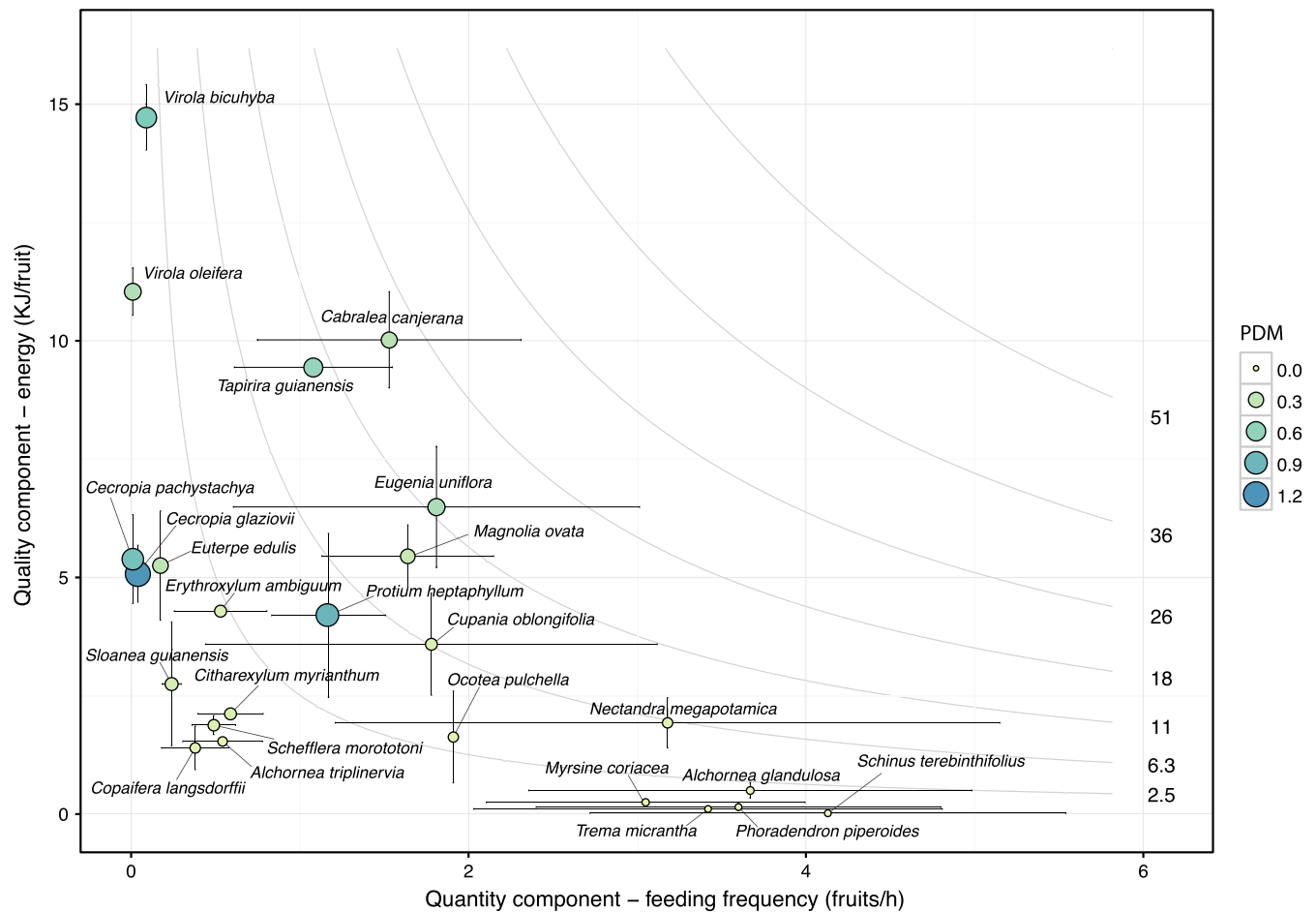
## 3 | RESULTS

### 3.1 | Overview of plant RPE

A total of 147 unique species-specific interactions were found, for which it was possible to calculate RPE values. Table 1 shows the  $RPE_T$  value of each fruiting plant, as well as the specific  $RPE_i$  values for each of the frugivores consuming the same plant species.

The effectiveness landscape for each frugivore species considered in the study can be found in Figure S3. Thrushes, tanagers and toucans were the species that consumed a particularly diversified set of fruit species with a greater fruit size range. Trogons, in contrast, were one of the groups with fewer records. The most complete RPE landscape we could obtain was for *Turdus rufiventris*, with the highest record of interactions reported in the literature ( $n = 23$ , Figure S3.6). *Euterpe edulis* and *Cecropia glaziovii* were





**FIGURE 3** Total resource-provisioning effectiveness ( $RPE_T$ ) landscape of plant taxa for all the avian species considered in the study. Each point corresponds to one fruit species and is located according to its average effectiveness across frugivore species with which it interacts.  $RPE$  is a product of its quantity component (number of consumed fruits per hour) on the X axis and its quality component (energy per fruit in kJ) on the Y axis. Points along the isolines have, by definition, equal  $RPE_T$ ; the numbers on the right of the graph indicate  $RPE_T$  values for the depicted isolines. Horizontal and vertical lines at each point represent  $\pm 1$  SE for the quantity and quality components of  $RPE_T$ . Point size and colour represent the actual energetic mass or pulp dry mass (PDM) of each fruit species [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

the food source that most overlapped in the diet of the species analysed.

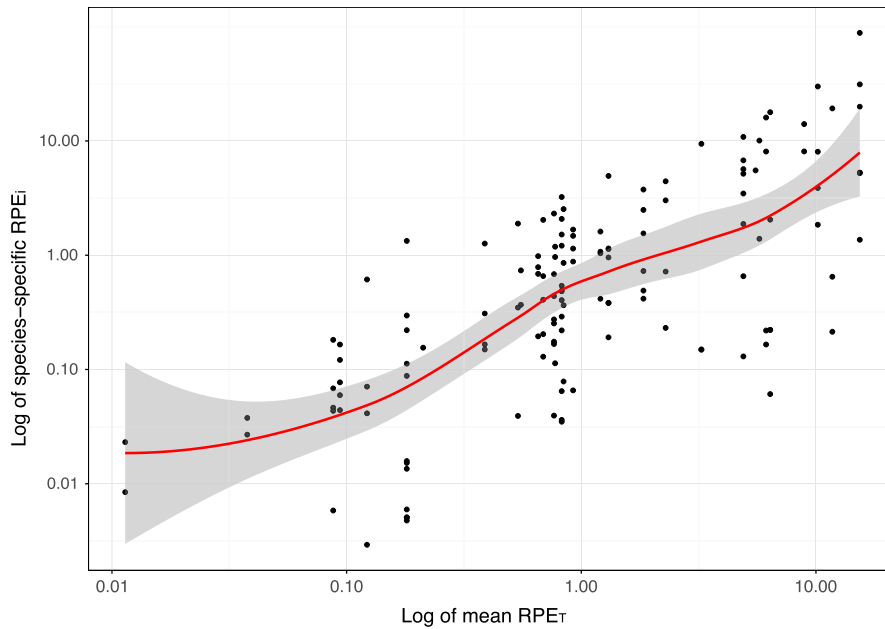
The  $RPE_T$  landscape (Figure 3) combines the information for all the frugivore species into a single graph, pooling the  $RPE_T$  value for each fruit species. If we divide the resulting plot with a diagonal line from the left-top corner to the right-down corner, all the  $RPE$  points remain restricted to the lower left half, this configuration seems to be consistent with the distributional pattern in the individual  $RPE_i$  landscapes (Figure 3; Figure S3). In order to describe the scattering of fruit species, the graph can be divided into four regions. The first region corresponds to those species located in the lower left corner, with very poor effectiveness values because of a low score in both components, such as *Schefflera morototoni*, *Citharexylum myrianthum* or *Copaifera langsdorffii*. Then, a second group of poorly energetic species, but with a high consumption rate, is located in the lower right sector of the landscape (e.g. *Trema micrantha*, *Alchornea glandulosa*, *Schinus terebinthifolius* and *Phoradendron piperoides*). The third group is composed of few species with very high-quality component, such as *Virola bicuhyba*, *Cabralea canjerana* and *Tapirira guianensis*, that are less

frequently consumed, but their quality component greatly increases their effectiveness. Finally, there is a fourth group composed of those species with medium-high pulp energy content that, depending on their consumption frequency, have higher or lower effectiveness. This is the group that shows the greatest variation in both components and is composed of several fruit species such as *Magnolia ovata*, *Eugenia uniflora*, *Cecropia* spp. or *Protium heptaphyllum*.

### 3.2 | Correlates of effectiveness variation in plants

The relation between the  $RPE_i$  values obtained for each frugivore species (i.e. interaction-specific) and the average  $RPE_T$  for each fruit species value showed a positive raw correlation of 0.554 ( $t = 7.85$ ,  $df = 139$ ,  $p < .001$ ) and 0.720 when log-transformed ( $t = 12.21$ ,  $df = 139$ ,  $p < .001$ ; Figure 4). This indicates that there is ample variation in  $RPE_T$  across fruits, and that the differences across the studied plant species (i.e. along the X axis) are not hidden by variation in the mode of interaction with frugivore species that widely differ in the way they





**FIGURE 4** Correlation plot for interaction-specific RPE ( $RPE_i$ ) and total fruit RPE ( $RPE_T$ ). The X axis is represented by the logarithm of the  $RPE_T$ , and the Y axis by the logarithm of frugivore species-specific interaction RPE. The red line shows local fitting and the shaded area a 95% confidence interval of fitted values. Pearson's correlation is  $r = .720$ ,  $p < .001$ ,  $n = 139$  (that comes from leaving out six  $RPE_T$  interactions with just one value) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

	Abouheif's C		Blomberg's K		Pagel's $\lambda$	
	$C_{\text{mean}}$	$p$ -value	K	$p$ -value	Lambda	$p$ -value
Quantity component	0.025	.127	0.085	.379	0.000	1.000
Quality component (fruit energy)	0.191	.052*	0.108	.241	0.232	.154
RPE	0.119	.116	0.092	.416	0.183	.409
Specific energy (kJ/g)	0.385	.001**	0.197	.002**	0.812	.139
Pulp dry mass	0.244	.018*	0.148	.045*	0.024	.906

\* $p \leq .05$ , \*\* $p < .01$ .

use the fruits (variation along the Y axis for each specific value on the X axis). Thus, the resulting  $RPE_i$  is positively related to the  $RPE_T$  that the fruit species has for the whole frugivore assemblage. This reveals that RPE, as defined here, is a characteristic feature of the fruit species, less dependent of the specific frugivore partner it has in a particular pairwise interaction. Yet we must note that our calculation of RPE implicitly assumes that different birds are equally able to extract energy from the same set of fruits, which is not guaranteed (see below).

When total RPE was recalculated using pulp digestibility data ( $RPE_d$ ), all  $RPE_d$  values consistently decreased (Figure S5). We caution about the interpretation of these results and their generalization due to the limited number of species we had available during our experiments. Yet, the limited sample points have a consistent direction for declining RPE when accounting for digestibility constraints.

### 3.3 | Phylogenetic signal of fruit RPE

All three phylogenetic signal statistics for each effectiveness component are presented in Table 2 together with their  $p$ -value (i.e. probability of finding the observed phylogenetic signal under a null model). The

**TABLE 2** Indices for Abouheif's C, Blomberg's K and Pagel's  $\lambda$  phylogenetic effects with their statistical significance ( $p$  value) for the quantity and quality components, resource-provisioning effectiveness (RPE), specific energy and pulp dry mass of 34 fruit species (Figure S4 includes the plant phylogenetic tree used)

quantity component and the  $RPE_T$  showed low values for phylogenetic signal (Table 2; see Figure S4 for the phylogenetic tree used). This suggests that fruit consumption frequency as well as fruit RPE do not appear to be marked with a significant phylogenetic signal across the set of taxa and species analysed. Fruit-specific energy instead showed significant phylogenetic signal for Abouheif's and Blomberg's indices, and the quality component and pulp dry mass were marginally significant for Abouheif's C. Overall, these results indicate that RPE values of closely related species are no more similar to each other than when compared with randomly selected species of the phylogenetic tree. However, fruit-specific energy appears influenced by the plant phylogeny, with significant—but reduced—phylogenetic signal values, implying closely related plant species showing more similar specific energy than expected for random comparisons.

## 4 | DISCUSSION

### 4.1 | Resource-provisioning effectiveness framework: A 'zoocentric' approach

The utility of the RPE landscape lies in providing a quantitative tool to assess how efficient fleshy-fruited plants are in providing

food resources to a diverse coterie of frugivores (Wheelwright & Orians, 1982). In general, the most energetically rich species fell in low positions on the quantity component axis, while the species with a lower energetic value reached the highest ranks on this quantity component. This energy-rich little-consumed pattern is mostly explained by fruit size and crop size, since bigger fruits tend to be less abundant and offer more food quantity and so take longer to process, causing lower total consumption in comparison to small fruits. Also, physiological constraints likely explain this pattern (Levey & Martínez del Rio, 2001), namely, energetically rich fruits are often lipid-rich ones, and lipids take longer than sugars to be metabolized and absorbed. Thus, birds that often ingest lipid-rich fruits cannot take many fruits at once (limited QTY component) simply because the gut takes longer to be emptied. Thus, the RPE landscape shows a well-documented gradient of fruit profitability for avian frugivores (Howe & Estabrook, 1977; McKey, 1975; Snow, 1971). Yet the RPE landscape informs about how subtle variations in these components may or may not determine major shifts to higher RPE in a particular fruit–bird interaction. While aspects of the quality component appear more fixed (i.e. constrained by digestibility or the species-specific nutrient combination in the pulp), those of the quantity appear more labile, related to for example variations in fruit supply that influence visitation and foraging rate. Our results show a covariation pattern across fruit species in RPE that modulates the outcomes of fruit–bird interactions along two directions. First, some fruit species appear more effective by representing a readily accessible food resource, allowing high visitation and high feeding rates, even with marginal quality in terms of gross energy assimilation. In contrast, some fruit species rely on lower consumption rates yet with higher per-interaction profitability. Most fruit species appear constrained to either trend, with no instances of simultaneously high-quantity and high-quality profitability.

The resulting effectiveness landscape (Figure 3) suggests that, as the quality component of a fruit impoverishes, the quantity component, related to frequency of consumption, has a wider margin to increase. Note that variation along the quantity X axis of the RPE landscape is influenced by fruit-use variables, directly related to the specific frugivore species; while the quality component is more related to intrinsic properties of the fruit pulp. Thus, there is more room for ecological factors (i.e. local abundance, visitation rate, importance of non-fruit food in the diet) to modulate variation along the X axis for the outcome of a particular bird–fruit interaction. Yet, the ‘opportunities’ for increases in the quantity component appear to be constrained by factors that prevent rich fruits from having higher consumption frequencies, as for example fruit size. The lack of data points in the upper right sector of the RPE landscape suggests constraints for any fruit species to move upwards along both axes. This pattern appears to reflect early proposals of two basic strategies in fleshy-fruited plants which, at their extremes, have generalized and specialized forms of interaction with avian frugivores (i.e. The Paradigm, Howe, 1993; Howe & Estabrook, 1977; McKey, 1975; Snow, 1971).

As suggested by Howe (1993), seed dispersal systems of fleshy-fruited plant species could be classified into two distinct groups depending on their fruiting strategy, that he called ‘The Paradigm’. The first group of plants would produce highly nutritious large fruits in small quantities and dispersed by specialized frugivores; while the second group would be integrated by plants that produce very abundant but small and poorly nutritious fruits that would be dispersed by opportunistic frugivores. The distribution pattern of fruit species across the RPE landscape partly supports this early paradigm of a dichotomy in fleshy-fruited plants. The highest-quality fruits are usually lipid-rich, large fruits that, by being large, are necessarily eaten in small quantities (with additional digestibility constraints, Levey & Martínez del Rio, 2001), while some of the lowest quality fruits are consumed with the highest frequency. Our RPE landscape results agree with The Paradigm if visitation frequency was only limited by the plant’s fruit production capacity. For example, some species like *Virola* spp., *Cabralea canjerana*, *Magnolia ovata* have low fecundities and high-quality, while *Trema micrantha*, *Schinus terebinthifolius* or *Alchornea glandulosa* have high fecundities and low-quality (see e.g. Pizo, 1997 for *Cabralea*; Cazetta, Schaefer, & Galetti, 2008 for *Schinus*). However, some of our results do not support The Paradigm. First is that our study assemblage is mainly composed by frugivores with a strong reliance on fruit food and less so by opportunistic species; only thruses, tityrids and tanangers may depend on other food resources, yet they are still much more dependent on fruits than more opportunistic species like the tyrannids or finches (Wilman et al., 2014). Second, we still have a bottom-left region in the effectiveness landscape (Figure 3) of medium-poor quality and barely consumed fruits that are not explained by the paradigm. The plants with these characteristics fall in between the two extremes, forming a cloud of plant species with varied dispersal strategies (also see Rother et al., 2016 for analysis of the quantity component of SDE).

#### 4.2 | Factors influencing RPE variability

Several factors shape and influence the outcomes of seed dispersal interactions (Schupp, Jordano, & Gómez, 2010). These factors can be categorized into following three types: morphological constraints such as beak–fruit size matching, manipulation effort, fruit position and accessibility; chemical constraints such as pulp nutrient composition, secondary compounds and physiological limitations; and context-dependent factors that comprise spatial, temporal and community-composition scenarios. While some of the effects may affect the quantity component (mainly fruit size and the context-dependent factors), those more related to intrinsic characteristics of the fruit affect the quality component can also affect both RPE components synergistically.

Morphological traits such as fruit and seed size affect fruits’ RPE. The ability to efficiently consume and disperse large-seeded species is usually restricted to the large-bodied disperser species (Galetti et al., 2013; Jordano, 2013; Levey, 1987). Thus, fruit and seed size

act as a primary filter for dispersers, yet avian species are also capable of consuming bigger fruits than their gape size by plucking on its pulp, known as mashers (Levey, 1987). This explains why in our study we have recorded many frugivores consuming bigger seeds than the gape sizes, for example *Thraupis* spp. feeding on *Virola* fruits and *Euphonia* spp. on *Protium heptaphyllum*. Furthermore, other factors such as fruit protection and accessibility may also act as deterrents for fruit consumption by some avian species (Denslow & Moermond, 1982; Pratt & Stiles, 1985).

Nutrient composition is variable among fruit species, and this triggers frugivore preferences for specific fruit nutritional contents (Cazetta, Galetti, Rezende, & Schaefer, 2012; Jordano, 2013). Lipids are one of the most variable nutrients in fruit pulp (Moermond & Denslow, 1985; Stiles, 1993), and are known to covary negatively with carbohydrate content (Herrera, 1987; Jordano, 1995, 2013; Valido, Schaefer, & Jordano, 2011; Witmer & Van Soest, 1998). Birds that mix their diets with insect and other lipid-rich sources have a better facility to absorb and assimilate lipid-rich fruits (White & Stiles, 1990); therefore, they prefer these fruit types. In contrast, strictly frugivorous species seem to prefer carbohydrate-rich fruit species with high watery content that acts as nutrient solvent and facilitates assimilation (Levey & Martínez del Río, 2001). We expect that many of the instances of low RPE scoring in the bottom-left corner of the RPE landscape are thus associated with partial or sporadic consumption of fruits by avian species with mixed diets. Yet low RPE values for a particular fruit may be also due to those instances of size misfitting or fruit-use yielding suboptimal foraging conditions for the frugivores (i.e. 'pulp theft', accessibility constraints, etc.).

Highly frugivorous species also tend to complement their diet with different fruit species to balance the nutrient intake (Jordano, 1987, 1988; Levey & Karasov, 1989; Witmer & Van Soest, 1998). Secondary metabolites are tightly related in frugivore-fruit interactions. These compounds have been proposed to be involved in several frugivory processes, acting as attractors, repulsors, mediators in gut retention time or intoxicators (Cipollini & Levey, 1997; Herrera, 1982). Regardless of the reason, secondary compounds in the pulp are believed to limit fruit ingestion through deterrent means (Izhaki & Safriel, 1989; Jordano, 2013). These negative effects of secondary compounds could explain why highly nutritious fruits are consumed less frequently. Following this proposition, it would be interesting to see the relation between energetic content or fruit size with secondary metabolites. Our RPE model also serves as a basis to test hypotheses based on differential preferences of frugivores and test if variable consumption rates of the same fruits are related to different nutrient composition or variable tolerance to secondary compounds. We expect heavily defended fruits to lie on the left sector of the RPE landscape due to a 'minoring' consumption pattern by frugivores (Jordano, 1988; Snow & Snow, 1988), with reduced but consistent consumption of small amounts of pulp in the frugivore's diet. This is a consumption pattern expected for fruit species contributing specific micronutrients or elements to the frugivore's diet (Jordano, 1988), in which case the location on the RPE landscape would be at the left-bottom corner.

In the Supporting Information we have shown how to improve RPE, including a preliminary analysis using fruit digestibility to refine the quality component. All individual pairwise interactions showed RPE values affected to variable extents when assessing digestibility. The energy assimilation measures used must be interpreted cautiously because digestive efficiency may depend on several factors such as gut transit time, food ingestion rate or differential enzymatic activities (Karasov, 1990; Levey & Martínez del Río, 2001; Worthington, 1989). However, despite the data used being limited, with these preliminary analyses we highlight the importance of including digestibility assimilation in RPE models. Their inclusion in effectiveness landscapes can re-scale the quality component for the different fruits and may facilitate the understanding of specific frugivore preferences. A deeper exploration of digestibility capabilities would be required to look at intraspecific variation among fruit species and the foraging ecology of the frugivore consumers.

### 4.3 | Phylogenetic trends in RPE

So far, differences in fruit effectiveness have proven to be more related to intrinsic characteristics of the fruit itself than to those of the frugivore consuming it, and the correlation result between  $RPE_T$  and frugivore-specific RPE supports this. A species-specific signal in RPE variation suggests a sizeable phylogenetic component of variation, so that closely related fruit species tend to show similar values, irrespective of the specific interactions with frugivores. However, our analysis revealed that only the subcomponent 'fruit-specific energy' had significant phylogenetic signal, this being consistent with results previously reported in comparative analyses (Cazetta et al., 2012; Jordano, 1995; Valido et al., 2011). Despite the imprecise branch length calculation method and the reduced sample of phylogenetic diversity of fruits, our results suggest that the sampling has been adequate, reflecting reasonably well the existing phylogenetic diversity of the Atlantic rainforest fleshy-fruited species. The missing phylogenetic signal in RPET probably emerges from extreme variation in the quantity component that is dependent on, for example local variation in interaction frequency; just this effect might be blurring any phylogenetic imprint of the quality component (Carnicer, Jordano, & Melian, 2009).

Most seed dispersal systems are usually generalized and asymmetric, that is most species are visited by several frugivores (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007; Howe, 2016; but see Guaraldo, Boeni, & Pizo, 2013). Several constraints operating against tight coevolution of high specificity have been already discussed in diverse studies (Herrera, 1986; Jordano, 1995; Wheelwright & Orians, 1982). Our results support the existence of phylogenetic constraints due to just pulp energy content that may limit among-species variation in RPE. Yet, the effect of interaction with a highly diversified frugivore assemblage appears to release these constraints and result in RPE variation not closely tied to the patterns of shared ancestry. Despite

phylogenetic constraints, RPE has an ample margin for fruit effectiveness to independently vary in seed dispersal systems. This might explain the ample scatter of RPE values among frugivores, even for the same fruit species. In addition, this is consistent with the frequent field observation of weak pairwise interactions, where RPE values for the frugivore do not match the resulting SDE values for the plant (Jordano, 2013).

#### 4.4 | Future perspectives

A potentially interesting field to be explored is the arrangement of the RPE landscape along a time window, that is, to test how changes in fruiting phenology affect the effectiveness of specific frugivores or the combinations of RPE values that occur seasonally. Because fruit availability determines shifts in frugivore diet (Loiselle & Blake, 1999) it is expected that fruit effectiveness will vary too. Using RPE landscapes will allow the visualization of seasonal changes in distributional patterns of fruit effectiveness (see Culot, Huynen, & Heymann, 2015; Pizo & Camargo, 2018).

Comparisons not only need to be performed from the 'zoocentric' point of view. A further ambitious objective is the comparison of RPE landscapes with SDE landscapes (Schupp et al., 2017). By looking at both mutualistic approaches we can better understand the dependencies and the tightness of fruit-frugivore links within multispecies mutualistic networks. Finally, RPEs can be applied in decision-making for conservation purposes, helping to develop more complete management strategies by identifying core groups of plant species within diversified plant-frugivore assemblages.

## 5 | CONCLUSIONS

The RPE model has been shown to be a useful tool for understanding the overlooked frugivore perspective in analyses of SDE, significantly expanding the conceptual breadth of the SDE framework (Schupp et al., 2017). Our study provides a preliminary foundation for future studies trying to address similar questions. The approach also offers the possibility to better understand the ecological fundamentals that generate mutual dependence between species partners, as well as the stability and maintenance of their interactions in time.

#### ACKNOWLEDGEMENTS

We are indebted to Mauro Galetti for useful and thoughtful discussion at different stages of this manuscript and help with logistic support during field work. We thank the Piracicaba Zoo for allowing us to work in their facilities. Comments and suggestions by Francisco Rodríguez-Sánchez, Antônio Fontanella, Carolina Bello, Carolina Carvalho, and Miguel Jácome were most helpful for improving the manuscript. The final manuscript was greatly improved by comments from Jörg Albrecht and two anonymous reviewers. E.Q. was funded by MSc grant from Tropimundo (European Commission)

and received the support of a fellowship from 'la Caixa' Foundation (ID LCF/BQ/DE18/11670007). P.J. was supported by a Junta de Andalucía Excellence Grant (RNM-5731), as well as grant CGL2017-82847-P from Agencia Estatal de Investigación, Ministerio de Ciencia, Innovación y Universidades and FEDER UE funding. M.A.P. was supported by a research grant from the Brazilian Research Council (CNPq).

#### AUTHORS' CONTRIBUTIONS

E.Q., M.A.P. and P.J. designed the study; E.Q. did the experimental work; E.Q. and P.J. carried out the data compilation and statistical analyses, and M.A.P. contributed to data compilation; all the three authors contributed to writing the paper and its final editing.

#### DATA AVAILABILITY STATEMENT

The data used in this article are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pk0p2ngj7> (Jordano, Quintero, & Pizo, 2020) and in our GitHub repository: [https://github.com/PJordano-Lab/MS\\_JEcol\\_Resource-provisioning-effectiveness](https://github.com/PJordano-Lab/MS_JEcol_Resource-provisioning-effectiveness).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Quintero E, Pizo MA, Jordano P. Fruit resource provisioning for avian frugivores: The overlooked side of effectiveness in seed dispersal mutualisms. *J Ecol*. 2020;108:1358–1372. <https://doi.org/10.1111/1365-2745.13352>



**Table S1.** List of bird species studied, taxonomic affiliation, size, body mass and gape size (Data source: Bello et al., 2017).

Species	Family	Common name	Size	Body mass (g)	Gape size(mm)
<i>Penelope obscura</i>	Cracidae	Dusky-legged Guan	Large	1770.00	22.35
<i>Aburria jacutinga</i>	Cracidae	Jacutinga	Large	1250.00	19.12
<i>Ramphastos vitellinus</i>	Ramphastidae	Channel-billed toucan	Large	343.50	30.11
<i>Ramphastos dicolorus</i>	Ramphastidae	Green-billed toucan	Large	331.00	30.10
<i>Procnias nudicollis</i>	Cotingidae	Bare-throated bellbird	Medium	200.00	23.61
<i>Selenidera maculirostris</i>	Ramphastidae	Spot-billed toucanet	Medium	164.00	25.04
<i>Bailloniuss bailloni</i>	Ramphastidae	Saffron toucanet	Medium	146.00	23.60
<i>Trogon viridis</i>	Trogonidae	Green-backed trogon	Medium	89.70	20.49
<i>Trogon surrucura</i>	Trogonidae	Surucua trogon	Medium	73.30	17.52
<i>Turdus rufiventris</i>	Turdidae	Rufous-bellied thrush	Small	69.50	13.25
<i>Tityra cayana</i>	Tityridae	Black-tailed tytyra	Small	68.10	16.57
<i>Turdus albicollis</i>	Turdidae	White-necked thrush	Small	54.00	11.15
<i>Thraupis palmarum</i>	Thraupidae	Palm tanager	Small	39.00	8.28
<i>Thraupis sayaca</i>	Thraupidae	Sayaca tanager	Small	32.50	8.92
<i>Tangara seledon</i>	Thraupidae	Green-headed tanager	Small	18.70	6.12
<i>Tangara cyanocephala</i>	Thraupidae	Red-necked tanager	Small	18.00	5.17
<i>Euphonia violacea</i>	Fringillidae	Euphonia violacea	Small	15.00	6.92
<i>Euphonia chlorotica</i>	Fringillidae	Purple-throated euphonia	Small	11.00	6.15

**Table S2.** List of the six plant species where the Pulp Dry Mass values (grams) were estimated using species-specific data, where FFM is Fruit Fresh Mass in g, pPFM is the proportion of pulp fresh mass, w% indicates water percentage of the fruit and SFM is the Seed Fresh Mass. Multiplication sign is represented as 'x'.

<b>Plant species</b>	<b>Value (g)</b>	<b>Calculation method</b>
<i>Acnistus arborescens</i>	0.026	FFM x pPFM x (1-w%)
<i>Alchornea glandulosa</i>	0.018	PFM x (1-w%)
<i>Citharexylum myrianthum</i>	0.133	PFM x (1-w%)
<i>Copaifera langsdorffii</i>	0.081	FFM x pPFM x (1-w%)
<i>Cupania oblongifolia</i>	0.132	(FFM-SFM) x (1-w%)
<i>Virola oleifera</i>	0.407	PFM x (1-w%)

**Table S3.** List of data imputed for 9 plant species using congeners data. Where pPFM is the proportion of Pulp Fresh Mass, pPDM is the proportion of Pulp Dry Mass, pPROT is proportion of Protein content, pNSC is the proportion of Non-Structural Carbohydrates, PDM is the Pulp Dry Mass (g) and Energy is the specific energy given in kJ g<sup>-1</sup>.

Plant species	Data imputed	Value	Congener species used
<i>Alchornea triplinervia</i>	pPFM	0.381	<i>Alchornea glandulosa</i>
<i>Cecropia glaziovii</i>	pPDM	0.080	<i>Cecropia pachystachia</i>
<i>Sloanea guinaensis</i>	pPDM	0.610	<i>Sloanea monosperma</i>
<i>Myrsine coriacea</i>	pPROT	0.046 ± 0.012	Mean of 5 <i>Myrsine</i> spp ( <i>gardneriana</i> , <i>parviflora</i> , <i>rubra</i> , <i>umbellata</i> , <i>venosa</i> )
<i>Nectandra megapotamica</i>	pNSC	0.199 ± 0.058	Mean of 4 <i>Nectandra</i> spp. ( <i> davidsoniana</i> , <i>gentlei</i> , <i>hypoglauca</i> , <i>salicina</i> )
<i>Phoradendron affine</i>	PDM	0.007 ± 0.004	Mean of 3 <i>Phoradendron</i> spp ( <i>hexastichum</i> , <i>inaequidentatum</i> , <i>robustissimum</i> )
	Energy	21.045 ± 2.729	Mean of 4 <i>Phoradendron</i> spp. ( <i>californicum</i> , <i>jenmanii</i> , <i>serotimun</i> , <i>sp1.</i> )
<i>Phoradendron crassifolium</i>	PDM	0.007 ± 0.004	Mean of 3 <i>Phoradendron</i> spp ( <i>hexastichum</i> , <i>inaequidentatum</i> , <i>robustissimum</i> )
	Energy	21.045 ± 2.729	Mean of 4 <i>Phoradendron</i> spp. ( <i>californicum</i> , <i>jenmanii</i> , <i>serotimun</i> , <i>sp1.</i> )
<i>Phoradendron piperoides</i>	PDM	0.007 ± 0.004	Mean of 3 <i>Phoradendron</i> spp ( <i>hexastichum</i> , <i>inaequidentatum</i> , <i>robustissimum</i> )
	Energy	21.045 ± 2.729	Mean of 4 <i>Phoradendron</i> spp. ( <i>californicum</i> , <i>jenmanii</i> , <i>serotimun</i> , <i>sp1.</i> )
<i>Miconia prasina</i>	pPDM	0.067 ± 0.079	Mean of 17 <i>Miconia</i> spp ( <i>valtheri</i> , <i>tristis</i> , <i>theaezans</i> , <i>sellowiana</i> , <i>rigidiuscula</i> , <i>racemifera</i> , <i>pusilliflora</i> , <i>latecrenata</i> , <i>incospicua</i> , <i>doriana</i> , <i>discolor</i> , <i>cubatanensis</i> , <i>cabucu</i> , <i>budlejoides</i> , <i>bipulifera</i> , <i>sp1.</i> <i>sp2.</i> )
	pNSC	0.744 ± 0.070	Mean of 2 <i>Miconia</i> spp ( <i>bipulifera</i> and <i>sp1.</i> )

**Table S4.** List of plant species indicating the Carbohydrates measurement that was used to calculate the fruit Specific Energy. Where NSC is the proportion of Non-Structural Carbohydrates, TC is the proportion of Total Carbohydrates and TSUG is the proportion of Total Sugar.

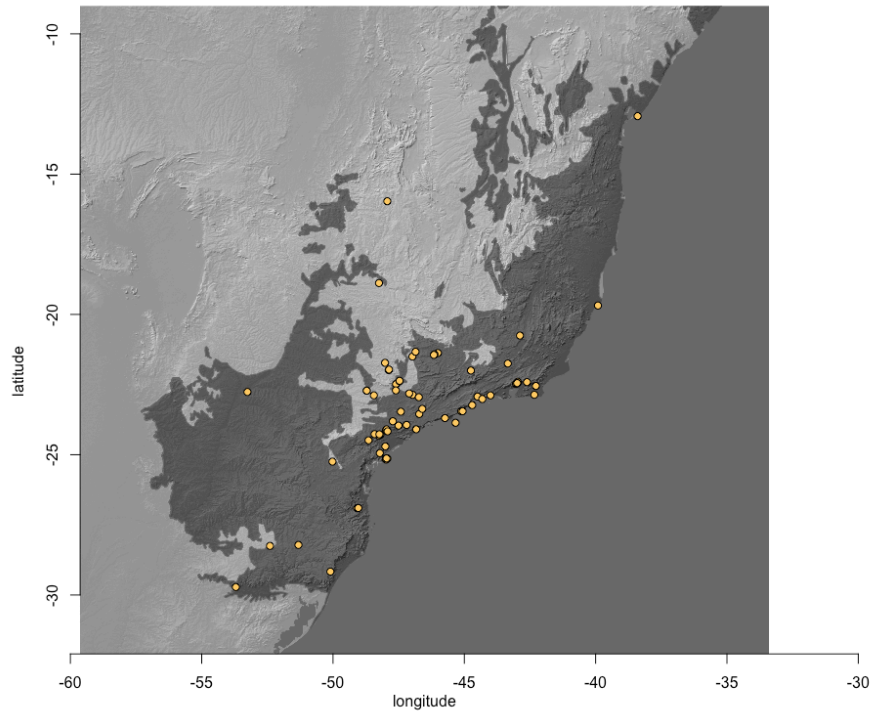
<b>Plant species</b>	<b>Family</b>	<b>Carbohydrates value used</b>
<i>Acnistus arborescens</i>	Solanaceae	NSC
<i>Eugenia uniflora</i>	Myrtaceae	NSC
<i>Ficus benjamina</i>	Moraceae	NSC
<i>Miconia prasina</i>	Melastomataceae	NSC
<i>Nectandra megapotamica</i>	Lauraceae	NSC
<i>Schefflera morototoni</i>	Araliaceae	NSC
<i>Tapirira guianensis</i>	Anacardiaceae	NSC
<i>Virola sebifera</i>	Myristicaceae	NSC
<i>Phoradendron affine</i>	Santalaceae	NSC
<i>Phoradendron crassifolium</i>	Santalaceae	NSC
<i>Phoradendron piperoides</i>	Santalaceae	NSC
<i>Alchornea glandulosa</i>	Euphorbiaceae	TC
<i>Alchornea triplinervia</i>	Euphorbiaceae	TC
<i>Cabralea canjerana</i>	Meliaceae	TC
<i>Cecropia pachystachya</i>	Urticaceae	TC
<i>Citharexylum myrianthum</i>	Verbenaceae	TC
<i>Copaifera langsdorffii</i>	Fabaceae	TC
<i>Cupania oblongifolia</i>	Sapindaceae	TC
<i>Erythroxylum ambiguum</i>	Erythroxylaceae	TC
<i>Euterpe edulis</i>	Arecaceae	TC
<i>Sloanea guianensis</i>	Elaeocarpaceae	TC
<i>Sorocea ilicifolia</i>	Moraceae	TC
<i>Virola oleifera</i>	Myristicaceae	TC
<i>Cecropia glaziovii</i>	Urticaceae	TSUG
<i>Eugenia umbelliflora</i>	Myrtaceae	TSUG
<i>Magnolia ovata</i>	Magnoliaceae	TSUG
<i>Miconia pusilliflora</i>	Melastomataceae	TSUG
<i>Myrsine coriacea</i>	Primulaceae	TSUG
<i>Myrsine gardneria</i>	Primulaceae	TSUG
<i>Myrsine umbellata</i>	Primulaceae	TSUG
<i>Ocotea pulchella</i>	Lauraceae	TSUG
<i>Protium heptaphyllum</i>	Burseraceae	TSUG
<i>Schinus terebinthifolius</i>	Anacardiaceae	TSUG
<i>Trema micrantha</i>	Cannabaceae	TSUG
<i>Virola bicuhyba</i>	Myristicaceae	TSUG
<i>Vitex polygama</i>	Lamiaceae	TSUG

**Table S5.** Experimental digestibility results for the 4 bird species studied. Columns show bird and plant species used, apparent digestibility mean values ( $\pm 1SE$ ), the number of digestibility replicate estimates (n), the energy per fruit in KJ, the quantity component, the quality component (defined as Energy x Digestibility), RPE (RPE= Quantity Component x Energy) and the RPE<sub>d</sub> value including digestibility estimates (RPE<sub>d</sub>= Quantity Component x Quality Component).

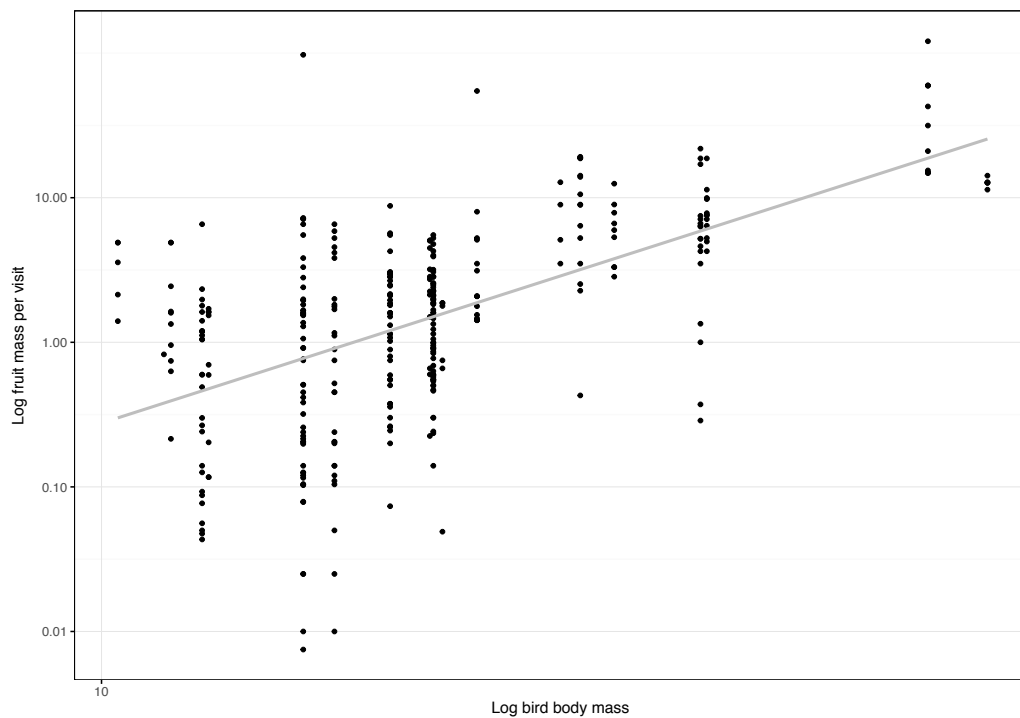
Frugivore species	Fruit consumed	n	Digestibility	Energy	Quality C	Quantity C	RPE	RPE <sub>d</sub>
<i>Ramphastos dicolorus</i>	<i>Cecropia glaziovii</i>	5	0.18 $\pm$ 0.06	5.08	0.93 $\pm$ 0.29	0.022 $\pm$ 0.021	0.11	0.02
<i>Ramphastos toco</i>	<i>Euterpe edulis</i>	9	0.31 $\pm$ 0.09	5.18	1.62 $\pm$ 0.43	0.043 $\pm$ 0.010	0.22	0.07
<i>Thraupis sayaca</i>	<i>Trema micrantha</i>	2	0.70 $\pm$ 0.07	0.11	0.08 $\pm$ 0.01	2.725 $\pm$ 2.267	0.31	0.22
<i>Turdus leucomelas</i>	<i>Trema micrantha</i>	3	0.60 $\pm$ 0.09	0.11	0.07 $\pm$ 0.01	11.15	1.27	0.76

## SUPPLEMENTARY MATERIAL

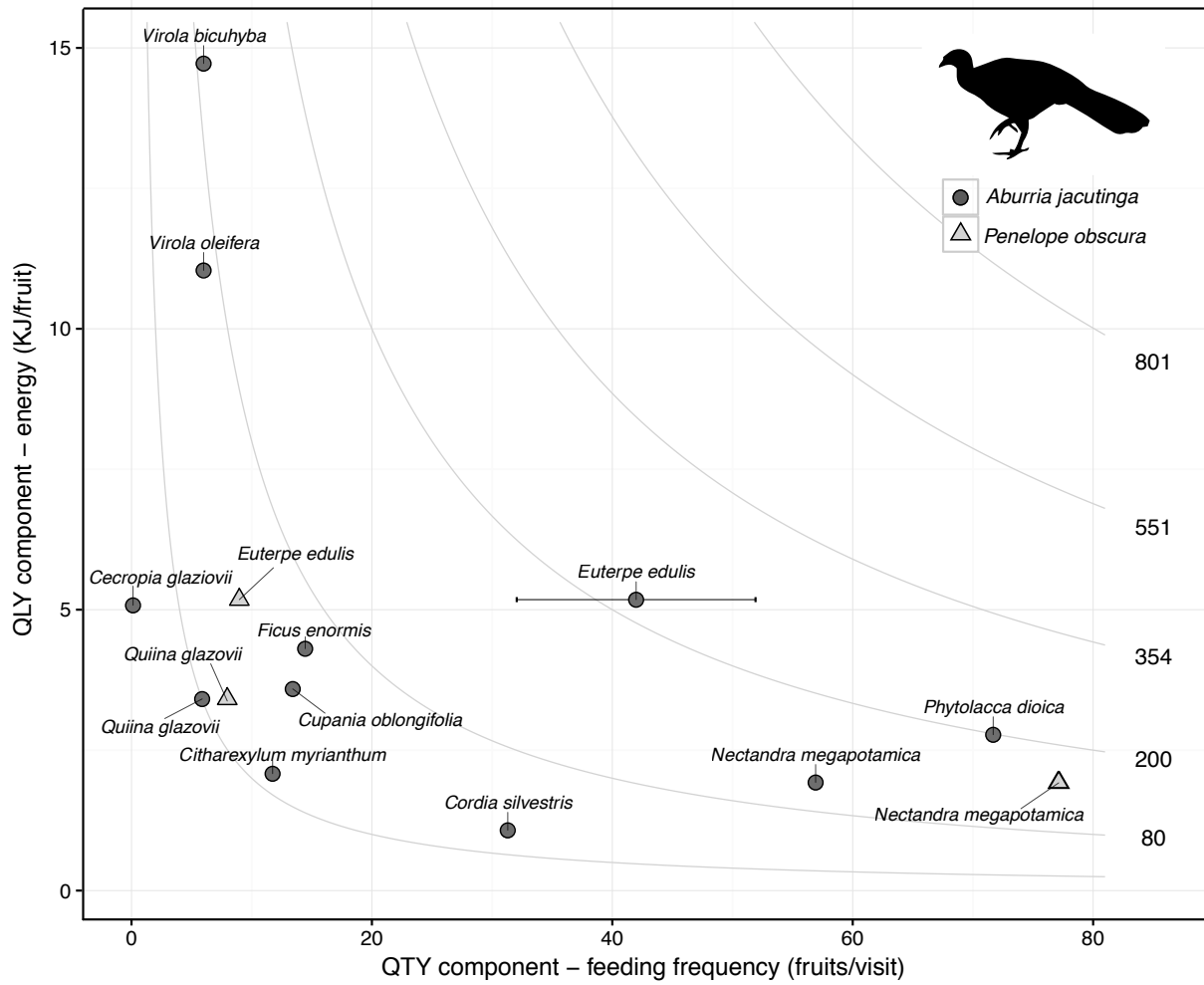
**Figure S1.** Map of Brazil indicating with yellow dots the location of the study sites from the bibliography. The Atlantic rainforest biome distribution is represented by the shadowed area.



**Figure S2.** Correlation plot of avian body mass and fruit mass ingested per visit for 541 observed interactions. Both variables log-transformed. Pearson's correlation is 0.588,  $df=354$ ,  $n = 18$  frugivore species.

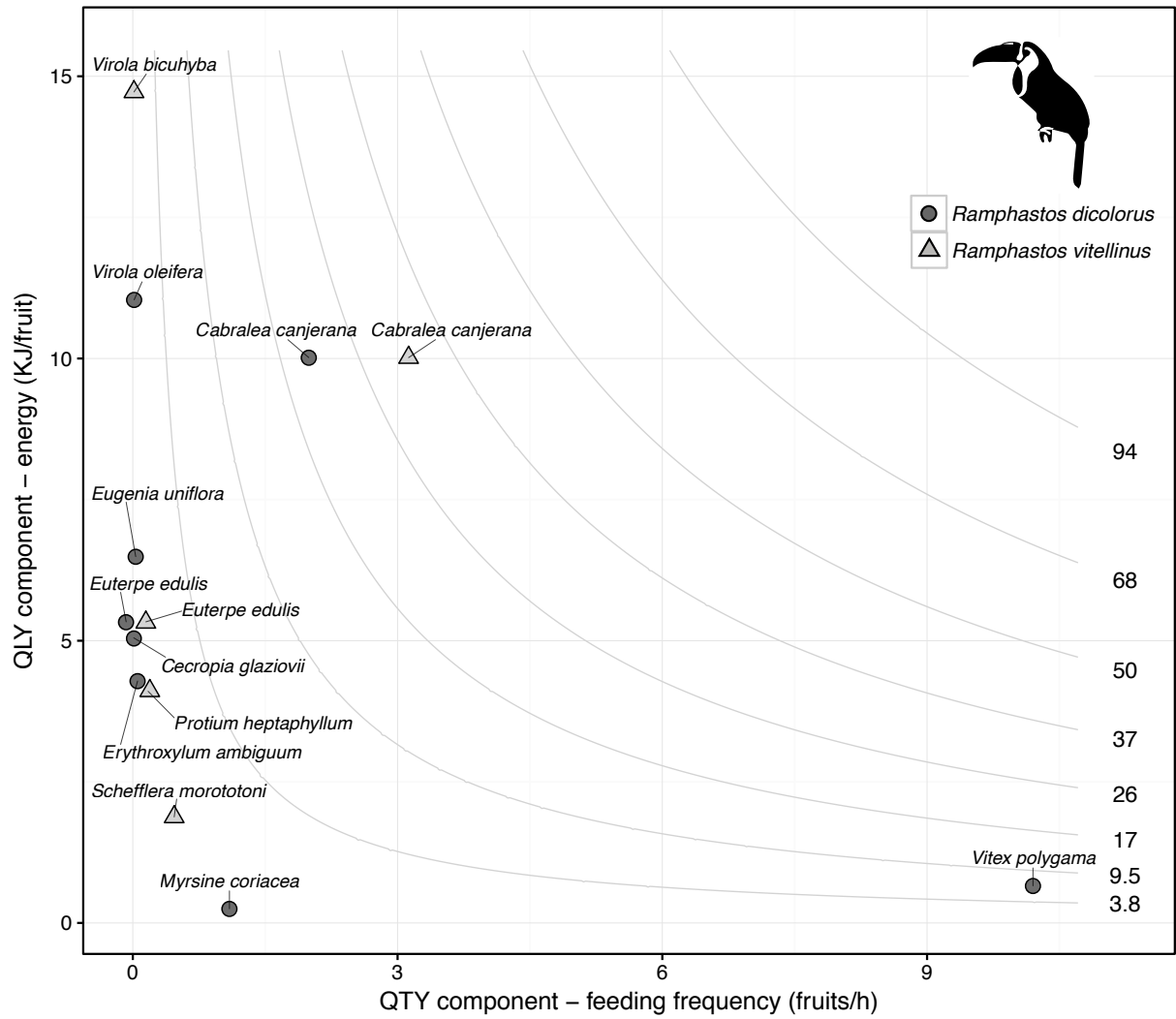


**Figure S3.1.** RPE landscape for Cracidae species: *Aburria jacutinga* and *Penelope obscura*. In order to avoid losing information for Cracidae species, it is the only case for which we created an effectiveness landscape using the estimated number of fruits per visit as the only subcomponent in the quantity axis.

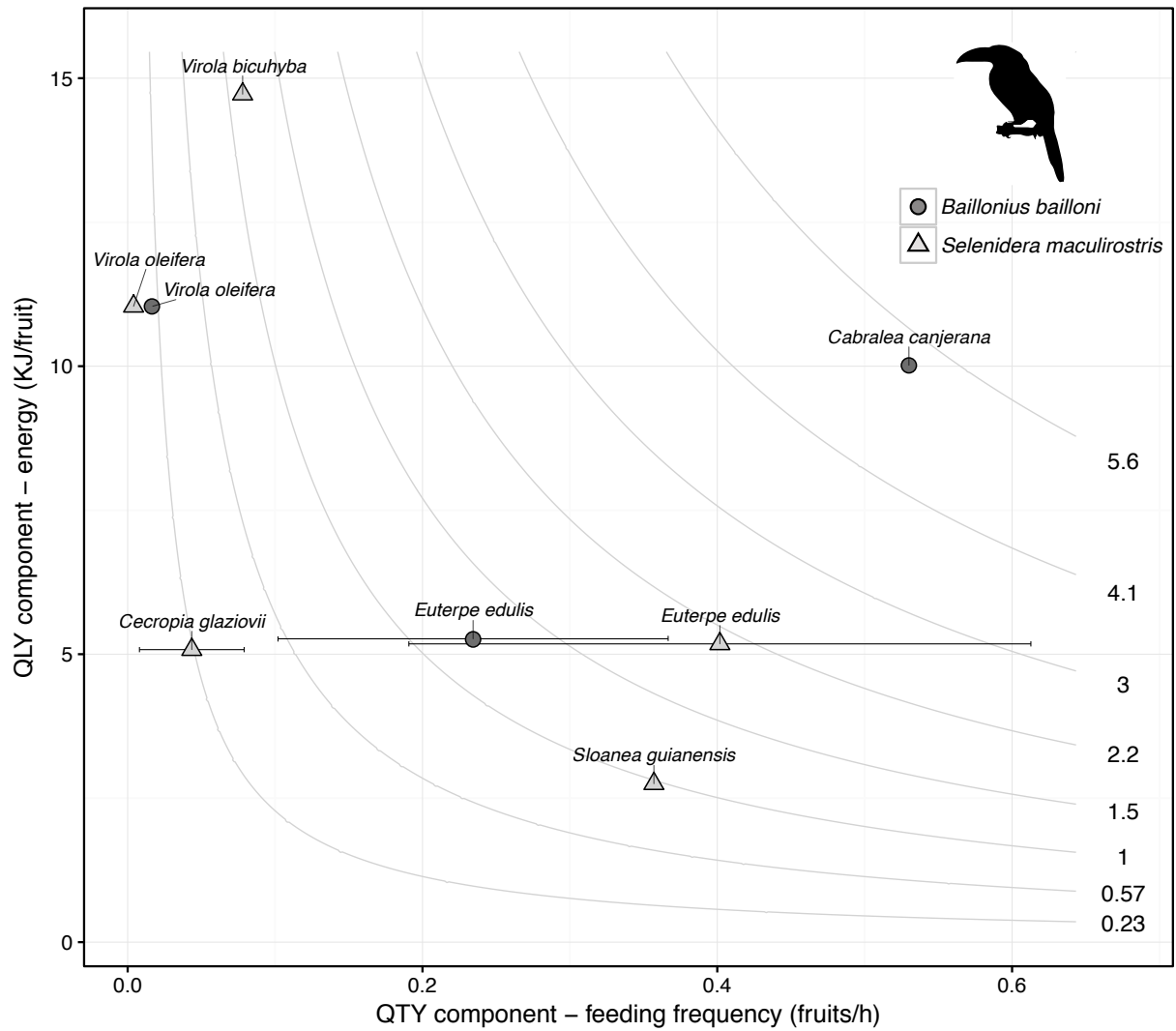




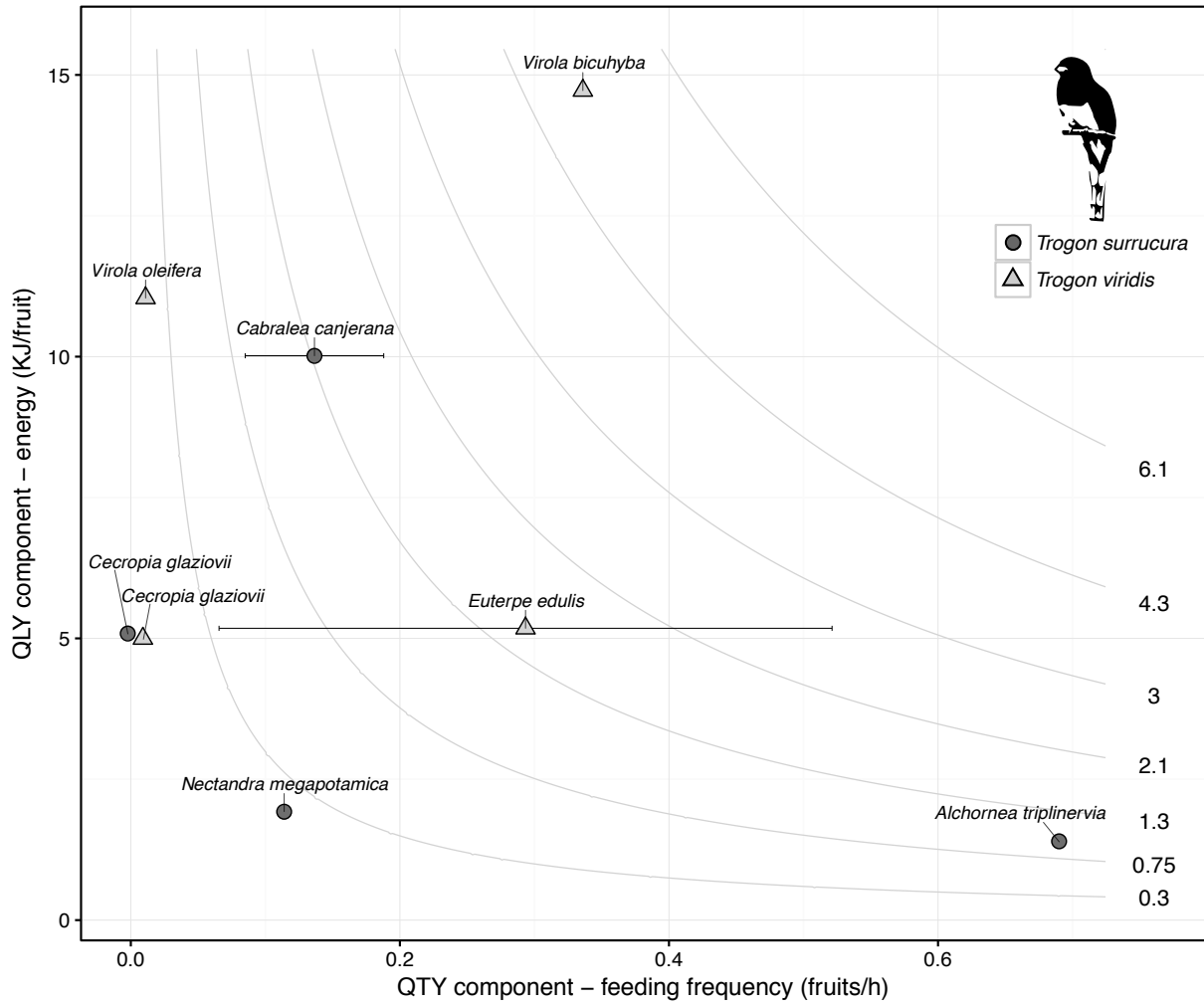
**Figure S3.2.** RPE landscape for Ramphastidae, big toucans species: *Ramphastos dicolorus* and *Ramphastos vitellinus*.



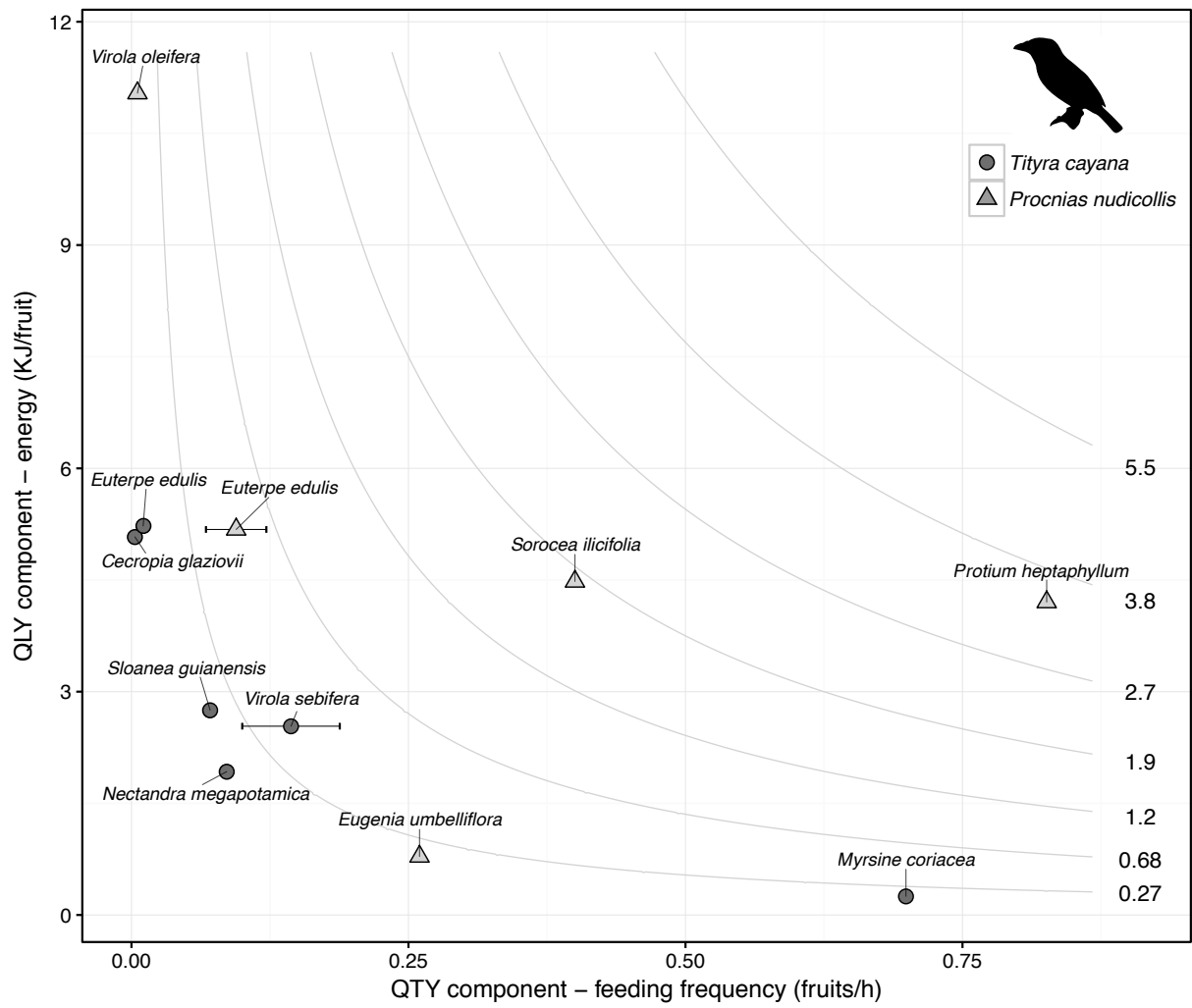
**Figure S3.3.** RPE landscape for Ramphastidae, toucanet species: *Bailloni* *bailloni* and *Selenidera maculirostris*.



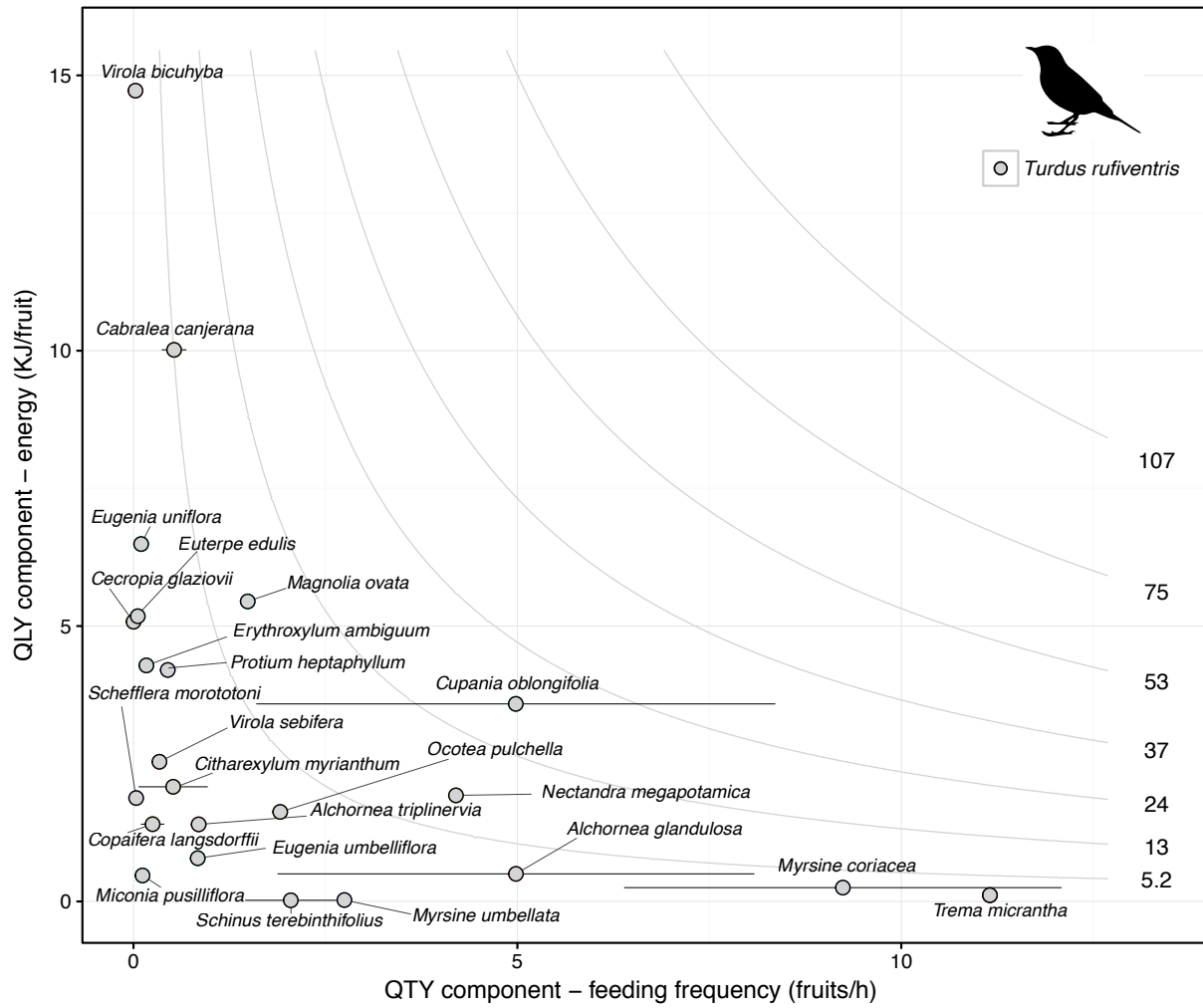
**Figure S3.4.** RPE landscape for Trogonidae species: *Trogon surrucura* and *Trogon viridis*.



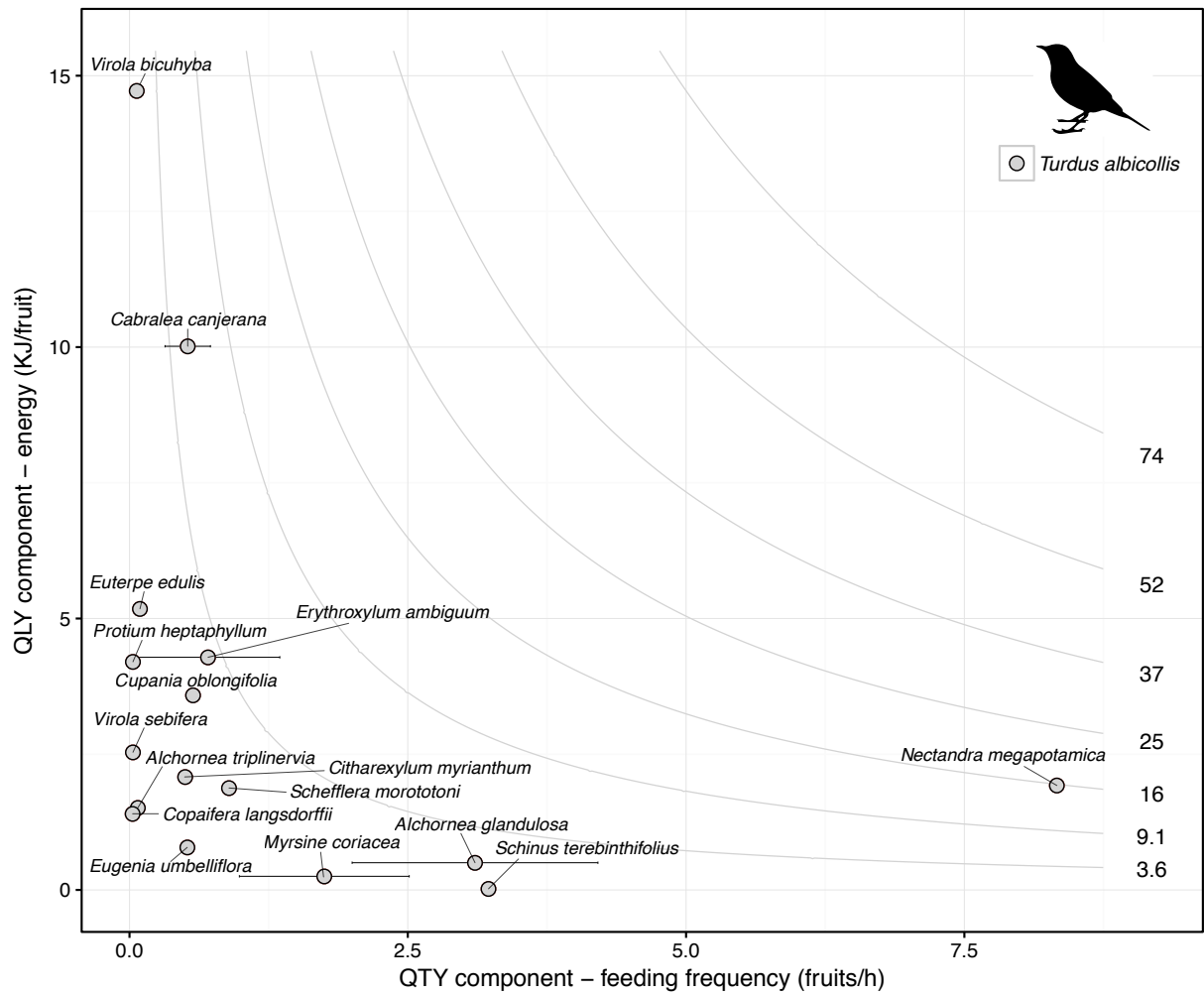
**Figure S3.5.** RPE landscape for Cotingidae and Tityridae species: *Procnias nudicollis* and *Tityra cayana*.



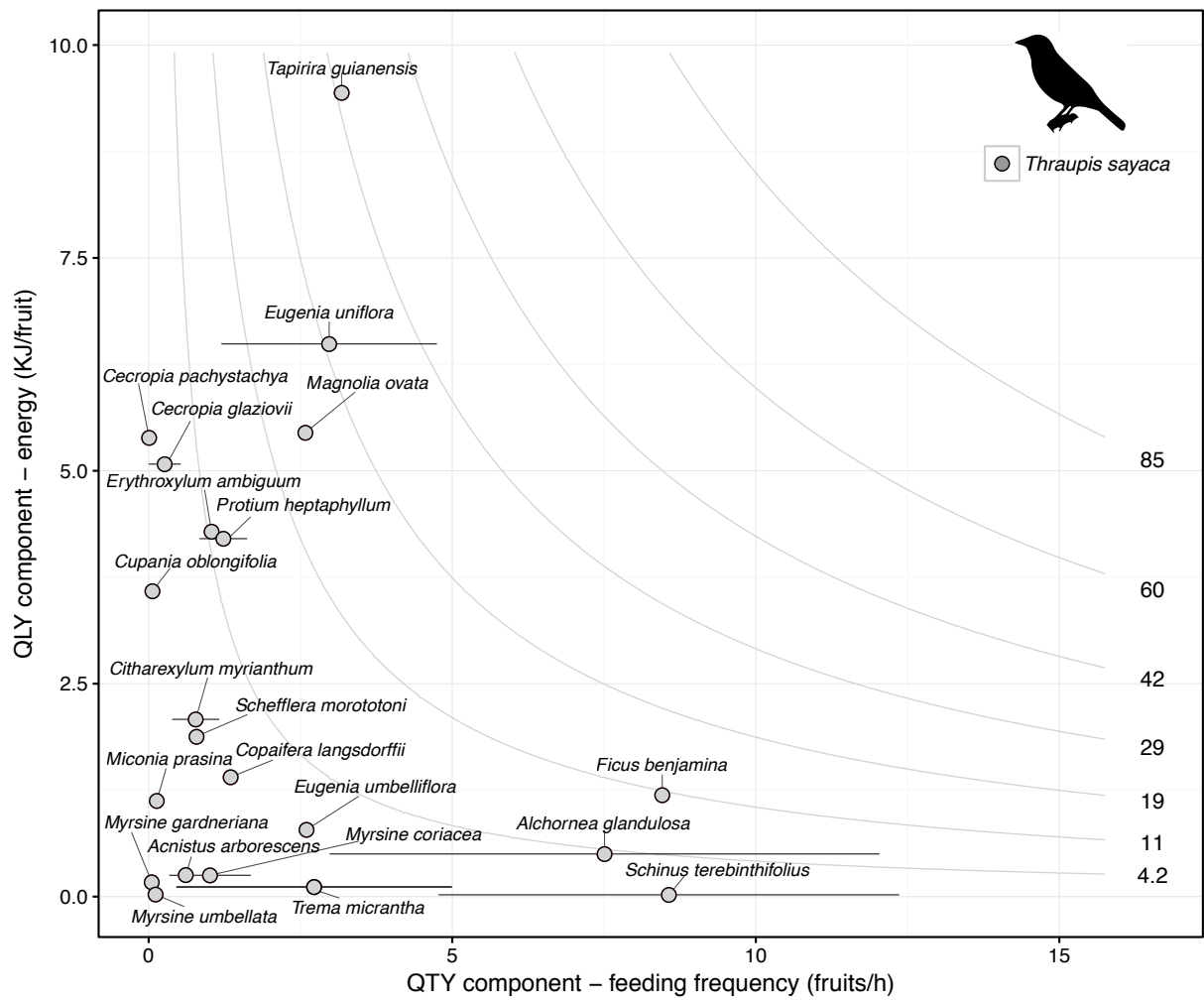
**Figure S3.6.** RPE landscape for the Turdidae species *Turdus rufiventris*.



**Figure S3.7.** RPE landscape for the Turdidae species *Turdus albicollis*.

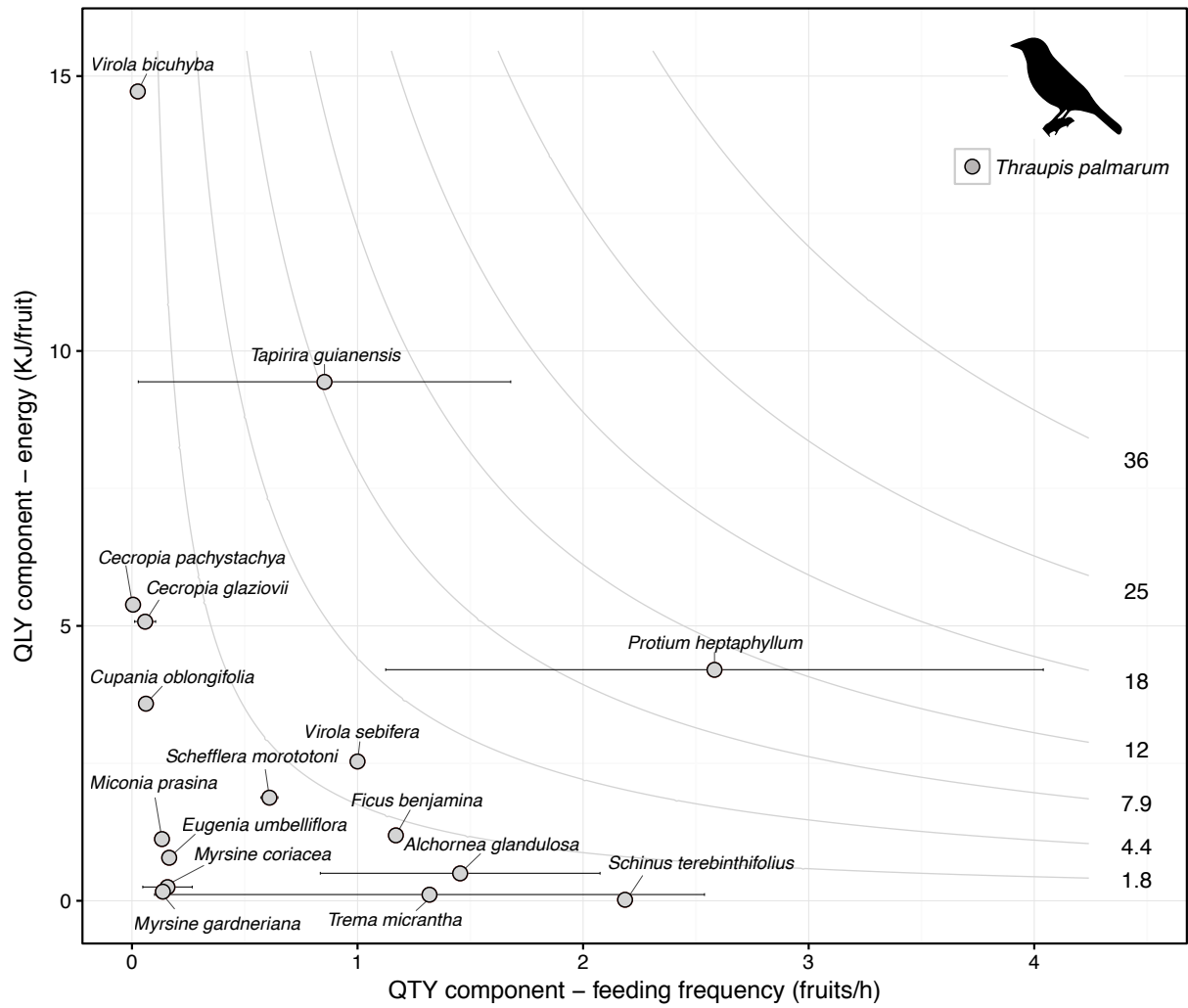


**Figure S3.8.** RPE landscape for the Thraupidae species *Thraupis sayaca*.

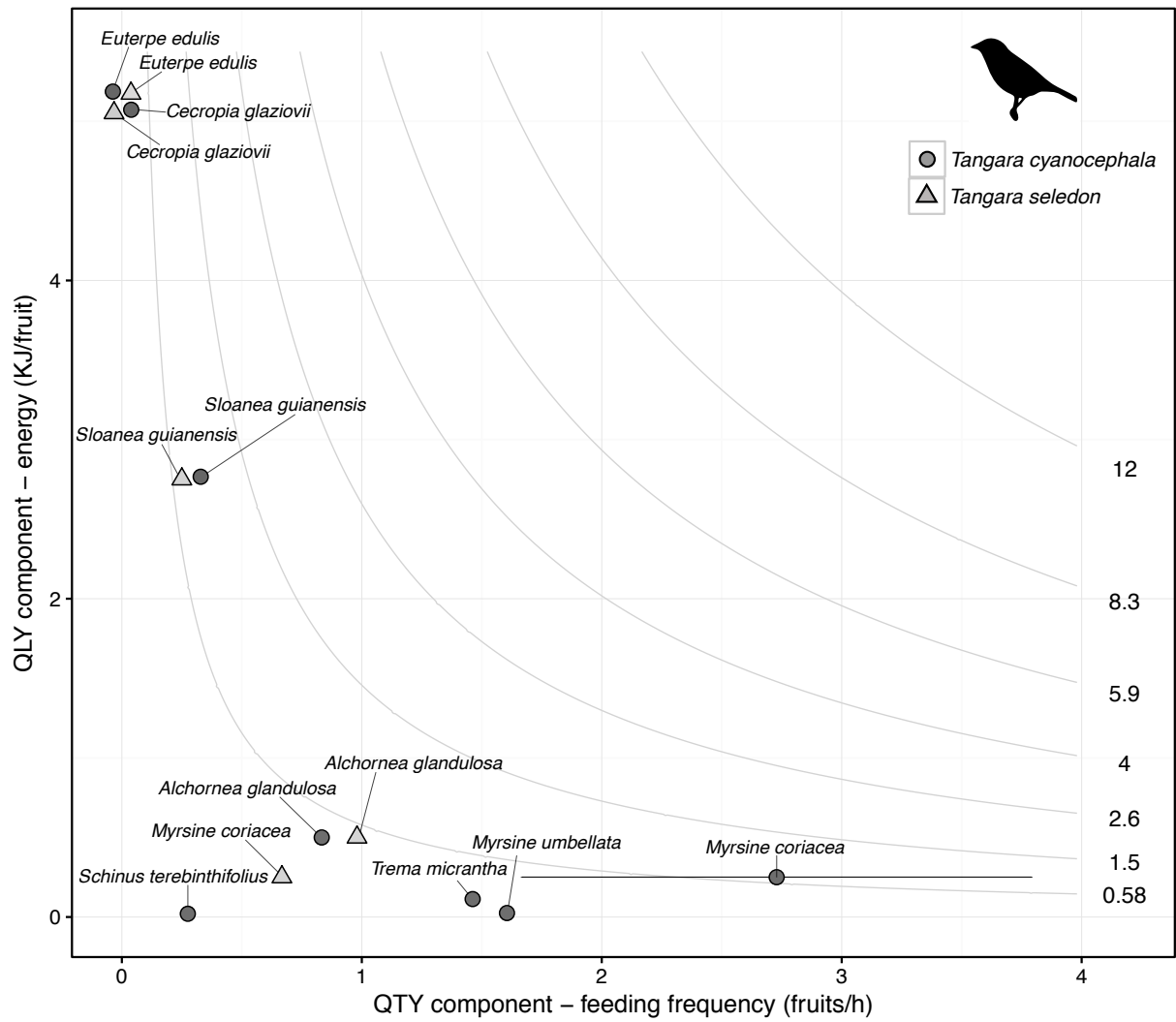




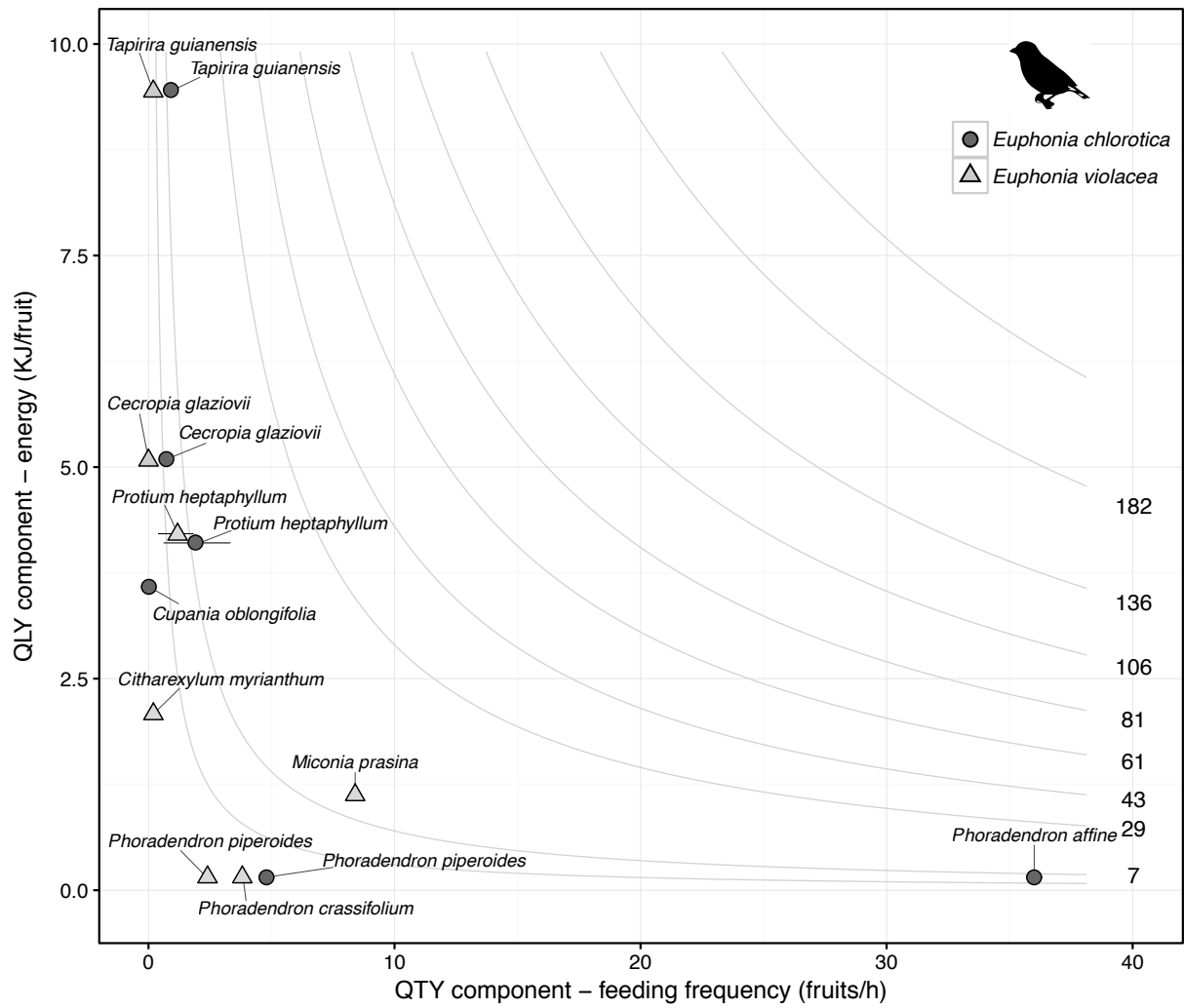
**Figure S3.9.** RPE landscape for the Thraupidae species *Thraupis palmarum*.



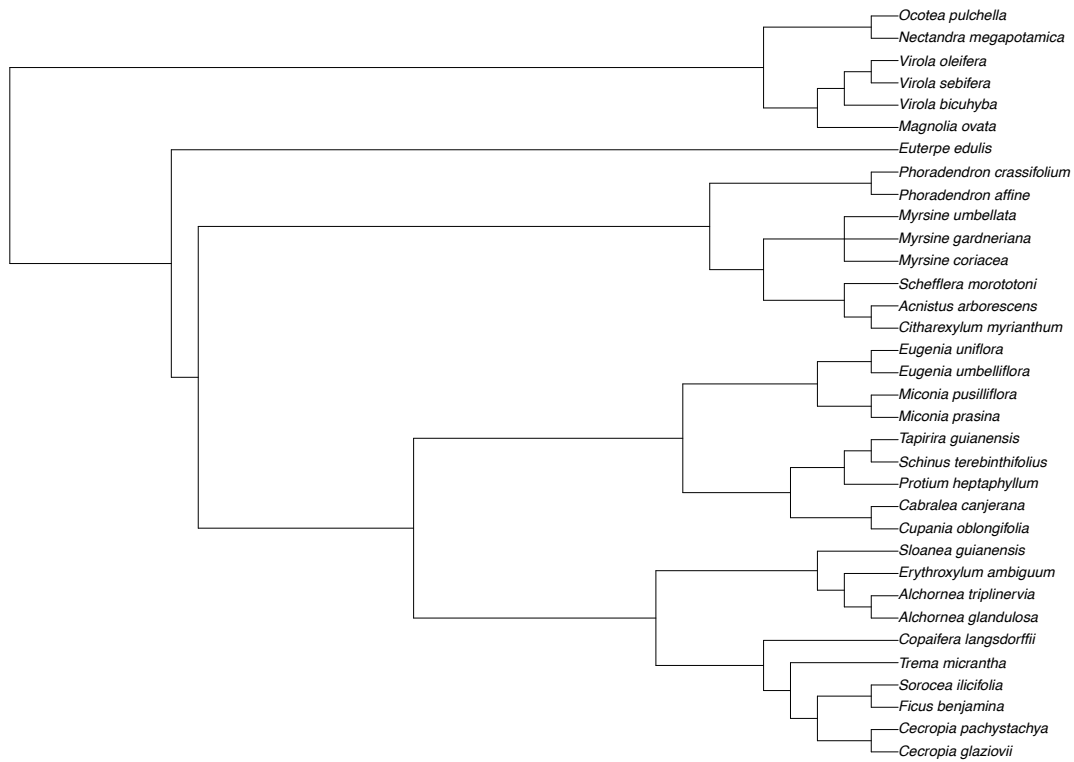
**Figure S3.10.** RPE landscape for Thraupidae species: *Tangara cyanocephala* and *Tangara seledon*.



**Figure S3.11.** RPE landscape for Fringillidae species: *Euphonia chlorotica* and *Euphonia pectoralis*.



**Figure S4.** Phylogenetic arrangement of the 34 plant species studied using Phylomatic R package.



**Table S1.** List of bird species studied, taxonomic affiliation, size, body mass and gape size (Data source: Bello et al., 2017).

Species	Family	Common name	Size	Body mass (g)	Gape size(mm)
<i>Penelope obscura</i>	Cracidae	Dusky-legged Guan	Large	1770.00	22.35
<i>Aburria jacutinga</i>	Cracidae	Jacutinga	Large	1250.00	19.12
<i>Ramphastos vitellinus</i>	Ramphastidae	Channel-billed toucan	Large	343.50	30.11
<i>Ramphastos dicolorus</i>	Ramphastidae	Green-billed toucan	Large	331.00	30.10
<i>Procnias nudicollis</i>	Cotingidae	Bare-throated bellbird	Medium	200.00	23.61
<i>Selenidera maculirostris</i>	Ramphastidae	Spot-billed toucanet	Medium	164.00	25.04
<i>Bailloniuss bailloni</i>	Ramphastidae	Saffron toucanet	Medium	146.00	23.60
<i>Trogon viridis</i>	Trogonidae	Green-backed trogon	Medium	89.70	20.49
<i>Trogon surrucura</i>	Trogonidae	Surucua trogon	Medium	73.30	17.52
<i>Turdus rufiventris</i>	Turdidae	Rufous-bellied thrush	Small	69.50	13.25
<i>Tityra cayana</i>	Tityridae	Black-tailed tytyra	Small	68.10	16.57
<i>Turdus albicollis</i>	Turdidae	White-necked thrush	Small	54.00	11.15
<i>Thraupis palmarum</i>	Thraupidae	Palm tanager	Small	39.00	8.28
<i>Thraupis sayaca</i>	Thraupidae	Sayaca tanager	Small	32.50	8.92
<i>Tangara seledon</i>	Thraupidae	Green-headed tanager	Small	18.70	6.12
<i>Tangara cyanocephala</i>	Thraupidae	Red-necked tanager	Small	18.00	5.17
<i>Euphonia violacea</i>	Fringillidae	Euphonia violacea	Small	15.00	6.92
<i>Euphonia chlorotica</i>	Fringillidae	Purple-throated euphonia	Small	11.00	6.15

**Table S2.** List of the 6 species where the Pulp Dry Mass values (grams) were estimated using species-specific data; where FFM is Fruit Fresh Mass in g, pPFM is the proportion of pulp fresh mass, w% indicates water percentage of the fruit and SFM is the Seed Fresh Mass. Multiplication sign is represented as 'x'.

Plant species	Value (g)	Calculation method
<i>Acnistus arborescens</i>	0.026	FFM x pPFM x (1-w%)
<i>Alchornea glandulosa</i>	0.018	PFM x (1-w%)
<i>Citharexylum myrianthum</i>	0.133	PFM x (1-w%)
<i>Copaifera langsdorffii</i>	0.081	FFM x pPFM x (1-w%)
<i>Cupania oblongifolia</i>	0.132	(FFM-SFM) x (1-w%)
<i>Virola oleifera</i>	0.407	PFM x (1-w%)

**Table S3.** List of data imputed for 9 plant species using congeneric species data. Where pPFM is the proportion of Pulp Fresh Mass, pPDM is the proportion of Pulp Dry Mass, pPROT is proportion of Protein content, pNSC is the proportion of Non-Structural Carbohydrates, PDM is the Pulp Dry Mass (g) and Energy is the specific energy given in kJ g<sup>-1</sup>. Values are represented with  $\pm$  1SE when possible.

Plant species	Data imputed	Value	Congener species used
<i>Alchornea triplinervia</i>	pPFM	0.381	<i>Alchornea glandulosa</i>
<i>Cecropia glaziovii</i>	pPDM	0.080	<i>Cecropia pachystachia</i>
<i>Sloanea guinaensis</i>	pPDM	0.610	<i>Sloanea monosperma</i>
<i>Myrsine coriacea</i>	pPROT	0.046 $\pm$ 0.012	Mean of 5 <i>Myrsine</i> spp ( <i>gardneriana</i> , <i>parviflora</i> , <i>rubra</i> , <i>umbellata</i> , <i>venosa</i> )
<i>Nectandra megapotamica</i>	pNSC	0.199 $\pm$ 0.058	Mean of 4 <i>Nectandra</i> spp. ( <i> davidsoniana</i> , <i>gentlei</i> , <i>hypoglauca</i> , <i>salicina</i> )
<i>Phoradendron affine</i>	PDM	0.007 $\pm$ 0.004	Mean of 3 <i>Phoradendron</i> spp ( <i>hexastichum</i> , <i>inaequidentatum</i> , <i>robustissimum</i> )
	Energy	21.045 $\pm$ 2.729	Mean of 4 <i>Phoradendron</i> spp. ( <i>californicum</i> , <i>jenmanii</i> , <i>serotimun</i> , <i>sp1.</i> )
<i>Phoradendron crassifolium</i>	PDM	0.007 $\pm$ 0.004	Mean of 3 <i>Phoradendron</i> spp ( <i>hexastichum</i> , <i>inaequidentatum</i> , <i>robustissimum</i> )
	Energy	21.045 $\pm$ 2.729	Mean of 4 <i>Phoradendron</i> spp. ( <i>californicum</i> , <i>jenmanii</i> , <i>serotimun</i> , <i>sp1.</i> )
<i>Phoradendron piperoides</i>	PDM	0.007 $\pm$ 0.004	Mean of 3 <i>Phoradendron</i> spp ( <i>hexastichum</i> , <i>inaequidentatum</i> , <i>robustissimum</i> )
	Energy	21.045 $\pm$ 2.729	Mean of 4 <i>Phoradendron</i> spp. ( <i>californicum</i> , <i>jenmanii</i> , <i>serotimun</i> , <i>sp1.</i> )
<i>Miconia prasina</i>	pPDM	0.678 $\pm$ 0.079	Mean of 17 <i>Miconia</i> spp ( <i>valtheri</i> , <i>tristis</i> , <i>theaezans</i> , <i>sellowiana</i> , <i>rigidiuscula</i> , <i>racemifera</i> , <i>pusilliflora</i> , <i>latecrenata</i> , <i>incospicua</i> , <i>doriana</i> , <i>discolor</i> , <i>cubatanensis</i> , <i>cabucu</i> , <i>budlejoides</i> , <i>bipulifera</i> , <i>sp1.</i> <i>sp2.</i> )
	pNSC	0.744 $\pm$ 0.070	Mean of 2 <i>Miconia</i> spp ( <i>bipulifera</i> and <i>sp1.</i> )

**Table S4.** List of plant species indicating the Carbohydrates measurement that was used to calculate the fruit Specific Energy. Where NSC is the proportion of Non-Structural Carbohydrates, TC is the proportion of Total Carbohydrates and TSUG is the proportion of Total Sugar.

<b>Plant species</b>	<b>Family</b>	<b>Carbohydrates value used</b>
<i>Acnistus arborescens</i>	Solanaceae	NSC
<i>Eugenia uniflora</i>	Myrtaceae	NSC
<i>Ficus benjamina</i>	Moraceae	NSC
<i>Miconia prasina</i>	Melastomataceae	NSC
<i>Nectandra megapotamica</i>	Lauraceae	NSC
<i>Schefflera morototoni</i>	Araliaceae	NSC
<i>Tapirira guianensis</i>	Anacardiaceae	NSC
<i>Virola sebifera</i>	Myristicaceae	NSC
<i>Phoradendron affine</i>	Santalaceae	NSC
<i>Phoradendron crassifolium</i>	Santalaceae	NSC
<i>Phoradendron piperoides</i>	Santalaceae	NSC
<i>Alchornea glandulosa</i>	Euphorbiaceae	TC
<i>Alchornea triplinervia</i>	Euphorbiaceae	TC
<i>Cabralea canjerana</i>	Meliaceae	TC
<i>Cecropia pachystachya</i>	Urticaceae	TC
<i>Citharexylum myrianthum</i>	Verbenaceae	TC
<i>Copaifera langsdorffii</i>	Fabaceae	TC
<i>Cupania oblongifolia</i>	Sapindaceae	TC
<i>Erythroxylum ambiguum</i>	Erythroxylaceae	TC
<i>Euterpe edulis</i>	Arecaceae	TC
<i>Sloanea guianensis</i>	Elaeocarpaceae	TC
<i>Sorocea ilicifolia</i>	Moraceae	TC
<i>Virola oleifera</i>	Myristicaceae	TC
<i>Cecropia glaziovii</i>	Urticaceae	TSUG
<i>Eugenia umbelliflora</i>	Myrtaceae	TSUG
<i>Magnolia ovata</i>	Magnoliaceae	TSUG
<i>Miconia pusilliflora</i>	Melastomataceae	TSUG
<i>Myrsine coriacea</i>	Primulaceae	TSUG
<i>Myrsine gardneria</i>	Primulaceae	TSUG
<i>Myrsine umbellata</i>	Primulaceae	TSUG
<i>Ocotea pulchella</i>	Lauraceae	TSUG
<i>Protium heptaphyllum</i>	Burseraceae	TSUG
<i>Schinus terebinthifolius</i>	Anacardiaceae	TSUG
<i>Trema micrantha</i>	Cannabaceae	TSUG
<i>Virola bicuhyba</i>	Myristicaceae	TSUG
<i>Vitex polygama</i>	Lamiaceae	TSUG

## Supplement 1. Model refinement, with digestibility experiments.

With the aim of improving the model and refine the estimates of effectiveness, we performed preliminary analysis including digestibility in the quality component. We conducted feeding experiments with four birds species in order to asses their digestibility with different fruits.

Trials were conducted with three toco toucans (*Ramphastos toco*) and one green-billed toucan (*Ramphastos vitellinus*) at the Piracicaba Municipal Zoo, in Piracicaba, São Paulo. The birds were offered *Euterpe edulis* and *Cecropia pachystachya* fruits respectively. Animals were starved overnight and given free access to water. Experiments lasted 1 to 2 hours, starting around 9:00AM and finishing at 11:00AM. Force-feeding experiments were also conducted with two frugivorous birds (*Thraupis sayaca* and *Turdus leucomelas*) captured with mist nets operated in the UNESP campus of Rio Claro, São Paulo. Fruits of *Trema micrantha* were force-fed to the birds, to ensure swallowing and total ingestion. Individual birds were kept in cloth bags and periodically checked until feces were found, and then released.

A precision balance was used to obtain the fruit mass before the offering and after the ingestion event in case it was not complete; this was considered as the ingested mass (IM). After the end of the experiment, feces were collected and weighed, this is referred as the excreted mass (EM). For *Euterpe edulis* fruits, the mass of regurgitated seeds (SM) was also included in the excreted material. The apparent fruit pulp digestibility formula used in this study was adapted from the apparent assimilation efficiency formulas frequently used in physiological avian studies (Worthington, 1989; Karasov, 1990; Brown & Downs, 2003). The apparent pulp digestibility was calculated using an apparent digestibility coefficient:

$$\text{Apparent digestibility coefficient} = \frac{IM - EM}{IM - SM}$$

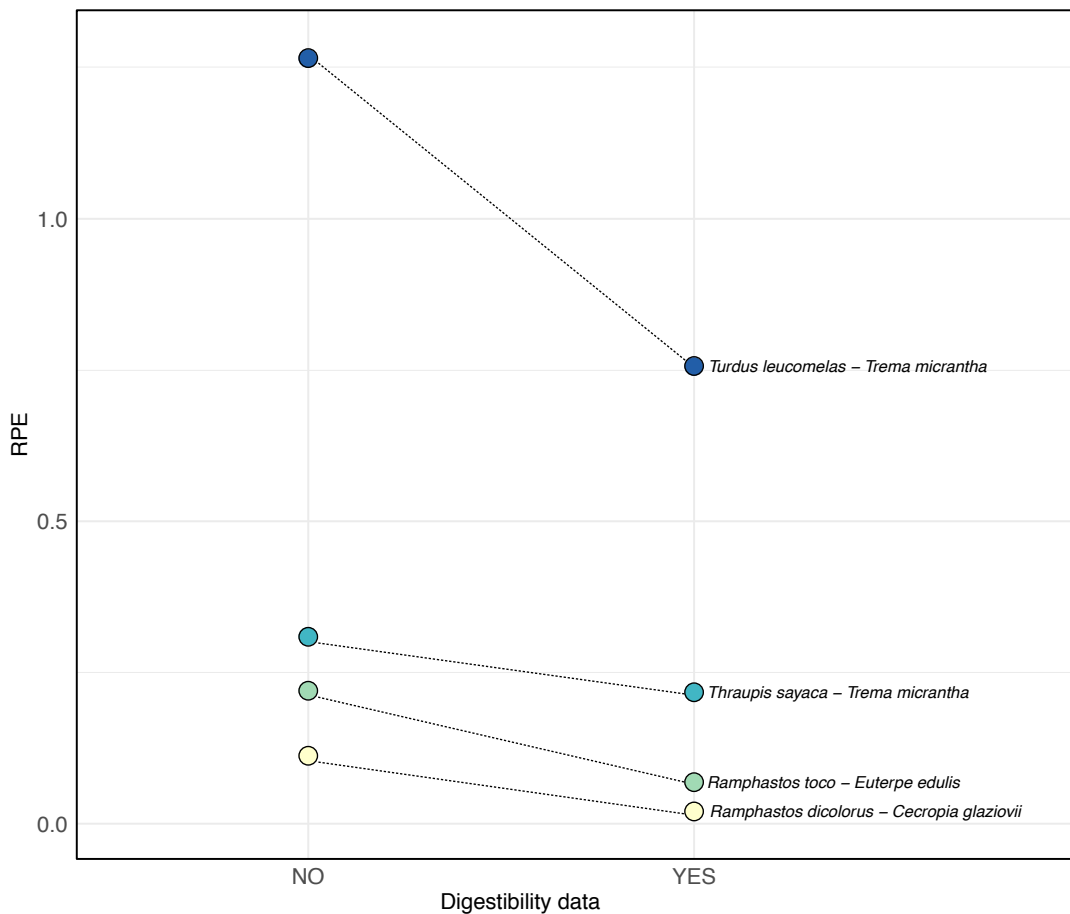
Apparent pulp digestibility is defined as the absorbed pulp mass (i.e. ingested mass minus the excreted mass), divided by the total pulp mass (i.e. ingested fruit mass minus the seed mass), providing a raw estimation of energy assimilation.

*Ramphastos toco* and *Turdus leucomelas* had no available information to calculate the quantity component, so we resorted to quantitative data on fruit consumption for their close congeneric species *R. dicolorus* and *T. rufiventris*.



**Table S5.** Experimental digestibility results for the 4 bird species studied. Columns show bird and plant species used, the number of digestibility replicate estimates (n), apparent digestibility mean values ( $\pm$  1SE), the energy per fruit in KJ, the quantity component, the quality component (defined as Energy x Digestibility), RPE (RPE= Quantity Component x Energy) and the RPE<sub>d</sub> value including digestibility estimates (RPE<sub>d</sub>= Quantity Component x Quality Component).

Frugivore species	Fruit consumed	n	Digestibility	Energy	Quality C	Quantity C	RPE	RPE <sub>d</sub>
<i>Ramphastos dicolorus</i>	<i>Cecropia glaziovii</i>	5	0.18 $\pm$ 0.06	5,08	0.93 $\pm$ 0.29	0.022 $\pm$ 0.021	0,11	0,02
<i>Ramphastos toco</i>	<i>Euterpe edulis</i>	9	0.31 $\pm$ 0.09	5,18	1.62 $\pm$ 0.43	0.043 $\pm$ 0.010	0,22	0,07
<i>Thraupis sayaca</i>	<i>Trema micrantha</i>	2	0.70 $\pm$ 0.07	0,11	0.08 $\pm$ 0.01	2.725 $\pm$ 2.267	0,31	0,22
<i>Turdus leucomelas</i>	<i>Trema micrantha</i>	3	0.60 $\pm$ 0.09	0,11	0.07 $\pm$ 0.01	11,15	1,27	0,76



**Figure S5.** Graph representing RPE changes when using data on fruit apparent digestibility determined experimentally. Each point color represents the RPE of single frugivore-fruit interaction including (YES) and not including (NO) digestibility data. The RPE values decrease when including apparent nutrient absorption data of each frugivore species. For those species that do not coincide with the ones selected in the study, the Quantity component has been estimated from its closest congeneric species.

Apparent nutrient absorption values obtained for the frugivores tested were varied (see Table S5). When total RPE was recalculated using these digestibility data ( $RPE_d$ ), all  $RPE_d$  values decreased (Fig. S5). Individual pairwise interactions were affected differentially in degree of magnitude, being the impact on the RPE higher for some than for others. *Turdus leucomelas* was the most affected in absolute terms by the reduction of the effectiveness value, this occurred because it obtained a very high quantity component score, which in turn made the total effectiveness of the fruit more susceptible to any minor change in the quality component. Yet, toucan species were the most affected in relative terms by refinement of the quality component, having their RPE reduced by more than half.

This results, yet raw and scarce, highlight the importance of including digestibility assimilation on RPE models. Their inclusion in effectiveness landscapes can re-scale the quality component for the different fruits and may facilitate the understanding of specific preferences of frugivores. Additionally, it will illustrate variation in digestibility, if any, of the same fruit species for different frugivores in the  $RPE_T$  landscape.

References not included in the main text:

Brown, K.J. & Downs, C.T. 2003. Digestive efficiency of a generalist avian feeder, the Cape White-eye (*Zosterops pallidus*). *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, 134(4), 739–748. doi: 10.1016/S1095-6433(03)00005-9