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Sowing forests: a synthesis of seed dispersal and predation by agoutis and their influence on plant communities

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ABSTRACT

Granivorous rodents have been traditionally regarded as antagonistic seed predators. Agoutis (*Dasyprocta* spp.), however, have also been recognized as mutualistic dispersers of plants because of their role as scatter-hoarders of seeds, especially for large-seeded species. A closer look shows that such definitions are too simplistic for these Neotropical animals because agoutis can influence plant communities not only through seed dispersal of large seeds but also through predation of small seeds and seedlings, evidencing their dual role. Herein, we summarize the literature on plant–agouti interactions, decompose agouti seed dispersal into its quantitative and qualitative components, and discuss how environmental factors and plant traits determine whether these interactions result in mutualisms or antagonisms. We also look at the role of agoutis in a community context, assessing their effectiveness as substitutes for extinct megafaunal frugivores and comparing their ecological functions to those of other extant dispersers of large seeds. We also discuss how our conclusions can be extended to the single other genus in the Dasyproctidae family (*Myoprocta*). Finally, we examine agoutis' contribution to carbon stocks and summarize current conservation threats and efforts. We recorded 164 interactions between agoutis and plants, which were widespread across the plant phylogeny, confirming that agoutis are generalist frugivores. Seed mass was a main factor determining seed hoarding probability of plant species and agoutis were found to disperse larger seeds than other large-bodied frugivores. Agoutis positively contributed to carbon storage by preying upon seeds of plants with lower carbon biomass and by dispersing species with higher biomass. This synthesis of plant–agouti interactions shows that ecological services provided by agoutis to plant populations and communities go beyond seed dispersal and predation, and we identify still unanswered questions. We hope to emphasise the importance of agoutis in Neotropical forests.

Key words: frugivory, granivory, plant–animal interactions, scatter-hoarding, Neotropics, carbon storage, synzoochory, acouchy

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I. INTRODUCTION

Granivorous animals rely mainly on the consumption of seeds rather than pulp and for this reason are mostly considered as seed predators. More recently, this assumption has been challenged by field studies showing that interaction outcomes between plants and granivores can be positive because the latter can also act as effective seed dispersers (Jansen *et al.*, 2012; Baños-Villalba *et al.*, 2017). Scatter-hoarding rodents, for instance, have been shown to provide important ecological services to plants both in temperate and tropical habitats (Vander Wall & Joyner, 1998; Haugaasen *et al.*, 2010). In the Neotropics, the agoutis (family Dasyproctidae, genus *Dasyprocta*) have the potential to act as mutualistic partners of plants (Fig. 1). Since the seminal work of (Smythe, 1970a, 1978) agoutis have been recognized not only as granivorous seed predators but also as important dispersers of seeds, but we still lack studies that synthesize both their mutualistic and antagonistic roles.

Positive outcomes from plant–agouti interactions arise from synzoochorous seed dispersal through the scatter-hoarding behaviour of agoutis (Gómez, Schupp & Jordano, 2019). In synzoochory, effective seed dispersal occurs when hoarders cache seeds for later consumption but do not retrieve them. Cache locations are often suitable for seed germination and seedling establishment can follow (Asquith *et al.*, 1999; Moore & Vander Wall, 2015). Many reasons enable seeds to escape agouti consumption after hoarding: seeds can germinate and deplete their reserves before cache retrieval, individuals might simply forget cache locations or rodents may die and leave their whole stock intact (agoutis are short-lived and have many predators; Emsens

et al., 2014). More importantly, seed escape mainly occurs because scatter-hoarding rodents usually stock more seeds than they will ever be able to consume during periods of scarcity (Vander Wall, 1990). Agoutis store in excess as insurance against harsher-than-expected lean periods, seed spoilage, seed germination and cache pilferage by other individuals (Jansen & Forget, 2001). Because agoutis are the largest scatter-hoarding rodents (2–6 kg) they can carry and disperse a wide range of seeds, including the heaviest ones (in contrast to many light-weight rodent species; Muñoz, Bonal & Espelta, 2012), making agoutis key dispersers of large-seeded (>20 mm) plants (Hallwachs, 1994; Galetti *et al.*, 2010).

Despite recent advances in the understanding of agoutis as mutualistic dispersers (e.g. Jansen *et al.*, 2012; Kuprewicz, 2015), a synthesis on the impact of seed dispersal by agoutis on seed germination and seedling establishment is still missing, as well as how seed traits influence decision choices by agoutis and how those traits affect interaction outcomes. Moreover, the extent of ecological services provided by this rodent is still largely understudied. For instance, by dispersing some of the largest seeds of a plant assemblage, agoutis are likely to have an important role in carbon storage, as has been shown for large frugivores (Bello *et al.*, 2015; Culot *et al.*, 2017). In addition, despite also acting as seed predators, agoutis have been suggested to act as substitute dispersers for megafaunal plants (Hallwachs, 1986; Jansen *et al.*, 2012). Given that agoutis are one of the most widespread frugivore genera in the Neotropics, and that several populations are threatened (Chiarello, 2000; Galetti *et al.*, 2017), a synthesis on the ecological roles of agoutis is necessary.



Fig. 1. A red-rumped agouti (*Dasyprocta leporina*) carrying a *Joannesia princeps* seed, a large-seeded species commonly dispersed by agoutis, and a *J. princeps* seedling emerging from a monitored agouti cache.

Here, we compile plant–agouti interactions reported in the literature, synthesize traits of plants consumed by these rodents and discuss the role of agoutis as seed dispersers and seed predators. First, we explore the taxonomic and phylogenetic distribution of plant species consumed by agoutis and map known plant–agouti interactions in the Neotropics in order to identify species and regions with information deficits. We then discuss the quantitative and qualitative components of agouti seed dispersal (*sensu* Schupp, Jordano & Gómez, 2010) exploring how plant traits and environmental factors affect dispersal rates, dispersal distances and seedling survival. We also look into the role of agoutis in a community context, comparing them to other dispersers of large seeds, and examine their overlooked contribution to maintenance of carbon stocks in tropical forests. We also discuss the role of agoutis in replacing seed dispersal services provided by extinct Quaternary megafauna. We finish by summarizing current agouti conservation efforts and by highlighting information gaps where most progress can be made. In this review, we aim to gather in one place data about plant–agouti interactions, summarize information on seed dispersal and predation by these animals and underline the importance of agoutis for the conservation of Neotropical forests.

II. METHODS AND DATA

(1) Data collection

To collect records of interactions between agoutis and fruits they feed upon, we conducted searches on the *Web of Science* (WoS) and *Google Scholar* using the following combination of terms: (seed dispers* OR seed predat* OR seed removal OR mutualis* OR frugivor* OR granivor*) AND

(*Dasyprocta* OR agouti). We also searched for documents in French, Spanish and Portuguese (languages also used by journals in Latin America) by combining the same search terms in these respective languages with the term ‘*Dasyprocta*’. Since we used two search platforms and multiple idioms, we were able to obtain studies including theses and dissertations, thus increasing the number of studies recorded by also covering the grey literature. We manually screened each reference to compile records of interactions between agoutis and plant species. We only registered interaction records from original data, therefore discarding records that cited other studies as references for plant–agouti interactions. Studies speculating that agoutis are the probable dispersers/consumers of a plant species but not presenting evidence for the interaction (e.g. studies on fruit/seed removal with no visual records of the interaction) were not included. We did not include either the consumption of leaves or flowers in our search. Although these items can sometimes be consumed by agoutis, they represent a minor percentage of their diet (Henry, 1999) and studies focusing on interactions between agoutis and flowers/leaves of plant species are scarce or non-existent.

We obtained a total of 153 studies containing interactions between seven species of agoutis and 164 different plant species. From the selected studies we recorded taxonomic information about the plant and agouti species, study location coordinates, country of study, biome type and study year. We used the *Handbook of Mammals of the World* (Wilson *et al.*, 2016) as the taxonomy source for current agouti species. Plant species names were standardized in cases of taxonomic changes according to *The Plant List* Version 1.1 (2013) with help of the ‘Taxonstand’ package (Cayuela *et al.*, 2012) in the R environment. For each plant species we assessed whether agoutis were reported to disperse their seeds or only to prey upon them. When studies reported only seed

removal but did not describe the seeds' final fates we tagged the plant species as removed but did not consider them as dispersed unless the same species was demonstrated to be dispersed by agoutis in another study. Although seed caching and eventual seed escape can follow seed removal events, we did not equate seed removal to seed dispersal because agoutis commonly carry seeds away to prey upon them in safer locations (Smythe, 1978; Hallwachs, 1994). From studies that presented evidence of seed dispersal by agoutis we recorded the maximum and mean dispersal distances and whether seed germination was observed as result of agouti dispersal, whenever this information was available.

Additionally, we collected information about plant species traits such as: fruit type, fruit length, fruit diameter, fruit mass, mean number of seeds per fruit, seed length, seed diameter, seed mass, mean tree wood density, and maximum mature tree height. When wood density data for a plant species could not be found we used the mean wood density value for the genus as a proxy. Plant trait data was often provided in articles reporting plant–agouti interactions, but most were obtained from online herbaria and databases [Royal Botanic Gardens Kew Seed Information Database, 2020; the TRY Plant Trait Database (Kattge *et al.*, 2020; try-db.org/TryWeb/Home.php) and the Brazilian Flora 2020 project (Brazil Flora Group, 2021; doi:10.15468/1mtkaw)]. Our final compilation of plant–agouti interactions is provided as online Supporting Information (Table S1).

We also compared plant–agouti interactions with those of acouchies (*Myoprocta* spp.), the only other member of the Dasyproctidae. For this we performed a systematic search for plant–acouchy (*Myoprocta* spp.) interactions with the same search terms but using ‘Myoprocta OR acouchi OR acouchy’ instead. We also used acouchy common names in Portuguese, French and Spanish as search terms. We obtained a total of 29 studies containing interactions between acouchies and 17 unique plant species (Table S2).

We also compiled plant–animal interactions involving three large tropical frugivores [tapirs (*Tapirus* spp.), spider monkeys (*Ateles* spp.) and woolly spider monkeys (*Brachyteles* spp.)], which are commonly known to disperse large seeds efficiently, in order to compare the dispersal roles of agoutis and large frugivores. We investigated if large frugivores and agoutis have redundant or complementary roles in terms of dispersal by assessing the seed mass of plants they interact with. We used seed mass as a proxy for seed size since data on seed mass were far more abundant than data on seed dimensions such as width or length. We gathered a total of 971 interactions between 8 frugivore species and plants from 21 studies (Table S3). We collected information on average seed mass for each plant species using the KEW and TRY databases.

(2) Data analyses

To test whether plant–agouti interactions were phylogenetically conserved or randomly distributed we measured the phylogenetic dispersion D (Fritz & Purvis, 2010) of plant

families that agoutis interact with. D varies from 0 to 1, with $D = 0$ denoting that the trait evolved according to a Brownian phylogenetic structure (a phylogenetically conserved trait) and $D = 1$ indicating that the trait has a random distribution in the phylogeny. We mapped plant families that interact with agoutis onto a fossil-calibrated phylogeny of seed plant families of the world (Harris & Davies, 2016) and trimmed the phylogeny to contain only those families present in the Neotropics (according to the Vascular Plants of Americas data set; Ulloa *et al.*, 2017).

To assess whether agoutis were more likely to disperse plant species with heavier seeds we compared seed mass of plant species dispersed by agoutis with those without any evidence of agouti dispersal using a t -test that allows for unequal variance (Welch test). We log-transformed the data and confirmed that this procedure resulted in a normal distribution of residuals.

Some plant species for which we could find no evidence of dispersal might actually have their seeds hoarded by agoutis but either this was not assessed, not reported (e.g. when seed dispersal was not within the scope of a study), or not detected. To assess whether our conclusions were affected by false negatives we compared the seed mass of dispersed species with those reported to be exclusively preyed upon (i.e. species where 100% of seeds with known fate were eaten by agoutis) using a Generalized Linear Model (GLM) with a binomial distribution (dispersed/not dispersed) in the *lme4* package in R (Bates *et al.*, 2014; R Core Team, 2020).

We used a linear model to investigate if the mean seed mass of dispersed plant species influenced the distance over which they were moved by agoutis. We evaluated whether we needed to account for phylogenetic structure in the models by checking if the residuals were distributed according to the phylogeny. Since the residuals did not show any correlation with phylogenetic structure (Moran test), applying a phylogenetic correction was not deemed necessary (Revell, 2010).

We used Kruskal–Wallis tests followed by Dunn's tests with *post-hoc* pairwise comparisons to compare the median seed mass and carbon storage capacity of plant species dispersed by agoutis, tapirs, spider monkeys and woolly spider monkeys. We used the Benjamini–Hochberg correction to adjust P values for multiple *post-hoc* pairwise comparisons. We evaluated whether the seed mass of species consumed by agoutis was related to their carbon storage capacity using a linear model. As a proxy for carbon storage we used the product of wood density and maximum mature size for each plant species. We assessed whether plant species with seeds dispersed by agoutis store more carbon than those preyed upon by agoutis with a t -test after checking for residual normality. We consider species to be prey rather than dispersed when their seeds weigh less than 0.8 g – the minimum seed mass for which there was evidence of dispersal – or when the species was reported in the literature to be exclusively preyed upon by agoutis.

III. DISTRIBUTION OF PLANT-AGOUTI INTERACTIONS

(1) Taxonomic distribution

Of the seven species of agoutis for which interactions with plant species were reported, the best studied were *D. leporina* and *D. punctata* (75% of studies) representing 41 and 33% of all interactions with plants, respectively. We found no information on interactions between agoutis and plants for *D. croconota*, *D. guamara*, *D. iacki*, *D. ruatanica*, *D. coibae* and *D. kalinowskii*. Most of these agouti species are endemic with small isolated distributions and are located in areas with difficult access that generally lack scientific ecological study. Agoutis interacted with a total of 164 plant species, which were distributed across 104 genera and 35 plant families (Fig. 2). Over 40% of all plant species recorded in interactions with agoutis were palms (Arecaceae) and legumes (Leguminosae), which are represented by 40 and 31 plant species, respectively. Nearly half of all plant families ($N=17$) were represented by only one plant species.

(2) Phylogenetic distribution of plants eaten and dispersed by agoutis

From the total of 164 plant species, seeds of 83 plant species were reported as being hoarded by agoutis in at least one study (Fig. 3). Twenty-two plant families on our database had one or more plant species dispersed by agoutis. In 16 cases all seeds with known fates were eaten by agoutis, representing a total of nine exclusively preyed plant species. Although absolute seed predation is not very common, scatter-hoarding rodents can occasionally consume nearly all the seed crop from a plant species (Hulme, 1998; Sun, Gao & Chen, 2004).

Seed traits may influence how agoutis interact with and hoard them (Kuprewicz, 2013; Kuprewicz & García-Robledo, 2019). Such seed characteristics could have a single or a few origins in the phylogeny, or have arisen on multiple occasions and be spread throughout the phylogenetic tree. Using the phylogenetic relationships of plant species consumed by agoutis (Fig. 3), we examined if plant-agouti interactions were phylogenetically conserved or randomly distributed. The phylogenetic dispersion value (D) was 0.772, rejecting the null hypothesis of phylogenetic structure in the plant families that agoutis interact with ($P=0.003$), and thus indicating a random distribution of plant families consumed by agoutis. Similar results were found when mapping synzoochorical dispersal by rodents in general (Gómez *et al.*, 2019). This result reinforces agoutis as generalist granivorous and frugivores that eat and disperse a variety of plant species which are not restricted to a single or a few phylogenetic clades and origins.

(3) Geographic distribution of studies

More than half of all studies were conducted in Brazil, Panama and Costa Rica (50, 34 and 19 studies respectively, Fig. 4). Although agoutis are present from central Mexico

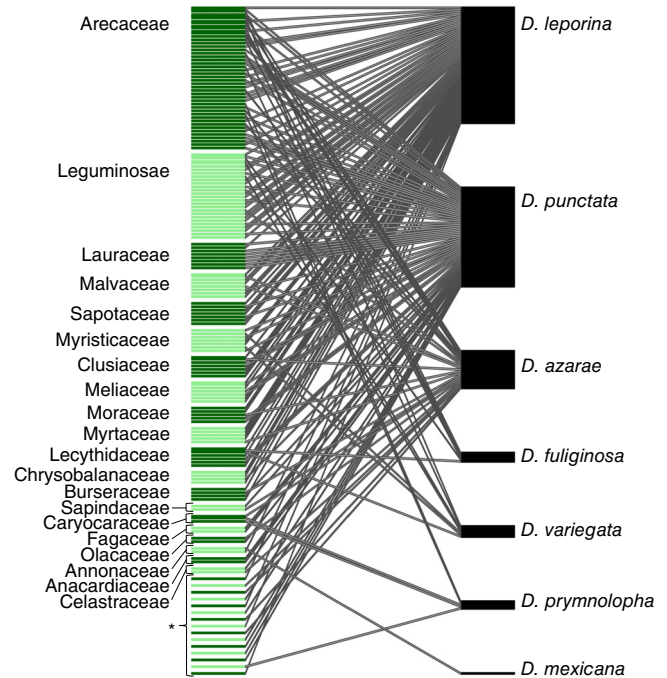


Fig. 2. Bipartite network showing interactions between plant species (green boxes) and agouti species (black boxes). Each green box represents one plant species, which are grouped by families (dark and light green colors are used to facilitate visualization of plant species belonging to the family indicated on the left). Grey lines indicate links between plant and agouti species. Eighteen interactions between plants and unidentified agouti species (*Dasyprocta* sp.) are not presented in this figure. *Plant families represented by only one species, in the following order: Connaraceae, Apocynaceae, Araucariaceae, Boraginaceae, Euphorbiaceae, Gnetaceae, Lamiaceae, Lythraceae, Malpighiaceae, Proteaceae, Rhamnaceae, Rosaceae, Rubiaceae, Rutaceae and Staphyleaceae.

to northern Argentina we did not find any publications recording agoutis' ecological interactions in Paraguay or Argentina, where *Dasyprocta azarae* occurs (Catzeflis *et al.*, 2014), nor in El Salvador, Honduras and Guatemala, where *D. punctata* is found (Emmons, 2016). Hotspots of agouti frugivory studies seem to be correlated with the distribution of universities and institutes of environmental science research in Latin America.

IV. QUANTITATIVE ASPECTS OF AGOUTI SEED DISPERSAL

(1) Number of seeds eaten and dispersed by agoutis

(a) Effects of seed mass

Seed mass is known to affect the decisions of scatter-hoarding rodents to prey on or to hoard seeds (Lichti, Steele & Swihart, 2017). Small scatter-hoarding animals like mice

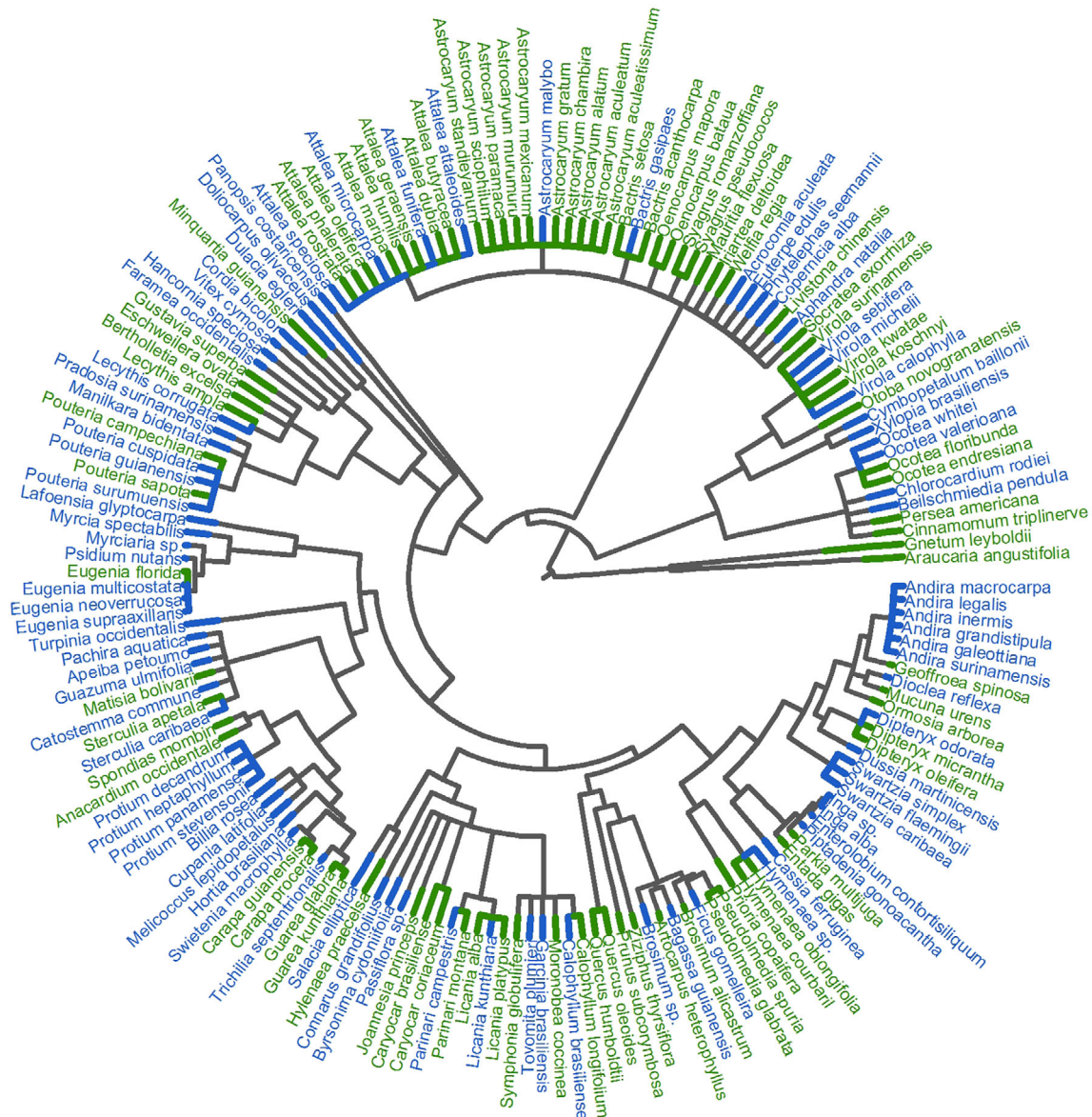


Fig. 3. Phylogeny of all plant species whose fruits and/or seeds were reported to be consumed by agoutis. Colours represent evidence of seed dispersal (green) or no evidence of seed dispersal (blue) for each plant species.

sometimes prefer to hoard lighter seeds which they are able to carry more easily (Muñoz & Bonal, 2008; Yi & Yang, 2011) but for larger rodents like agoutis seed mass is not likely to represent a significant burden (the heaviest seed registered here weighs less than 2% of agouti body mass) and thus agoutis can carry almost any seed they naturally encounter. We found evidence for agoutis interacting with seeds weighing from less than 0.01 g (*Ficus gomelleira*) to more than 50 g (*Chlorocardium rodiei*) (Fig. 5). Furthermore, agoutis occasionally carry whole fruits and were recorded moving *Bertholletia excelsa* fruits that weigh more than 1 kg (Tuck Haugaasen et al., 2012).

Since agoutis rely on their cached seeds during periods of food scarcity (Henry, 1999) they are expected preferentially

to hoard seeds with greater nutritional value. It is likely to be more energetically efficient for agoutis to manage a smaller stock of large nutrient-rich seeds than stocks of many small, nutrient-poor seeds. Heavier seeds also usually have larger reserves that take longer to be depleted during germination, making them better candidates for storage. Thus, we expect that heavier, more durable seeds of higher nutritional value are more likely to be hoarded than lighter ones.

We confirmed that plant species with greater seed mass were more likely to be hoarded than those with lighter seeds (*t*-test: $N = 140$, $df = 88.489$, $t = 6.5085$, $P < 0.0001$; GLM: $N = 84$, $df = 82$, $z = 2.284$, $P = 0.0224$). Some studies also show that among conspecific seeds the heavier ones are more likely to be hoarded by agoutis (Hallwachs, 1994; Jansen,

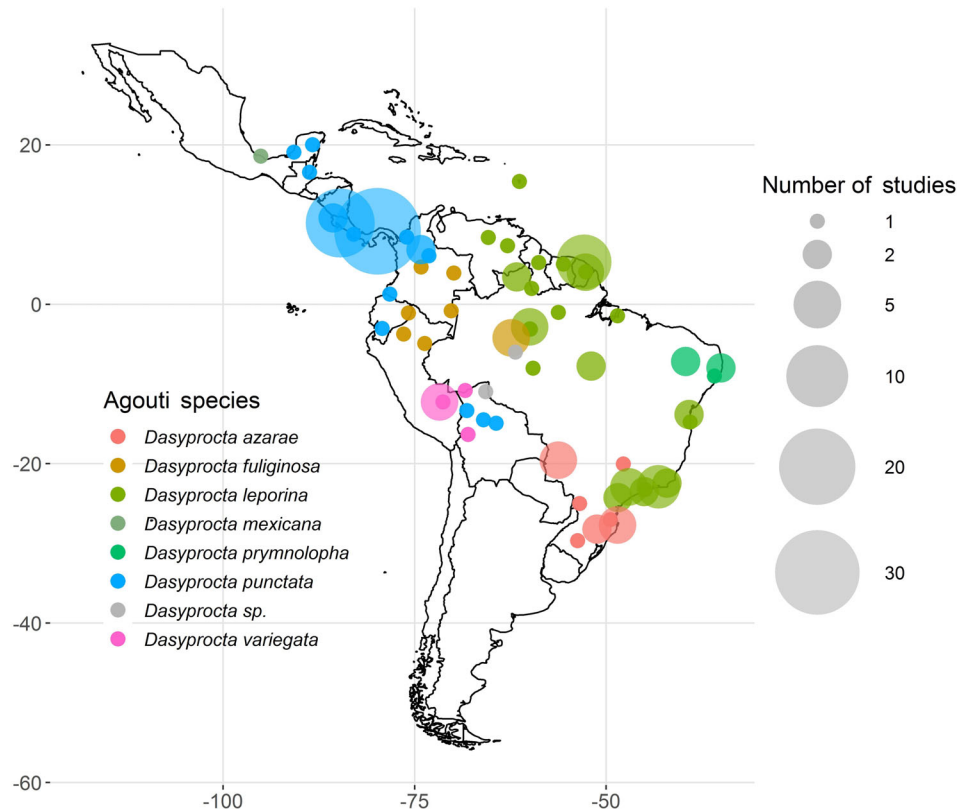


Fig. 4. Location of studies reporting interactions between agoutis and plants. Larger circles represent a greater number of studies at that site.

Bongers & Hemerik, 2004). The same is true for artificial seeds (Kuprewicz & García-Robledo, 2019) and among interspecific seeds in a previous study on six plant species (Galetti *et al.*, 2010). Galetti *et al.* (2010) reported that agoutis do not cache seeds lighter than 0.9 g; this is consistent with our literature review where *Guarea glabra* was the plant species dispersed by agoutis with seeds of the smallest mass, 0.8 g. However, Hallwachs (1994) reported that coconut pieces weighing 0.5 g are rarely cached by agoutis ($\leq 1\%$ of cases).

A similar pattern of greater dispersal probability as a function of seed mass might not be extended to other smaller scatter-hoarding rodents because of size matching between seed mass and animal body mass. The long-tailed field mouse *Apodemus sylvaticus* and the western Mediterranean mouse *Mus spretus*, for example, never hoarded acorns that weighed more than 70% of their body mass (Muñoz & Bonal, 2008). This limitation on body mass/seed mass ratio can result in preferential dispersal of seeds of intermediate mass by some rodents (Rusch, Midgley & Anderson, 2013; Wang *et al.*, 2013; Cao *et al.*, 2016), or greater dispersal of the lightest seeds by the smallest rodents (Brewer, 2001; Tamura & Hayashi, 2008; Yi & Yang, 2011).

Seed mass influences the dispersal process beyond the probability of hoarding. Species with larger seeds also have a higher proportion of dispersed seeds (Jansen *et al.*, 2004; Kuprewicz & García-Robledo, 2019), a greater dispersal

distance (Gálvez *et al.*, 2009; Galetti *et al.*, 2010; Kuprewicz & García-Robledo, 2019) and a higher survival probability in caches (Jansen *et al.*, 2002). Thus, plant species hoarded by large rodents might be under selection for heavier seeds (Vander Wall, 2010), particularly for plants that depend almost exclusively on agoutis for their dispersal. Nut-bearing plants dispersed by scatter-hoarding rodents in temperate systems have increased their propagule size since the Paleocene (~60 million years ago), possibly because of selection imposed by scatter-hoarding dispersal (Vander Wall, 2001).

(b) Effects of other seed traits

Besides seed mass, the nutritional composition of a resource can influence its perceived value and the probability that agoutis will interact with and hoard it. For example, lipids and proteins are generally more highly valued than carbohydrates by frugivores because they are scarcer macronutrients (Jordano, 2000). Fruit pulp tends to be composed mainly of carbohydrates and water, while seeds are richer in protein and lipids, thus granivory allows access to these important macronutrients. It thus can be predicted that agoutis will preferentially harvest and cache lipid- and protein-rich seeds, as has been shown for other scatter-hoarding rodents (Yadok *et al.*, 2020), but there is a lack of studies investigating how macronutrient content influences agouti seed-dispersal

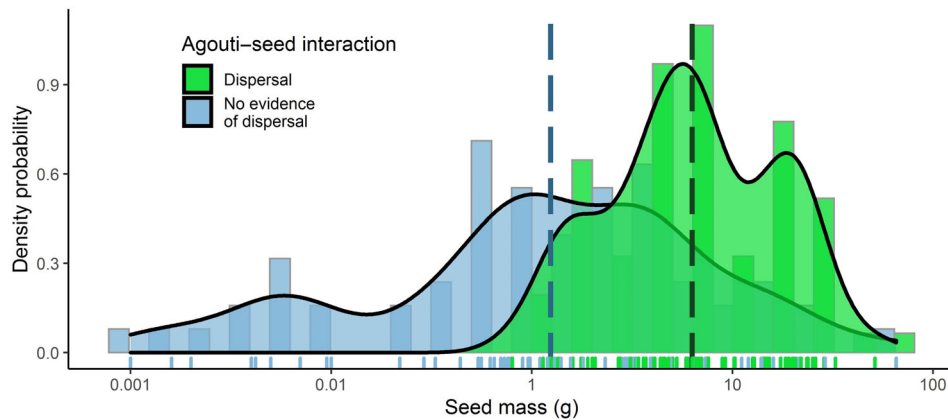


Fig. 5. Plant species with heavier seeds are more likely to be dispersed by agoutis. Density curves represent the seed mass distributions of species known to be dispersed and those for which there is no evidence of dispersal. Dashed lines are mean values for each distribution.

probability. For hoarders in general, the evidence suggests higher dispersal of protein- and lipid-rich seeds but other variables may also be involved, such as the presence of secondary metabolites and seasonal and geographical scarcity of macronutrients (Lichti *et al.*, 2017).

Other important traits affecting the decision of agoutis to hoard or consume seeds are seed perishability, dormancy and germination speed. Caches that are less likely to spoil or germinate represent a more reliable long-term food resource and thus are more likely to be stored and less likely to be recovered quickly (Sutton, Strickland & Norris, 2016). Ribeiro & Vieira (2014) observed that a very low proportion of *Araucaria angustifolia* seeds were hoarded by *D. azarae* in an araucaria forest. *A. angustifolia* seeds are large and heavy but are highly perishable and germinate rapidly on the ground; these traits are likely to decrease the probability that they are cached by agoutis.

Indigestible carbohydrates such as lignin and cellulose are likely to discourage seed consumption (Chen, Cannon & Conklin-Britton, 2012). Toxic secondary metabolites can also deter hoarders; *Mucuna holtonii* seeds, for example, are not consumed by agoutis due to the presence of the toxic amino acid L-dopa (Kuprewicz, 2013). Despite this, agoutis can ingest seeds containing certain levels of tannin, which is a common defensive secondary metabolite found in seeds (Kuprewicz & García-Robledo, 2019), suggesting that they can acclimate to a high-tannin diet like other seed-hoarding animals (Shimada, 2006). Some rodents have tannin-binding proteins in their saliva (Robbins *et al.*, 1991; Hagerman & Robbins, 1993), although whether this is the case for agoutis is not known. Agoutis include a higher proportion of protein in their diet than expected from their body size, mainly due to the consumption of insects (Dubost & Henry, 2006). Higher levels of protein consumption could represent a strategy to compensate for high levels of tannin consumption which decrease protein digestion and absorption (Chung-MacCoubrey, Hagerman & Kirkpatrick, 1997; Nersesian *et al.*, 2012).

While non-lethal toxic seeds are a poor choice for immediate consumption in a resource-abundant environment, they can serve as reserve in times of resource scarcity. Additionally, secondary compounds of some seeds degrade over time making hoarding a good strategy to reduce seed toxicity and improve palatability (Torregrossa & Dearing, 2009). Consequently, less-toxic seeds are expected to be consumed first, while toxic ones are more likely to be spared, hoarded and retrieved later from caches. Accordingly, Guimarães *et al.* (2003) observed that toxins in *Ormosia arborea* seeds discourage consumption but not caching by agoutis.

(c) Effects of seed abundance

Resource abundance is known to influence scatter-hoarders' decisions to hoard or eat seeds and the survival of seeds in caches (Vander Wall, 2002; Jansen *et al.*, 2004; Moore & Swihart, 2008). In seed-rich years and in areas with high resource abundance a greater proportion of seeds are dispersed [although over shorter distances (Jansen *et al.*, 2004; Liu *et al.*, 2013)], cache recovery is diminished and seedling establishment consequently increases (Jansen *et al.*, 2004; Gálvez *et al.*, 2009). This might happen because hoarders stock more seeds after they become satiated (the predator satiation hypothesis; Janzen, 1971). A surplus of resources thus could satiate hoarders and enable a substantial proportion of seeds to be hoarded. Greater cache survival and seed germination then possibly occurs because hoarders cannot manage their numerous caches. In addition, the frequency of partial rather than complete consumption increases when seeds are abundant (Steele, Gavel & Bachman, 1998; Yang & Yi, 2012) with many seeds still able to germinate after partial consumption (Pérez *et al.*, 2008; Perea, San Miguel & Gil, 2011). Pilferage rates are also diminished when resources are abundant (Muñoz & Bonal, 2011; Cao *et al.*, 2018). Because individual hoarders have large numbers of stocked seeds with known locations, they are less motivated to spend time looking for other individual's caches.

Since abiotic factors like temperature and rainfall are determinants of plant phenology and seed crop sizes, seasonality also plays an important role in the proportion of seeds hoarded by agoutis. Generally, agoutis consume more pulp and hoard more seeds in the wet season when resources are abundant, whereas in the dry season they feed mostly from their caches (Henry, 1999). The peak of seed storing often occurs at the end of the wet season when resources are still abundant (Forget *et al.*, 2002; Haugaasen *et al.*, 2010).

(d) Effects of conspecific and heterospecific density

The number of seeds being dispersed by agoutis is also affected by the abundance of other seed predators including other agoutis, scatter-hoarding rodents and granivores like the collared peccary (*Pecari tajacu*) and white-lipped peccary (*Tayassu pecari*) (Hallwachs, 1986; Akkawi *et al.*, 2020). While the amount of resource is correlated with agouti abundance and activity, the relationship is not exact (Gálvez *et al.*, 2009); the ratio of resources per hoarder is a better predictor of the proportion of seeds dispersed than is seed or animal abundance alone (Theimer, 2006; Xiao, Zhang & Krebs, 2013).

Agouti abundance has a complex relationship with seed dispersal: a high density of agoutis increases competition for food resources and therefore seed value, resulting in more pilferage events, seed predation and fewer dispersed seeds. However, when agouti numbers are too low, the total number of dispersed seeds will also be diminished due to a reduction in seed encounter and seed removal rates. Thus, seed dispersal rates by agoutis might be highest at intermediate densities of agoutis where there are sufficient seed-dispersal events without an accompanying burden of seed and cache predation (Mittelman, Pires & Fernandez, 2021).

Many environmental and anthropogenic factors, including habitat fragmentation, hunting and changes to habitat characteristics are likely to influence both resource and animal densities, thus affecting agoutis' scatter-hoarding dynamics (Carrillo, Wong & Cuarón, 2000; Jorge & Howe, 2009; Ferreguetti, Tomas & Bergallo, 2018).

V. QUALITATIVE ASPECTS OF AGOUTI SEED DISPERSAL

(1) Dispersal distances

We found 41 studies that reported mean dispersal distances and 45 that reported maximum dispersal distances. These studies used different methods for assessing dispersal, which greatly affected the mean and maximum measured distances (Fig. 6). Seed radio-tracking, for example, allowed the best detection of seed dispersal over longer distances (Hirsch, Kays & Jansen, 2012a). Different studies measure seed dispersal over different lengths of time which also affects assessment of dispersal distances. Studies conducted over longer periods will involve more pilferage and re-caching events; these studies have

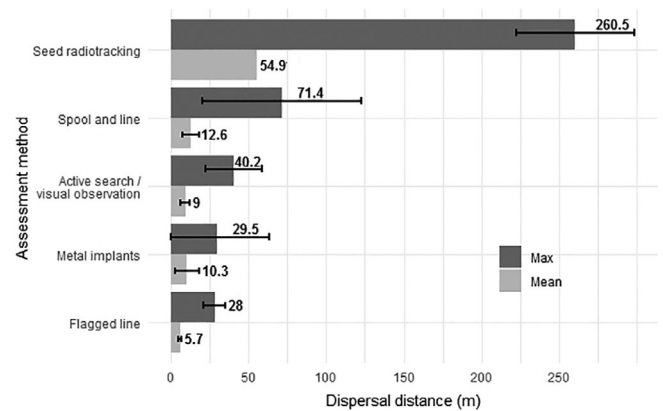


Fig. 6. Mean values for the maximum and mean dispersal distances recorded in 45 studies of seed dispersal by agoutis, presented according to different methods used to assess seed dispersal. Error bars are 95% confidence intervals.

provided evidence that seeds can be taken further away from the source by multistep re-caching (Jansen *et al.*, 2012).

Factors that can influence the distance that a seed is transported by agoutis include seed traits (Kuprewicz & García-Robledo, 2019), seed abundance (Jansen *et al.*, 2004; Gálvez *et al.*, 2009), plant density (Hirsch *et al.*, 2012b; Jansen *et al.*, 2014) and seasonality (Haugaasen *et al.*, 2010). These factors probably explain the variation in dispersal distances among studies. Larson & Howe (1987), for instance, reported that seeds of a *Virola* species are only moved a few meters away from the trunk of mother trees, with most seeds remaining below the tree crown. On the other hand, Hallwachs (1986) found that guapinol (*Hymenaea courbaril*) can be dispersed over long distances by agoutis (up to 225 m). More recently, Jansen *et al.* (2012) recorded dispersal of *Astrocaryum standleyanum* palm seeds over distances longer than 200 m from the source.

We found no consistent relationship between mean dispersal distance and seed mass of the dispersed species (linear model, $N = 41$, $df = 39$, $t = -0.823$, $P = 0.415$). Galetti *et al.* (2010) similarly found no evidence for an influence of seed mass on dispersal distances by agoutis when comparing multiple plant species. Nevertheless, given the many factors influencing dispersal distances we do not dismiss this possibility. The studies compiled herein used different methodologies and were carried out at different sites, making it difficult to compare them directly. Studies that attempted to control for the influences of other variables by using artificial seeds or that were carried out in the same habitat over equivalent periods have identified a correlation between dispersal distance and seed mass, with heavier seeds being carried further away (Hallwachs, 1994; Jansen *et al.*, 2004; Gálvez *et al.*, 2009; Kuprewicz & García-Robledo, 2019).

(2) Secondary seed dispersal and re-caching

Most studies of seed dispersal by agoutis only involve primary dispersal: the removal and burial of seeds after fruitfall. But seeds are often recovered from caches by the same rodent

or by pilfering individuals (Jansen *et al.*, 2012; Dittel, Perea & Vander Wall, 2017). Indeed, most primarily dispersed seeds do not remain where they were buried; animals tend to re-cache seeds elsewhere or to recover caches to feed on the stored seeds. Jansen *et al.* (2012) showed that 99% of caches were recovered by agoutis after one year and Vander Wall & Jenkins (2003) estimated daily pilferage rates of 2–30% of seeds depending on rodent species. Because agoutis repeatedly steal and re-cache each other's buried seeds, seeds can be transported over greater distances (>100 m, equivalent to dispersal by large mammals) to beyond an individual's home range. Such long-distance dispersal events are important because, in addition to removing seeds from the parent plant's vicinity where seeds are more vulnerable to attack by invertebrates or pathogens, they also allow for colonization of new sites (Jansen, Bongers & Van Der Meer, 2008; Jansen *et al.*, 2012).

Agoutis are common secondary dispersers of seeds following primary dispersal by abiotic factors and by other animals like birds and primates (Forget & Milleron, 1991; Andresen, 1994; Wenny, 2005). Wenny (1999) provided indirect evidence that agoutis act as secondary dispersers of two *Guarea* species in Costa Rica by removing intact seeds found in faeces. In diplochory (seed dispersal by a distinct two-step process), primary dispersal usually moves seeds longer distances but does not place them in safe sites; thus seed survival and seedling establishment after primary dispersal is relatively low. Agouti secondary dispersal complements this process by reducing seed predation and providing seeds with a favourable micro-site that improves the likelihood of germination (Vander Wall & Longland, 2004).

(3) Seed deposition and seedling fate

Deposition patterns and placement of dispersed seeds are important factors affecting the survival of seeds and seedlings (Schupp, 1993; O'Farrill, Chapman & Gonzalez, 2011; Bewley & Black, 2013). Seed burial by agoutis is known to protect seeds from other predators, from desiccation and to improve establishment success by depositing seeds in micro-environments with favourable germination conditions (Asquith *et al.*, 1999; Jansen & Forget, 2001; Draxler & Forget, 2017). For large-seeded species, most often dispersed by agoutis, burial can be even more important for germination since they usually require more humidity to germinate but absorb less water [due to a smaller surface area to volume ratio (Harper, Lovell & Moore, 1970; Kikuzawa & Koyama, 1999)]. Burial can maintain seeds in a high-moisture micro-environment and allow water absorption and germination (Kollmann & Schill, 1996; Perea *et al.*, 2012). Additionally, agoutis improve seed survival by carrying seeds towards locations with lower conspecific tree densities, thus facilitating the escape of seeds from natural enemies (Hirsch *et al.*, 2012b).

We found a total of 33 studies that followed seeds after hoarding or mimicked seed burial by agoutis; all observed germination of a portion of the buried seeds. Such studies provide important data on how many cached seeds are

recruited into seedlings. Several studies compared the survival and germination rates of non-harvested seeds found on the soil surface with those of hoarded seeds, and found advantages in survival and greater germination probability for hoarded seeds (e.g. Sork, 1987; Smythe, 1989; Brocardo, Pedrosa & Galetti, 2018). Together with rates of predation/dispersal by agoutis, this information will help us to understand whether agoutis have mutualistic or antagonistic interactions with plant species (Zwolak & Crone, 2012).

Even after seed germination, seeds can still be subject to predation by agoutis (Kuprewicz, 2015). In fact, during the germination period seeds can be more vulnerable to predation since emerging sprouts give rodents cues about seed location (Pyare & Longland, 2000; Jansen & Forget, 2001). This may result in selection for rapid seedling emergence and depletion of seed reserves. Rodents can also manipulate seeds to slow down germination by removing the protruding radicle and epicotyl, therefore stalling seedling development, a process resulting in so-called “zombie seeds” (Jansen, Bongers & Prins, 2006).

(4) Impact of agoutis on plant populations

Seed removal by agoutis is not always beneficial to plants. This is clear when all seeds found by agoutis are eaten. When seed dispersal occurs it does not mean that hoarders have a positive impact on plant populations; sometimes only a few seeds are cached and the majority of caches are recovered and eaten later. In these scenarios, seed hoarding does not compensate for intense predation (e.g. Bogdziewicz, Crone & Zwolak, 2020). Even when seed dispersal and cache survival rates are significant, seeds might not benefit from hoarding because burial can be detrimental for some species (e.g. Kuprewicz, 2015) or because seeds might have other dispersal mechanisms that allow germination without the predation cost associated with hoarding (e.g. Russo, 2005). In other plant species, however, seed burial is highly beneficial or even required for germination (Forget, 1990; Draxler & Forget, 2017; Mittelman *et al.*, 2020).

The ratio of seeds dispersed/eaten and the relative survival and germination of caches compared with non-dispersed seeds are the main factors that determine if the plant–agouti interaction is positive for the plant (Zwolak & Crone, 2012; Sawaya *et al.*, 2018). Additionally, the negative impact of agoutis on emerging seedlings must be taken into account.

A comparison of rates of seedling establishment and survival with and without agoutis can determine the ultimate impact of agoutis on a plant population; this could be done by contrasting seedling establishment and survival rates between harvested and non-harvested seeds or between areas with agoutis and areas where agoutis are locally extinct. Overall, plant–agouti interactions have been identified as positive for large-seeded plants, since synzoochorous species have evolved traits that encourage removal and dispersal by scatter-hoarding animals (Vander Wall, 2010).

VI. COMPARISON WITH ACOUCHIES

The acouchies (*Myoprocta* spp.) are the only other group of animals belonging to the family Dasyproctidae. Although less studied, acouchies are also known for their scatter-hoarding behaviour and are important dispersers and predators of seeds in the Amazon (Morris, 1962; Jansen *et al.*, 2004). Acouchies are smaller than agoutis and weigh 2–6 times less (16–20 cm, 0.8–1.5 kg; Dubost, 1988). There are two species: the green acouchy (*Myoprocta pratti*), which occurs primarily in the western Amazon region, and the red acouchy (*Myoprocta acouchy*) present in the northeastern Amazon (Catzeffis & Weksler, 2016a,b), although disputes remain about the accuracy of this division (Ramírez-Chaves, Suárez-Castro & Patterson, 2014; but see Teta, 2019).

Acouchies fill a similar ecological role to agoutis in terms of seed dispersal and predation (Jansen & Forget, 2001; Jansen *et al.*, 2004). Of the 17 acouchy–plant interactions we identified in the literature (Table S2), agoutis were found to share 14 (82%) of them. Nevertheless, rodent body size is known to affect predation and dispersal rates, seed size preference, and maximum carrying capacity (Muñoz & Bonal, 2008; Zhang *et al.*, 2015; Wróbel & Zwolak, 2017). Thus, because of their smaller size, acouchies could scatter-hoard some small seeds not dispersed by agoutis and have a lower threshold of maximum seed mass for dispersal. For instance, dispersal distances of *Carapa procera* seeds carried by acouchies seem to be reduced for seeds weighing more than 30 g (Jansen *et al.*, 2002). In terms of numbers of hoarded seeds (quantitative dispersal), however, acouchies might be even better seed dispersers than agoutis; in studies where acouchies co-occur with agoutis they removed more seeds than agoutis (Jansen *et al.*, 2002, 2004) and hoarded a larger proportion of removed seeds (Forget, 1990). However, other studies found that acouchies removed disproportionately fewer seeds compared to agoutis (Haugaasen *et al.*, 2010).

Conservation of acouchies deserves special attention because we lack important data on their population trends (Catzeffis & Weksler, 2016a) and they are likely to be very susceptible to habitat disturbance and fragmentation (Dubost, 1988; Jorge, 2008). Although there are differences between acouchies and agoutis, in terms of body mass, population turnover and site fidelity (Dubost, 1988; Jorge & Howe, 2009) that might influence the fate of dispersed seeds, it is likely that acouchies play a seed-dispersal role similar to agoutis. We strongly recommend that future studies focus on the conservation of acouchies and clarify their role as seed dispersers.

VII. AGOUTI SEED DISPERSAL AND PREDATION IN A COMMUNITY CONTEXT

In tropical systems, large frugivores are usually associated with dispersal of seeds of a wide size range, including the largest seeds, while small mammals interact mostly with small seeds (Jordano, 2000; Dylewski *et al.*, 2020). Agoutis, however, do not fit well into this generalization; they have a small

mass compared to large terrestrial frugivores like peccaries and tapirs but are known to interact with and disperse large seeds.

We found that agoutis interact with plant species that have heavier seeds than those consumed by large Neotropical frugivores (tapirs, spider monkeys and woolly spider monkeys) (Kruskal–Wallis: $N = 453$, $df = 3$, $\chi^2 = 105.55$, $P < 0.0001$; Dunn's test: $P < 0.0001$ for all comparisons between agoutis and other frugivores). Agoutis also seem to be the main dispersers of species at the high end of the seed mass distribution (>10 g, Fig. 7). This may be because fruit consumption by tapirs and ateline monkeys is largely limited by mouth width, whereas agoutis are able to take hold of a fruit with their teeth, a behaviour that allows them to transport a fruit in its entirety without having to fit it into their mouth. For example, agoutis commonly transport whole avocado fruits (*Persea americana*, 80 mm diameter; P. Mittelman, personal observation), and *Bertholettia excelsa* fruits (110 mm diameter; Tuck Haugaasen *et al.*, 2012).

While all animals in these groups are able to disperse large seeds to some extent, they are not functionally redundant: agoutis, tapirs and large primates each interact with particular subsets of plant species (Vander Wall & Beck, 2012; Bueno *et al.*, 2013), have different dispersal distances, and distinct spatial patterns of seed deposition (Russo, 2005; Gálvez *et al.*, 2009; Bueno *et al.*, 2013). Tapirs and ateline monkeys disperse great numbers of seeds of a wide range of sizes, usually in a clumped pattern [seeds are deposited in the faeces and frequently in the same defecation sites such as latrines and around sleeping trees (Fragoso, 1997; González-Zamora *et al.*, 2012)] and over longer distances, facilitating colonization of new sites; whereas agoutis hoard larger seeds, move them shorter distances, and cache them in micro-environments that often favour germination. Thus, agoutis can act as primary seed dispersers or can complement large-frugivore seed dispersal by scattering and burying seeds found in the faeces of these animals through diplochory. Moreover, in defaunated fragmented areas, where large frugivores have been extirpated, agoutis might provide important dispersal services for large-seeded plants that would otherwise have no other dispersal agent.

VIII. AGOUTIS AND CARBON STORAGE

Recent studies have linked seed dispersal by large frugivores to the maintenance of carbon stocks in tropical forests (Bello *et al.*, 2015; Peres *et al.*, 2016; Culot *et al.*, 2017; Chanthorn *et al.*, 2019). Since large frugivores usually consume and disperse fruits with larger seeds compared to small animals (Jordano, 2000; Galetti *et al.*, 2013) and large-seeded tree species tend to have greater wood density and height (Bello *et al.*, 2015), seed dispersal by large frugivores helps to sustain high levels of above-ground biomass and carbon storage (except in biomes where most seeds are abiotically dispersed; Osuri *et al.*, 2016). Seed dispersal by frugivores also helps to

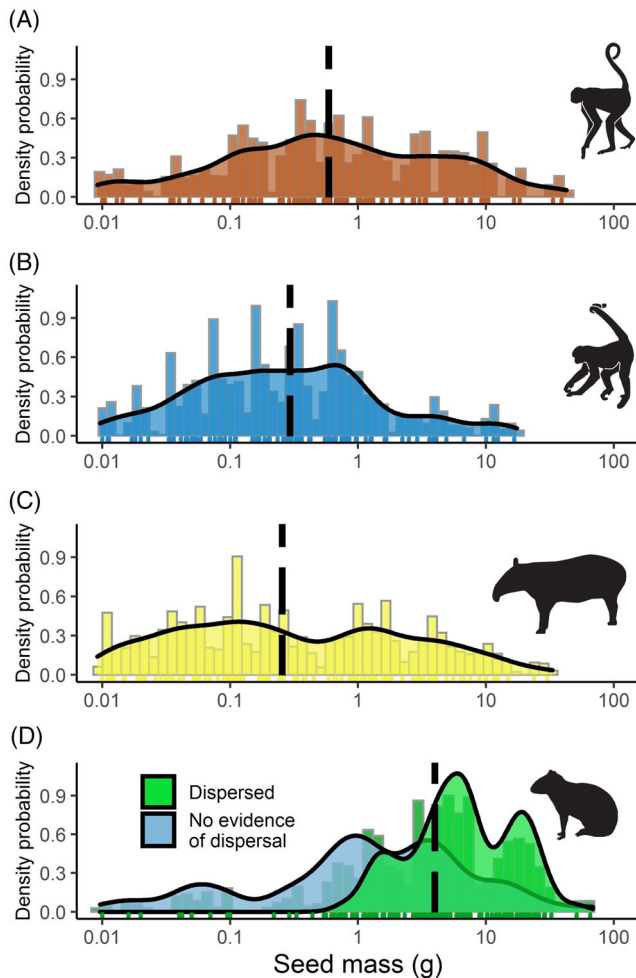


Fig. 7. Agouti interactions with plant species involve heavier/larger seeds compared with large Neotropical frugivores. The graphs show the distribution of seed masses for plants in interactions with (A) *Ateles* monkeys, (B) *Brachyteles* monkeys, (C) tapirs and (D) agoutis. Dashed black lines indicate the median seed mass for each animal group. Plant–agouti interactions are shown separately for seeds known to be dispersed and those where seeds are predated but with no evidence for dispersal.

promote plant diversity (Terborgh *et al.*, 2002; Bascompte & Jordano, 2007) which is also linked to higher above-ground biomass in tropical forests (Cavanaugh *et al.*, 2014).

Agoutis are also dispersers of large-seeded plants but their contribution to carbon storage in tropical systems remains unexplored. To fill in this gap, we assessed the relationship between seed mass and carbon storage for species consumed by agoutis, confirming that large-seeded species have a greater capacity for carbon storage (Fig. 8; $N = 85$, $df = 83$, $z = 3.27$, $R^2 = 0.115$, $P < 0.005$).

Given that agoutis tend to disperse larger seeds compared to other genera of Neotropical frugivores (*Ateles*, *Brachyteles* and *Tapirus*) (Fig. 7) we investigated if these differences could be translated to dispersal of plant species that store more carbon. We found that agoutis tend to disperse plant species that

on average store more carbon than those dispersed by *Brachyteles* and *Tapirus* (Fig. 9; Kruskal–Wallis: $N = 452$, $df = 3$, $\chi^2 = 35.95$, $P < 0.0001$; Dunn’s test: $P < 0.01$ for a comparison of species dispersed by agoutis with species dispersed by tapirs and *Brachyteles* monkeys; differences not statistically significant between agouti and *Ateles* monkeys; $P = 0.664$).

We also found that plant species whose seeds are hoarded by agoutis make a greater contribution to carbon stocks than species whose seeds are mostly preyed upon by agoutis (*t*-test: $N = 70$, $df = 67.99$, $t = 3.2908$, $P < 0.005$). Therefore, agoutis make a double contribution to maintenance of carbon storage in tropical forests: they favour plant species that have a high biomass by dispersing their seeds and negatively select species with low biomass by preying upon them.

IX. AGOUTIS AS FRUGIVORES AND MEGAFANAL SEED DISPERSERS

In general, large fruits provide greater rewards than small fruits due to their higher nutritional value (Galetti *et al.*, 2010; Lichti *et al.*, 2017) and are often exclusively dispersed by large frugivores due to size constraints. Agoutis, however, are reported mainly to eat and hoard seeds after discarding the pulp rather than ingesting entire fruits; this behaviour will allow them to disperse larger seeds than most animals in a disperser assemblage would not be able to ingest. In the Neotropics, agoutis are believed to be the main or exclusive seed dispersers of plants with very large fruits (Asquith *et al.*, 1999; Jansen *et al.*, 2012; Mittelman *et al.*, 2020) due to a shortage of dispersers of large-seeded fruits hypothesized to be caused by the extinction of Pleistocene megafaunal herbivores that used to interact with these fruits (Janzen & Martin, 1982; Guimarães, Galetti & Jordano, 2008). The megafaunal dispersal syndrome refers to oversized fruits that show adaptations to dispersal by extinct mega-herbivores, with no substitute disperser in contemporary fauna. Several authors suggest that after megafauna went extinct in the Neotropics, agoutis adopted a more central role in the dispersal of type I megafauna fruits [fruits with few (<5) but large (>20 mm) seeds (*sensu* Guimarães *et al.*, 2008)] due to extensive dietary overlap with the diets of megafaunal frugivores (Pires *et al.*, 2014). This hypothesis has been challenged by evidence that seed-dispersal services provided by agoutis to large-seeded plants are unlikely to be as effective as those provided by the extinct megafauna. For example, while megafauna could potentially have been able to disperse seeds over thousands of meters, agoutis often only move seeds a few meters away from parent plants. However, the dispersal effectiveness of agoutis is likely to have been underestimated by seed-tracking methods that limit the evaluation of dispersal distances. By using a method not biased against longer dispersal distances and higher-order movements to track seed-dispersal distances, Jansen *et al.* (2012) showed that agoutis can disperse seeds over much larger distances than previously thought, confirming that agoutis could indeed be substitute dispersers of megafaunal fruits.

Despite more reliable seed-tracking methods providing better evidence for the role of agoutis as substitute megafaunal

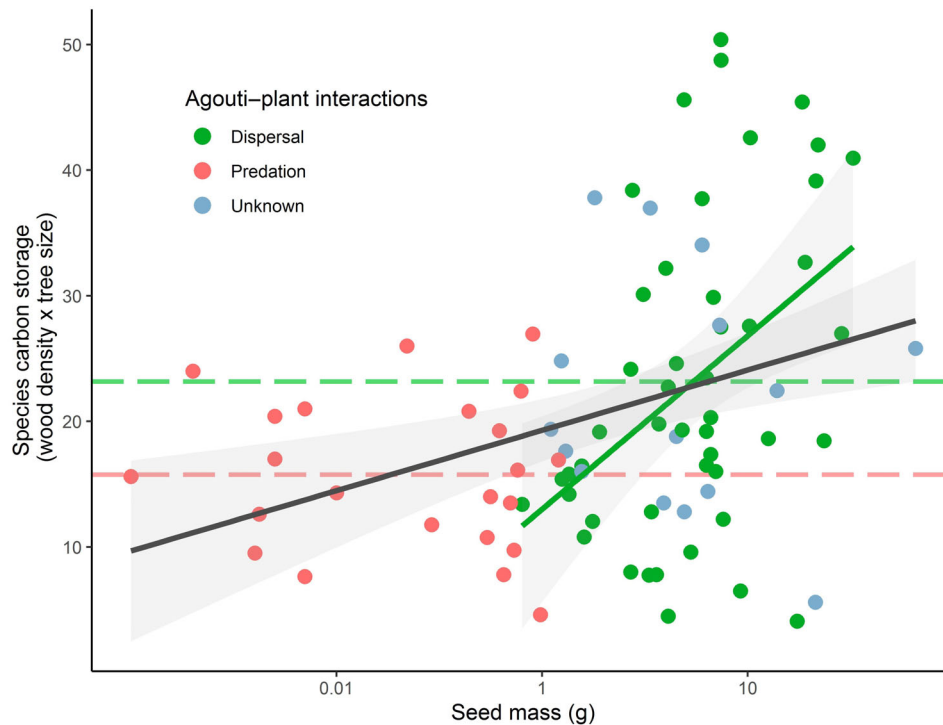


Fig. 8. Relationship between seed mass and carbon storage (estimated as wood density \times mature tree size) according to plant-agouti interaction type. Heavier seeds are produced by plants that store more carbon and are more likely to be dispersed by agoutis. Dashed horizontal lines represent mean carbon storage for plants with seeds dispersed and eaten by agoutis. The solid black line is the linear regression for all plant species known to interact with agoutis and the solid green line for species known to be dispersed by agoutis. We consider that all species that have seeds weighing less than 0.8 g (the minimum seed mass for which we found evidence of dispersal) are exclusively predated (no dispersal) by agoutis. Seeds weighing more than 0.8 g but with no record of seed dispersal were deemed neither dispersed nor eaten and placed in the ‘unknown’ category.

dispersers, dispersal services provided by agoutis are unlikely to be exact substitutes due to differences in the magnitude of quantitative (e.g. number of seeds dispersed) and qualitative (e.g. dispersal distances) contributions provided by these two groups. However, in the absence of megafauna, agoutis play an essential role in the dispersal and regeneration of megafaunal fruits.

We found that agoutis interact with 42 plant species that fit the definition of type I megafaunal fruits in 51 unique plant–agouti interactions. Among the megafaunal fruits dispersed by agoutis, half are from the palm family (Arecaceae; $N = 21$ spp.) family and nine from the Leguminosae family, including genera known to be dispersed mainly by scatterhoarding rodents (Muñoz, Trøjelsgaard & Kissling, 2019).

Almost all reports of interactions between agoutis and megafaunal fruits indicate that agoutis act as effective dispersers of these fruits. The exceptions are two studies that show that agoutis act exclusively as seed predators, suggesting no benefits for the plants involved. One of these two cases involves the palm *Syagrus romanzoffiana*, whose seeds were exclusively predated by *D. leporina*, a result that is attributed by the authors to trait-related choices in the decision-making process by agoutis (Galetti *et al.*, 2010). However, most records provide strong evidence for an effective role of agoutis as mutualistic dispersers.

Palms include 21 species that were probably dispersed by megafauna but that are also reported to be a main item in the diet of agoutis. A classic example on the benefits provided by agoutis for oversized fruits comes from Smythe (1989), who showed that seeds of *Astrocaryum standleyanum* buried by agoutis had much higher germination success (29.6%) than those left on the forest ground surface (2.6%). More recently, Kuprewicz (2015) showed that seeds of a congeneric palm species (*A. alatum*) are also effectively dispersed by agouti, and that hoarded seeds benefit from seed escape and have an increased probability of germination. Pires & Galetti (2012) used seed-fate field experiments to show that agoutis hoard rather than eat most *A. aculeatissimum* seeds that they interact with, a process that has been suggested by other authors to be crucial for seedling establishment of this palm (Dracxler & Forget, 2017). These examples show that seed caching by agoutis is likely to be a key step for seedling regeneration of megafaunal palm fruits, possibly because palm seeds found on the forest floor are highly susceptible to seed predation by invertebrates (Dracxler, Pires & Fernandez, 2011; Kuprewicz, 2015).

Agoutis may not entirely substitute the services provided by extinct megafauna frugivores in terms of dispersal distances and numbers of dispersed seeds, but the evidence compiled here suggests that agoutis act as key dispersers of

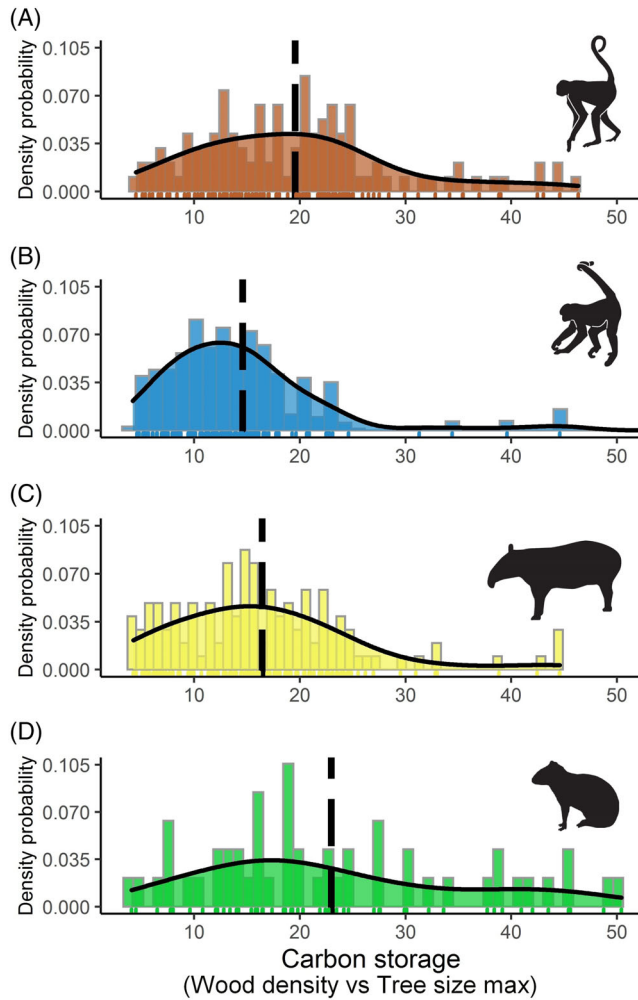


Fig. 9. Agoutis disperse plant species that have higher carbon storage potential compared with species dispersed by large Neotropical frugivores. The graphs represent the distribution of plant–animal interactions in relation to a carbon storage proxy (plant wood density \times maximum tree size) for (A) *Ateles* monkeys, (B) *Brachyteles* monkeys, (C) tapirs and (D) agoutis. Dashed lines are the median carbon storage capacity of all plant species for each animal group.

many species once consumed by megafauna, sometimes as the main or sole disperser of large-seeded plant species. Their possibly unique role as substitutes of extinct megafauna may be because agoutis interact with larger seeds than other mammals do on average (Fig. 7) and are the only species able to disperse the largest seeds.

X. AGOUTI CONSERVATION, REWILDING AND RESTORATION OF ECOLOGICAL INTERACTIONS

Four agouti species are of ‘Least Concern’ according to the IUCN *Red List* because of their wide range and large populations.

Indeed, agouti populations in the Amazon and in Central American lowland forests are generally in high numbers (Jorge & Peres, 2005; Emmons, 2016), nevertheless, even in these areas, agoutis are often consumed as bushmeat and suffer constant hunting pressures (Carrillo *et al.*, 2000; Cummins *et al.*, 2015). Some species elsewhere are showing declining populations and these species are considered ‘Threatened’ because of habitat reduction due to agricultural and urban expansion (e.g. *D. mexicana*; Vázquez *et al.*, 2008) or hunting (e.g. *D. ruatanica*; Schipper, Emmons & McCarthy, 2016). Many agouti species have very small geographic ranges, making them vulnerable to extinction, and for which we lack important ecological information that is essential for conservation (e.g. *D. iacki*; Roach & Naylor, 2016).

Local extinctions of agouti populations are common in fragmented landscapes (Galetti *et al.*, 2017), presenting a threat for the dispersal of large-seeded plants in these areas. Impacts on plant populations in areas where agoutis are now absent can take many decades to appear as most large-seeded plants are long-lived trees. This creates extinction debts on local floras that, over time, will adversely affect plant populations. In such locations, agouti reintroduction programs might be appropriate to reverse the loss of seed dispersers. For instance, in Tijuca National Park (Rio de Janeiro, Brazil) agoutis have been successfully reintroduced (Cid *et al.*, 2014), resulting in a well-established and growing population (Kenup *et al.*, 2018) and on the restoration of dispersal interactions with large-seeded species (Zucaratto, 2013; Mittelman *et al.*, 2020).

XI. FUTURE RESEARCH

Although recent research has substantially improved our knowledge about the dynamics of plant–agouti interactions, many questions remain unanswered. For instance, does greater cache retrieval by agoutis benefit plants? The advantages of cache recovery by agoutis are clear for seeds that are re-cached: they are dispersed away from the parent plant, over greater distances and have a greater survival probability (Hirsch *et al.*, 2012b; Jansen *et al.*, 2012). However, buried seeds retrieved by agoutis may be eaten instead of re-dispersed. Since each time a cache is found by a hoarder there is a probability of predation, greater numbers of cache-retrieval events will cumulatively increase cache predation and decrease the final number of hoarded seeds. Thus, it remains unclear whether the benefits of the multi-step re-caching process for some seeds outweigh the costs of a higher cache predation for seeds in general.

Most studies do not follow the fates of hoarded seeds for lengthy periods and thus do not provide information on the proportion that sprout into seedlings, or how many of these seedlings survive. Those are important pieces of evidence for understanding which interactions between agoutis and plants are mutualistic and which are antagonistic (Zwolak & Crone, 2012). The potential role of agoutis in controlling populations of small-seeded plants through predation also requires further investigation. Since we suggest that agoutis are

invariably predators of small seeds they might have an influence on the demographics of small-seeded plant species. This could be especially relevant for controlling dominant and invasive species. Future studies should also explore if agoutis can act as endozoochorous seed dispersers, i.e. whether they are effective dispersers of seeds following passage through the gut. Although this type of dispersal is uncommon for granivorous animals, there is evidence that other rodent species disperse seeds endozoochorically (Campos *et al.*, 2008; Lessa, Paula & Pessoa, 2019; Yang *et al.*, 2019).

We also lack studies about the effects of agouti local extinction on large-seeded plant populations. How population structure and dispersal processes are affected by the absence of agoutis, and how do they change over time? Areas without agoutis might serve as control areas to elucidate these ecological roles of agoutis in more detail.

XII. CONCLUSIONS

- (1) Agoutis are generalist frugivores that consume a wide range of fruits, seeds and even newly sprouted seedlings. Plant-agouti interactions are randomly distributed across the entire Neotropical plant phylogeny, confirming their broad diet. However, Arecaceae and Leguminosae seem to be the families in which seeds are most commonly eaten by agoutis.
- (2) Seed traits greatly influence whether agoutis eat or hoard seeds. Larger seeds have a greater probability of being hoarded, dispersed further and surviving to germination. Plant species with seeds weighing less than 0.8 g are hardly ever dispersed by agoutis. Agoutis also appear to favour durable, protein- and lipid-rich seeds and those containing secondary metabolites that hinder but do not impede consumption. Resource abundance positively affects the number of seeds dispersed by agoutis, whereas interspecific and intraspecific competition has the opposite effect.
- (3) In most cases, agoutis are efficient dispersers of large-seeded plants, and some plant species rely mainly or exclusively on agoutis for their dispersal. Seed burial and directed dispersal by agoutis can result in positive outcomes because seeds are often placed in germination-suitable micro-environments and in new areas, away from conspecific plant individuals. Agoutis can act as primary dispersers of seeds or as secondary dispersers, complementing other dispersal processes by caching seeds in safe sites.
- (4) The general conclusion that agoutis are effective seed dispersers of large seeds is very likely to hold for acouchies. Although understudied, acouchies are likely to have an important role for the natural regeneration of plants in Amazonian ecosystems.
- (5) Agoutis interact with and disperse seeds that are often larger than those consumed and dispersed by large Neotropical frugivores, such as the tapir. Plant species with the largest and heaviest seeds (> 10 g) seem to be dispersed

almost exclusively by agoutis. This information together with studies compiled herein suggests that agoutis are one of the most important dispersers of megafaunal fruits. Agoutis contribute to carbon stocks in tropical forests by dispersing seeds of plants that have the highest carbon storage capacity and by preying upon seeds of species with low biomass.

- (6) Agoutis are widely poached as bushmeat and extirpation of their populations is common in fragmented landscapes, which also hinder the maintenance of large-seeded plant populations. Agouti reintroduction might be a good strategy to reverse the loss of seed-dispersal processes in areas that are now under low or no hunting pressure.

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XV. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Data set on plant–agouti interactions.

Table S2. Data set on plant–acouchi interactions.

Table S3. Data set on interactions between plants and large Neotropical frugivores.

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