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Seed Removal by an Introduced Scatter-hoarder on a Caribbean Island

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Abstract.–The introduction of non-native seed dispersers has the potential to significantly alter distributions and relative abundances of native plants. Although effects of introduced seed predators have been documented, little is known about how introduced dispersers influence seed movement patterns. We investigated seed removal of seven rainforest species on the island of Dominica in the Lesser Antilles by the entire seed-remover community and specifically by the Red-rumped Agouti, *Dasyprocta leporina*, a scatter-hoarding rodent introduced to the island approximately 2500 years ago. We recorded removal rates in three regions of Dominica from 168 experimentally placed seed groups containing a total of 1356 seeds. Seed groups were either accessible to the entire seed-remover community or placed within exclosures designed to exclude agoutis. Within 13 days, 47 percent and 28 percent of seeds had been removed from control groups and agouti exclosure groups, respectively, leading to 19 percent of seed removal being attributed to agoutis. Species with smaller seeds were preferentially taken by seed removers other than agoutis, whereas agoutis were responsible for the majority of the removal of larger-seeded species. Seed removal was greater in areas with higher regional conspecific adult densities regardless of treatment, but agoutis had a greater impact relative to other seed removers on the seed removal of the study's rarest species. The results of this study highlight the potential impacts that introduced dispersers may have on native plant communities and call for further study of disperser introductions worldwide.

Keywords.–*Dasyprocta leporina*, Dominica, Neotropics, scatterhoarding, seed dispersal

Introduction

The movement of seeds by terrestrial mammals is a critical part of many plant life cycles, and can greatly affect the spatial distribution of tree species (Howe and Smallwood 1982, Morales and Carlo 2006). This process stands to be heavily impacted by changes in the local seed disperser community. Rodents are a group of seed predators and dispersers that are commonly introduced to island systems where they have the potential to significantly alter plant distributions through direct seed predation and seed movement patterns (Campbell and Atkinson 1999, Meyer and Butaud 2009, Chimera and Drake 2011, Shiels and Drake 2011). Most of our current knowledge on the effects of these introductions is based on rats, which are considered primarily seed predators (but see Shiels and Drake 2011). Much less is known about how the introduction of terrestrial mammals known to be primarily seed dispersers will affect seed movement and plant distributions on islands where they are introduced.

In the Neotropics, agoutis (Dasyprocta spp.: Dasyproctidae) are key dispersers of rainforest seeds, and these large rodents (2-5kg) commonly occur throughout dry and moist Neotropical forests (Silvius 2003). As scatter hoarders, agoutis store seeds in shallow caches for later consumption, but effectively disperse the seeds that are cached and never recovered (Galvez *et al.* 2009, Henry 1999). Agoutis are traditionally thought of as dispersing seeds distances less than 20 m (Haugaasen *et al*. 2010, Peres and Baider 1997), however recent evidence suggests that agoutis often re-cache seeds several times, dispersing seeds up to 280 m from the parent plant (Jansen et al. 2012). In many continental Neotropical rainforests, agoutis (*Dasyprocta* spp.) are the main dispersers of numerous plant species (Forget 1992, Galetti *et al.* 2006, Guimaraes *et al.* 2005, Peres *et al.* 1997) and are the only known dispersers of many larger-seeded species (Asquith *et al.* 1999, Hallwachs 1986). While common throughout their native range, agoutis have been introduced to many islands of the Lesser Antilles.

One such island is Dominica, to which

the Red-rumped Agouti (*Dasyprocta leporina*; Linnaeus 1758) was introduced circa 2500 ybp (Wing 2001). Dominica experiences naturally low diversity of both native trees and seed dispersers, with large ground-dwelling seed dispersers being historically absent. The low diversity of native ground-dwelling dispersers in Dominica likely influenced seed dispersal patterns on the island. Moreover, the historic lack of large-bodied, ground-dwelling dispersers suggests that the introduction of agoutis may have significantly altered seed movement patterns in Dominican forests, especially for large-seeded species.

In order to understand the seed-movement patterns on the forest floor in Dominica, and specifically how those patterns are affected by agoutis, we documented the removal (dispersal and predation) of seeds of six species of canopy trees and one species of liana (*Connarus grandifolius*; Table 1). Specific questions addressed in this study were the following: 1) What proportion of seeds lying on the forest floor is removed by the seed- remover community? 2) How much of the removal can be attributed to agoutis? 3) Do agoutis tend to remove different seeds than the rest of the seed remover community? and 4) Does local abundance of conspecific adult trees affect seed removal?

Methods

The island of Dominica (15°25'N, 61°20'W) encompasses 724 km^2 and lies at the center of the Lesser Antillean archipelago, 560 km north of the coast of Venezuela (Fig. 1). Since its formation, Dominica has experienced numerous large-scale volcanic eruptions (Sigurdsson & Carey 1981) as well as a regular regime of hurricane damage (Tanner *et al.* 1991), both of which have undoubtedly influenced the biota present on the island. However, Dominica has experienced relatively little human development compared to other islands in the Caribbean. Dominican forests have naturally low tree diversity compared to continental Neotropical rainforests; Fisher's α diversity of trees ≥ 10 cm in diameter is 9.8 for Dominican rainforests (K. Ickes and S. J. DeWalt, unpublished data) as compared to 41.9 at La Selva, Costa Rica (Lieberman & Milton 1987), 37.7 on Barro Colorado Island, Panama (Leigh 1999), and 89.5 at Cocha Cashu, Peru (Gentry 1988). Common ground-dwelling species capable of seed dispersal other than agoutis on this island include crabs (*Guinotia dentate*), mice (*Mus musculus*), rats (*Rattus rattus, Rattus norvegicus*), and possums (*Didelphis marsupialis*), of which crabs are the only native dispersers. Flight-based rainforest seed dispersers are limited to several small bird

Table 1. Seed mass, length, width, ± 1 standard deviation and the average adult densities in each study region (individuals/ha) of each study species. Adult densities were estimated from 0.25-ha tree plots found in each region (6 in the NE, 4 in the NW, and 7 in the SE).

Species	Family	Species code	Seed mass (g)	Seed length (cm)	Seed width (cm)	Adult density		
						NE	NW	SW
Connarus grandifolius	Connaraceae	CONNGR	3.13 ± 0.41	2.93 ± 0.24	1.56 ± 0.1	26.7	0.0	13.1
Dussia martinicensis	Fabaceae	DUSSMA	21.38 ± 6.19	5.41 ±0.6	2.90 ± 0.42	0.0	1.0	0.6
Sterculia caribaea	Malvaceae	STERCA	2.68 ± 0.48	2.43 ± 0.15	1.51 ± 0.12	54.7	49.0	74.3
Swartzia caribaea	Fabaceae	SWARCA	11.13 ± 3.9	3.41 ± 0.71	2.56 ± 0.31	4.7	6.0	24.6
Tovomita plumieri	Clusiaceae	TOVOPL	4.92 ± 1.06	3.98 ± 0.4	1.57 ± 0.13	6.7	4.0	0.6
Trichilia septentrionalis	Meliaceae	TRICSE	1.94 ± 0.31	2.56 ± 0.2	1.21 ± 0.1	2.0	3.0	7.4
Turpinia occidentalis	Staphyleaceae	TURPOC	3.94 ± 1.06	2.18 ± 0.22	2.13 ± 0.21	0.0	0.0	0.0

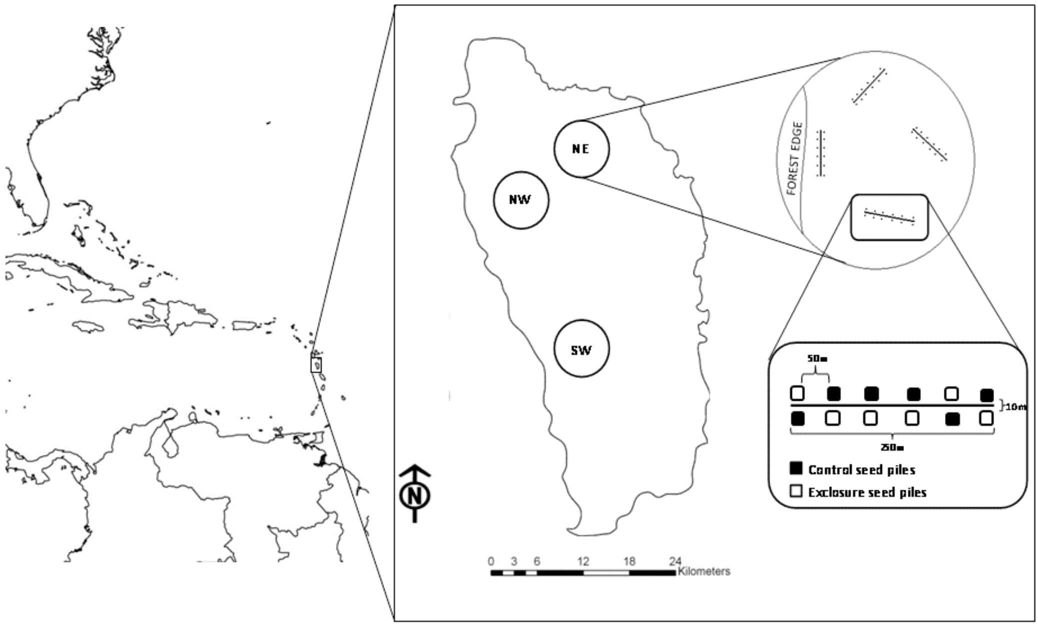

Fig 1. Diagram of the three study regions on the island of Dominica, the placement of transects within each region (NE, NW, SW), and the placement of seed groups along each transect.

species, one species of large pigeon (*Columba squamosa*), and four species of frugivorous bats (*Brachyphylla cavernarum, Ardops nichollsi, Artibeus jamaicensis, Sturnira lilium*).

We followed the removal of 1356 seeds experimentally placed on the forest floor either in open control groups (available to all seed removers) or within exclosures designed to exclude only agoutis (available to all seed removers except agoutis). Seeds were collected from the forest floor or fruiting branches and cleaned of any aril material (all species produce dry, dehiscent fruits). Aril material often detaches from the seed naturally and was highly variable upon seed collection, thus removal of aril material assured consistency within species while still presenting removers with seeds in a way that they commonly occur on the forest floor. Guimaraes *et al.* (2006) also demonstrated that the presence of pulp on a seed does not significantly affect the likelihood that *D. leporina* will take the seed. Seeds were checked for signs of viability, and seeds that were hollow (undeveloped) or showed signs of pathogen damage were discarded prior to placement in experimental groups. Leaf litter was not removed under experimentally placed seeds as earlier studies showed a significant effect of leaf litter clearing on seed removal (B. Taylor, unpublished data).

A total of 168 experimental seed groups were placed on the forest floor in 250 m transects, with a pair of seed groups (one control, one exclosure) placed every 50 m for a total of 12 seed groups per transect (Fig. 1). Within each pair, seed groups were placed 10 m apart, which doubles conservative estimates of olfactory detection of seeds by agoutis (Aliaga-Rossel *et al.* 2008). Transects were distributed across three environmentally distinct regions of Dominica (southwest, northwest, northeast) and were oriented both adjacent to the forest edge and along random trajectories within the forest interior.

Agouti exclosures were constructed of wire mesh (2.5 cm^2 mesh size) set up in a 1 m x 1 m square with an open top and a 7-cm gap between the bottom of the mesh and the ground. This design allowed for entry of avian seed removers through the open top as well as small, ground-dwelling seed removers through the gap beneath the bottom of the mesh. Similar design and dimensions have previously been used to exclude agoutis in seed dispersal studies (Paine & Beck 2007). Because control seed groups were accessible by the entire seed remover community and exclosure seed groups were accessible to the entire seed remover except agoutis, we use the difference in seed removal between these groups as the proportion of seed removal being carried out by agoutis.

Recognizing potential deterrence effects that the exclosure material might have on seed removers, even those that could physically gain access into exclosures, we constructed a dummy exclosure 1 m above the forest floor over one control seed group in each transect. This dummy exclosure presented the exclosure material while allowing ample space beneath for all species of seed removers to access these seed groups. The lack of difference between seed removal from these and the other control piles on each transect indicated that the exclosures likely did not deter species other than agoutis from removing seeds ($F_{5,521} = 0.93$, $P = 0.33$).

Seeds were placed into experimental seed groups within 7 days of collection. Each seed group contained one seed from each of the study species (Table 1) except for *Trichilia septentrionalis* for which there were three seeds due to an abundance of seeds collected for this species. This resulted in a total of nine seeds per seed group. Visual assessment of removal was made 3, 6, and 13 days after placement of seeds. If a seed was not immediately visible, a thorough search was made within a 1-m^2 area making sure to minimize leaf litter disturbance.

Local densities of conspecific adults were measured using data from a set of 17 0.25-ha permanent forest dynamic plots established in each of the three study regions (DeWalt and Ickes, unpublished data). For each study region, mean density of adults ($\geq$ 10 cm diameter at breast height for trees and $\geq$ 2 cm diameter for the liana species) was calculated for each of the study species and used as the local conspecific adult density.

We first tested whether the predicted probability of seed removal depended on main fixed effects of treatment (control or exclosure), species of seed, and position (forest edge or interior) as well as interaction effects of treatment*species, treatment*position, and species*position. A second model was then used to test the effect of adult plant density on the predicted probability of seed removal. This model used the fixed effects of treatment and conspecific adult plant density within a region as well as the interaction between the two. A third model was used to determine the relationship between seed mass and the predicted probability of seed removal and how this relationship may differ between agoutis and the rest of the seed remover community. This model used fixed effects of treatment, seed mass (average mass for each species), and their interaction as well as random effects of region, transect, and station within transect.

All statistical analyses were performed using the GLIMMIX procedure in SAS v.9.2 (SAS Institute Inc., Cary, NC), specifying a binomial error distribution and logit link and accounting for random effects of region, transect, and station within transect. Denominator degrees of freedom for all tests were calculated using the Kenward-Rogers adjustment, which is recommended for unbalanced data and inclusion of between-site random effects (Littell *et al.* 2006). This method resulted in non-integer denominator degrees of freedom in many cases.

Results

Of the 1356 seeds used in this study, only 38 % (510) were removed (47% from control groups and 28% from exclosure groups). More than half of the removed seeds were taken within 3 days of placement, which is consistent with predictions made by Aliaga-Rossel *et al.* (2008). The majority of seeds remaining on day 13 had germinated, were damaged, or were beginning to decompose. We found no significant difference in probabilities of seed removal for seeds placed in the forest interior compared with those placed adjacent to the forest edge ($F_{1,7.9} = 0.00$, $P = 0.99$). Removal was positively correlated to conspecific adult density ($F_{1,1040}$ = 29.23, $P <$ 0.001), indicating that seeds were more likely to be removed when conspecific adults were locally common.

Nineteen percent of observed seed removal was attributed to agoutis (difference in removal between control and exclosure groups), and the probability of removal from control seed groups was significantly greater than from seed groups within agouti exclosures ($F_{1,1006}$ = 50.89, $P <$ 0.001). Species preferences of agoutis differed significantly from those of the rest of the remover community (Fig. 2). Agoutis had a greater effect on removal of larger seeds than of smaller seeds (seed mass*treatment interaction: $F_{1,1040}$ = 9.17, $P <$ 0.01). Agoutis also constituted a higher proportion of the seed removal of locally rare species than that of more common species (adult density*treatment interaction: $F_{1,1040}$= 4.78, P= 0.029; Fig. 3).

Discussion

Sixty-two percent of seeds were left untouched after nearly two weeks, suggesting that many seeds in Dominican rainforests are likely left to germinate where they land. However, because aril material was removed in this study, this may have decreased the detectability of study seeds (Moles and Drake 1999) and contributed to a lower removal rate than might otherwise occur under natural conditions. Of the seeds that were removed from the forest floor following primary dispersal, a significant number of them were removed by agoutis. For five of our seven study species, the introduction of agoutis to the island of Dominica may have significantly increased the removal of their seeds (Fig. 2).

The effect that agoutis have on seed removal varies by plant species, and this variation correlates with seed size. Agoutis actually removed more small seeds than large seeds, but due to low overall removal rates of large seeds, agoutis were responsible for a disproportionately high percentage of the removal of our large-seeded study species (*i.e.*, > 5 g seed mass). Nutrient content or the presence of chemical and physical defenses in certain seeds are possible reasons why some species' seeds would be preferred over others (Janzen 1969, Janzen 1971). However, given the strong correlation between treatment effect and seed mass, it is likely that the largest seeds in Dominican forests exceed the maximum size that smaller local seed removers can handle (Munoz and Bonal 2008). Moreover, scatterhoarders like agoutis tend to cache rather than immediately consume large seeds due to their higher nutritional value (Forget *et al.* 1998, Galetti *et al.* 2010, Jansen *et al.* 2004). In Dominica, not only are agoutis the primary remover of large seeds, but they likely also disperse these large seeds more often than smaller seeds.

The interaction between treatment effect and adult conspecific density (Fig. 3) indicates that agoutis tend to constitute a larger proportion of the seed removal of rarer plant species. Our three rarest study species, *Turpinia occidentalis*, *D. martinicensis*, and *Trichilia septentrionalis*, were also the three species whose seed removal was influenced most by agoutis. Given the importance of seed dispersal and predation on plant distributions (Morales and Carlo 2006), it is likely that the introduction of agoutis to Dominica has altered the relative distributions of native rainforest plants. McConkey *et al.* (2012) note that alien dispersers can have a positive impact where introduced so long as they are not competing with native seed dispersers for fruit. The absence of large-bodied, ground-dwelling native seed dispersers in Dominica suggests that the introduction of agoutis may therefore be beneficial to native seed dispersal in this system. Future studies should therefore investigate whether or not the potential benefits of dispersal provided by the scatter hoarding of agoutis are outweighed by the negative impacts of predation on those large-seeded species utilized most frequently as a food resource.

A limited set of camera traps capturing images of seed removal of our study species suggest that the overwhelming majority of seed removal in Dominican rainforests is carried out by some type of introduced rodent. All of the 15 removal events captured on camera were

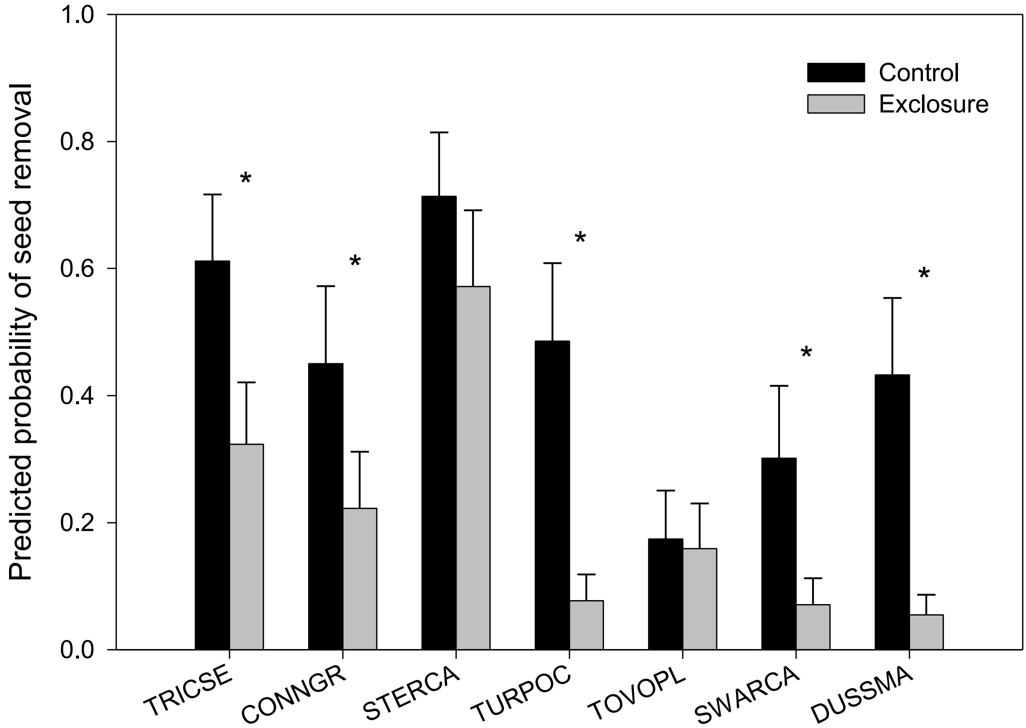

FIG 2. Predicted probability of seed removal (+ 1 SE) for each study species in control treatments (all seed removers allowed) and exclosure treatments (agoutis excluded). Species are arranged in order of increasing seed mass. Asterisks indicate species for which the probability of a seed being removed differed significantly between control and exclosure treatments. Species codes correspond to those presented in Table 1.

conducted by introduced rodents (13 by rats, 2 by agoutis), suggesting that the introduction of seed-eating rodents to Dominica has substantially changed the seed removal patterns of rainforest plants. Rats are well known introduced seed predators on islands worldwide (Shiels and Drake 2011), and agoutis are shown to be effective seed dispersers and seed predators in their native range. In the absence of native ground-dwelling seed predators and dispersers, this highlights not only the overall influence of introduced rodents on seed removal in Dominica, but also the importance of potential seed dispersal that agoutis carry out in this system.

Due to the limited ranges of most plant species used in this study, relatively little is known about their natural dispersal vectors. The four species of frugivorous bats that are known to inhabit Dominica are the most likely native primary dispersers of large seeds on the island. Of these bats, the largest species is the Jamaican Fruit-eating Bat (*Artibeus jamaicensis*), which is capable of carrying even our largest study species at least short distances (Gardner 1977). Although no literature exists reporting that *A. jamaicensis* consumes any of our study species, Janzen *et al.* (1976) reported that this species removes whole legume fruits, consuming at least part of the fleshy aril and dropping the seed intact below feeding roosts. However, bats do not remove fruits from the ground, and therefore their activities would be limited to primary seed dispersal. Moreover, bats typically deposit seeds in high densities below feeding roosts, where the seeds may be more susceptible to density dependent sources of mortality. Scatter-hoarders such as agoutis, conversely, tend to spread seeds spatially to reduce cache robbery (Galvez *et al.* 2009). In Dominican forests, it is possible that

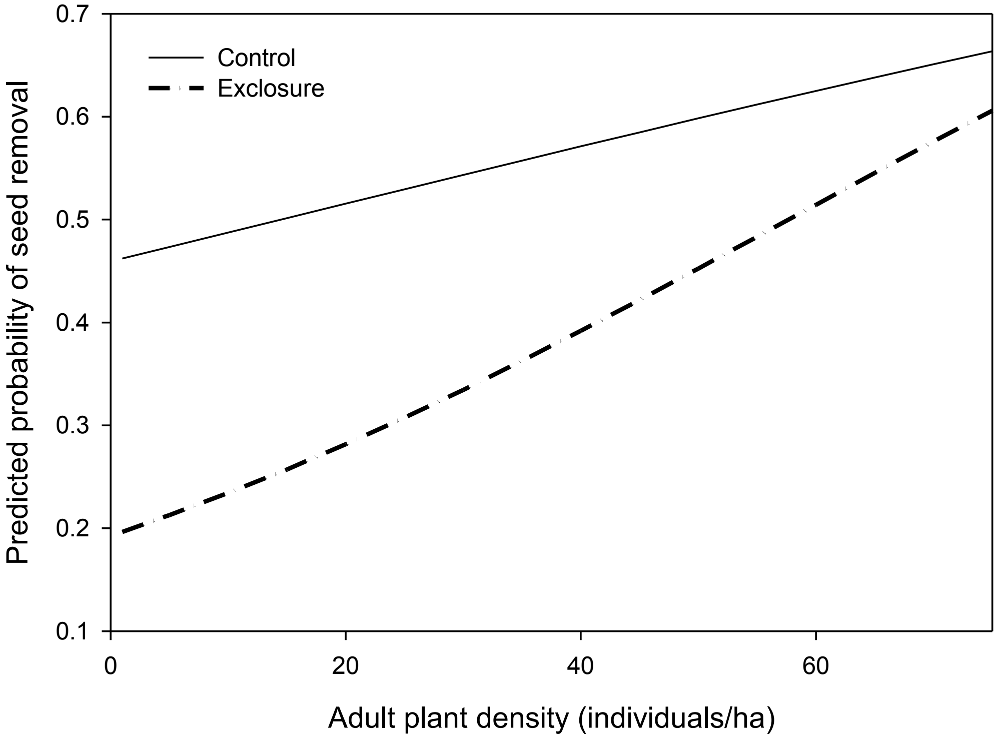

Fig 3. Predicted probability of seed removal in control and exclosure treatments as a function of regional conspecific adult plant density.

the more even distribution of seeds following secondary dispersal by agoutis has affected seedling competition and plant distributions of species that agoutis scatter-hoard.

Ground-dwelling seed dispersers, such as agoutis, are known to have substantial impacts on plant distributions in their native ranges (Peres and Baider 1997, Silva and Tabarelli 2001, Silvius and Fragoso 2003), but we know surprisingly little about the impact that alien dispersers have on the local plant community where they are introduced (but see Castro *et al.* 2008). Several studies have highlighted the importance of agoutis in taking over seed dispersal roles following the extinction or extirpation of large-bodied seed dispersers (Asquith *et al.* 1999, Galetti *et al.* 2010, Hallwachs 1986), yet the influence of agoutis when introduced into a new system, especially one lacking many large-bodied dispersers, remains largely unexplored. Studies investigating the role of introduced dispersers in determining native and endemic plant distributions, determining seed choices of native dispersers, and possibly facilitating the introduction of non-native plant species would provide critical insight into the preservation and management of forests where non-native dispersers have been introduced.

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