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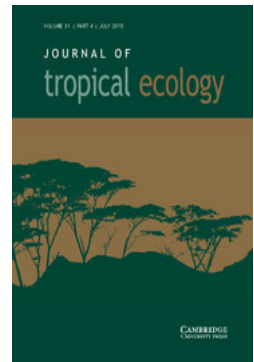
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Primary seed dispersal by a sigmodontine rodent assemblage in a Peruvian montane forest

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Abstract: We examined quantity and quality components of primary seed dispersal for an assemblage of sigmodontine rodents in a high-elevation montane tropical forest in Peru. We collected faecal samples from 134 individuals belonging to seven rodent species from the subfamily Sigmodontinae (Cricetidae) over a 2-y period. We conducted seed viability tests for seeds found in faecal samples. We identified seeds from eight plant families (Bromeliaceae, Annonaceae, Brassicaceae, Ericaceae, Melastomataceae, Myrtaceae, Rosaceae, Solanaceae), nine genera and 13 morphospecies. The most abundant seeds belonged to *Gaultheria* sp. 1 (46% of total) and *Miconia* sp. 1 (31% of total), while the most viable seeds belonged to *Greigia* sp. (84% viability) and *Guatteria* sp. (80% viability). We utilized relative rodent abundance, seed species diversity, seed abundance and seed viability per rodent species to calculate an index of rodent disperser effectiveness, and found that *Thomasomys kalinowskii* was the most effective disperser, followed by *Akodon torques*, *Calomys sorellus*, *Thomasomys oreas*, *Oligoryzomys andinus* and *Microryzomys minutus*. Plant genera dispersed by sigmodontine rodents overlapped more with bird- and terrestrial-mammal-dispersed plants than with bat-dispersed plants. Future neotropical seed dispersal studies should consider small rodents as potential seed-dispersers, especially in tropical habitats where small-seeded, berry-forming shrubs and trees are present.

Key Words: frugivory, Peru, rodents, seed dispersal, Sigmodontinae, tropical montane forest

INTRODUCTION

In neotropical rain forests, seed dispersal by rodents has been shown to play an important role in plant reproduction via scatterhoarding, seed caching and/or secondary seed dispersal (Forget 1990, 1992; Forget & Milleron 1991, Forget *et al.* 2002, Jansen *et al.* 2012). Rodents shown to disperse seeds of neotropical plants via these mechanisms are generally medium- to large-bodied, and consume fruit and/or seeds of canopy tree species (Adler & Kestell 1998, Dittel *et al.* 2015, Forget 1990,

1991, 1992; Haugaasen *et al.* 2010, Hoch & Adler 1997, Smythe 1989). Small-bodied rodents, on the other hand, are widely considered to be seed predators (Demattia *et al.* 2004, Denslow & Moermond 1982, Grenha *et al.* 2010, Griscom *et al.* 2007, Ostfeld *et al.* 1997, Pinto *et al.* 2009). Because of their influence on seed survivorship and seedling recruitment, several authors have called for inclusion of small rodents in guild/community studies of seed dispersal, but mostly to investigate their influence via seed predation (Demattia *et al.* 2004, Grenha *et al.* 2010). However, recent evidence for the neotropical rodent subfamily Sigmodontinae (Cricetidae) indicates that several species consume fruit and/or pass intact seeds

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in diverse neotropical habitats such as the montane forests in Peru (Noblecilla & Pacheco 2012, Sahley *et al.* 2015), scrub habitats in Chile (Meserve 1981) and the Atlantic forests in Brazil (Vieira *et al.* 2003). Despite these findings, only one published account for cricetid rodents (< 100 g) noted primary seed dispersal occurring via the digestive tract by *Necomys lasiurus* (formerly *Bolomys lasiurus*) after consumption of *Miconia albicans* fruit (Magnusson & Sanaïotti 1987). Data on diet of small-bodied rodents and their potential for primary seed dispersal are therefore limited (Sahley *et al.* 2015).

Determining the role that small-bodied (<100 g) rodents might play in seed dispersal is crucial, given the importance of dispersal for plant reproductive success (Dalling *et al.* 2002, Howe & Smallwood 1982, Wunderle 1997), re-establishment of plants in disturbed ecosystems (Medellin & Gaona 1999, Parrotta *et al.* 1997, Tabarelli & Peres 2002, Wunderle 1997), and the ubiquity of small rodents in neotropical habitats (Voss & Emmons 1996). During a study examining potential impacts on small-rodent populations due to construction of a natural gas pipeline through a montane tropical forest, Sahley *et al.* (2015) found that seven species of sigmodontine rodent had intact seeds present in their faecal samples. In this study we tested the following hypotheses: (1) small rodents belonging to the subfamily Sigmodontinae (Cricetidae) have viable seeds in their faeces and function as seed dispersers; (2) based on a previous diet study (Sahley *et al.* 2015) the genus *Thomasomys* would disperse a greater diversity and abundance of seeds as well as seeds with a higher viability, therefore species belonging to this genus would be the most effective seed dispersers at the site; and (3) small rodent-dispersed plant families and genera would be more similar to those dispersed by birds than by bats.

METHODS

Study site

Our study site was located near Chiquintirca, department of Ayacucho, in the province of La Mar (13°03'34''S, 73°42'25''W), Peru. It is near the upper limit of montane forests of the Apurimac River valley ranging in altitude from 3200 to 3500 m asl. This area is categorized as pluvial montane subtropical forest (Instituto Nacional de Recursos Naturales 1995), upper montane pluvial forest of the yungas (Josse *et al.* 2003) and the Apurimac river valley montane forest ecotone (Langstroth *et al.* 2013). Vegetation consisted of a mosaic of tropical forest dominated by *Polylepis* spp. co-occurring with tropical shrubs (Langstroth *et al.* 2013, Servat *et al.* 2013). Rainfall at the site in 2011 and 2012 ranged from 30 mm in June to 388 mm in February 2012 (Sahley *et al.* 2015).

Rodent captures and sample collection

In 2011 and 2012, we used nine trapping grids 20 × 150 m in size to live-trap rodents, following the protocol outlined in Pacheco *et al.* (2013). Each grid was made up of two parallel lines separated by 15–20 m each, and each line had 16 capture stations 10 m apart. Each station consisted of two Sherman traps that were 7.6 × 8.9 × 22.9 cm. When possible, one of the Sherman traps was placed on a branch or shrub of a tree, 1–2 m above ground. Traps were baited and opened in the late afternoon and checked the following morning. In 2011, one trapping session was conducted in October and another in November (just prior to the rainy season) and in 2012 one trapping session was conducted in May (just after the rainy season). Traps were left open for a total of four nights in each session, for a total capture effort of 6912 trap nights. Captured rodents were identified to species, age class and weighed before being tagged and released.

Faecal pellets in each trap were collected and placed in labelled aluminium paper for storage. All faecal samples were transported in a cooler with silica gel to reduce humidity and stored at 0°C.

Plant species richness and reference material

We collected leaves, stems, fruits and their seeds in 2012 to establish a reference collection for seed identification. All material was deposited in the Herbarium of the Universidad Nacional Mayor de San Marcos Natural History Museum. We used Servat *et al.* (2013) and Sahley *et al.* (2015) for plant identifications.

Seed identification and quantification

We placed 12 seeds from each aluminium packet in a 140 × 20-mm Petri dish. We used distilled water to disaggregate faecal pellets and locate seeds. We used a 20× Leica RX stereoscope to determine seeds to family, genus and morphospecies when possible using our reference collection and identification keys found in Caceres (2004), Cornejo & Janovec (2010), Gentry (1993), Ponte (1988) and Rios *et al.* (2004).

All seeds were photographed with a 1-mm grid paper placed below a Petri dish. Seed length was measured with a 1-mm grid paper placed below a Petri dish. We utilized the program Image J (www.imagej.nih.gov) to determine the length for seeds smaller than 1 mm. We calculated the mean and standard deviation for seed length in our samples.

Seed viability

We assessed seed viability using a 1% solution of tetrazolium. This test allows for determination of cellular respiration, which turns the seed embryo tissues a scarlet red colour and allows for an efficient estimate of germination capacity (ISTA 1996). In most cases, we determined viability for a minimum of 10 seeds per plant and per rodent species. We were unable to conduct viability test for Rubiaceae sp. 1 and we tested only one seed for *Myrteola* sp. To conduct viability tests, we made a small cut in the seed coat on the side opposite from the embryo. The seed was soaked in distilled water for 24 h. We then removed the distilled water and we added the tetrazolium solution and soaked the seeds in complete darkness for an additional 24 h. We then removed the seed coat to evaluate viability via embryo examination. We scored the embryo as viable only when it was scarlet red; if it was partially coloured, pink, or not coloured at all we classified the seed as non-viable. Because partially coloured or pink seeds can sometimes be viable (ISTA 1996), our viability analysis is conservative and may underestimate the proportion of viable seeds.

Analysis of data

We calculated the relative abundance of each rodent species by dividing the number of individuals captured per species by the total number of rodents captured for all species combined. We utilized 12 faecal pellets per individual rodent captured to quantify the total number of seeds for each species of plant and rodent; this allowed us to standardize the relative seed quantity estimates across rodent taxa. We calculated the mean and standard deviation of seed abundance in faecal samples per individual for each rodent species and the mean and standard deviation of seed number per sample (one sample = 12 faecal pellets) for each plant species.

We calculated the proportional abundance of seeds dispersed by each rodent species by dividing the total number of seeds found for each rodent species by the total number of seeds found for all rodent species combined. The proportion of plant species diversity for each rodent species was calculated by dividing the total number of plant species found for each rodent species by the total number of plant species in all rodent species combined. The proportion viability of plant species for each rodent species was calculated by dividing the total number of scarlet-coloured seeds for each plant species per rodent species by the total number of seeds evaluated for viability for that plant species. The total combined seed viability for each rodent species was calculated by adding the number

of all viable seeds and dividing this value by the total number of seeds evaluated. Total seed viability for plant species was calculated by dividing the total number of viable seeds for each plant species by the total number of seeds evaluated.

A Kruskal–Wallis test was calculated to examine differences in frequency distributions among plant species abundance in faecal samples across rodent species and also for differences in frequency distributions among plant species abundance in faecal samples across plant species. We calculated a chi-square statistic to examine differences in proportion seed viability by plant species for which we had $n > 10$ viability tests, as well as a chi-square statistic to test for differences in proportion seed viability among rodent species.

We calculated an index of disperser effectiveness for each species of rodent by utilizing the following equation:

$$\begin{aligned} \text{Disperser effectiveness} &= \text{Relative abundance each rodent species} \\ &\times \text{proportion intact seeds in faecal samples} \\ &\times \text{proportion number plant species in samples} \\ &\times \text{proportion viable seeds} \times 100 \end{aligned}$$

Statistical analyses were performed using SPSS version 21.

RESULTS

Rodent captures

We captured and released a total of 134 rodents from seven species belonging to the subfamily Sigmodontinae (Cricetidae) in 2011–2012. These were *Akodon torques* (Thomas, 1917) ($n = 49$); *Calomys sorellus* (Thomas 1900) ($n = 20$); *Microrhynchomys minutus* (Tomes, 1860) ($n = 5$); *Oligoryzomys andinus* (Osgood, 1914) ($n = 3$); *Thomasomys kalinowskii* (Thomas, 1894) ($n = 34$); *T. oreas* Anthony, 1926 ($n = 21$); and *T. aureus* (Tomes 1860) ($n = 2$).

Plant families and species

We found seeds of a total of eight plant families, nine genera and 13 morphospecies in faecal samples collected in 2011–2012. Plant families and genera recorded include Annonaceae (*Guatteria* sp.), Brassicaceae (Brassicaceae sp. 1), Bromeliaceae (*Greigia* sp.), Ericaceae (*Gaultheria* sp. 1 and *G.* sp. 2), Melastomataceae (*Miconia* sp. 1 and *M.* sp. 2), Myrtaceae (*Myrteola* sp. 1), Rosaceae (*Rubus* sp. 1) and Rubiaceae (Rubiaceae sp. 1 and sp. 2). We found intact seeds and/or evidence of fruit pulp in faecal samples in all species of rodent. For this study, we only found fruit pulp in the faecal samples of *T. aureus* and

Table 1. Mean (\pm SD) length of seeds in rodent faecal samples for 2011–2012, Chiquintirca, Ayacucho, Peru. n = sample size. Seed size was very small in all cases.

Family	Species	n	Mean seed length (mm)
Bromeliaceae	<i>Greigia</i> sp.	5	3.60 \pm 0.43
Annonaceae	<i>Guatteria</i> sp.	12	4.43 \pm 0.50
Brassicaceae	Brassicaceae sp. 1	56	0.64 \pm 0.07
Ericaceae	<i>Gaultheria</i> sp. 1	55	0.63 \pm 0.09
Ericaceae	<i>Gaultheria</i> sp. 2	20	0.56 \pm 0.06
Melastomataceae	<i>Miconia</i> sp. 1	75	0.84 \pm 0.08
Melastomataceae	<i>Miconia</i> sp. 2	31	0.78 \pm 0.09
Myrtaceae	<i>Myrteola</i> sp.	9	1.83 \pm 0.07
Rosaceae	<i>Rubus</i> sp.	12	2.58 \pm 0.11
Rubiaceae	Rubiaceae sp. 1	12	2.58 \pm 0.11
	Rubiaceae sp. 2	2	0.84 \pm 0.04
Solanaceae	Solanaceae sp. 1	18	1.67 \pm 0.12
Solanaceae	Solanaceae sp. 2	17	2.53 \pm 0.02

Table 2. Total and mean seed abundance \pm SD for plant species recorded in 12 faecal samples per rodent, Chiquintirca, Ayacucho Peru, 2011–2012. Plant species are listed in order of abundance.

Species	Total number seeds in samples	Proportion seeds of total	Mean \pm SD seed number per sample (range) n = 132
<i>Gaultheria</i> sp. 1	2158	0.46	16.34 \pm 25.05 (0–145)
<i>Miconia</i> sp. 1	1459	0.31	11.05 \pm 27.04 (0–220)
Brassicaceae sp. 1	351	0.08	2.66 \pm 21.7 (0–223)
<i>Gaultheria</i> sp. 2	225	0.03	1.70 \pm 6.52 (0–39)
<i>Greigia</i> sp.	202	0.04	1.53 \pm 6.35 (0–42)
<i>Miconia</i> sp. 2	167	0.035	1.27 \pm 7.64 (0–75)
Rubiaceae sp. 2	33	0.007	0.25 \pm 2.87 (0–33)
<i>Rubus</i> sp.	30	0.006	0.23 \pm 1.80 (0–17)
<i>Guatteria</i> sp.	10	0.002	0.076 \pm 0.87 (0–10)
<i>Myrteola</i> sp.	6	0.001	0.045 \pm 0.37 (0–3)
Solanaceae sp. 1	6	0.001	0.045 \pm 0.36 (0–4)
Solanaceae sp. 2	6	0.001	0.045 \pm 0.36 (0–4)
Rubiaceae sp. 1	1	0.0002	0.008 \pm 0.09 (0–1)
All seeds	4654	1.00	35.3 \pm 38.2 (0–234)

could not conduct seed viability tests. Average seed length found in samples ranged from 0.56 mm to 4.43 mm, with *Gaultheria* sp. 2 having the smallest seeds and *Greigia* sp. having the largest (Table 1).

Seed abundance and distribution across samples

We found a total of 4654 seeds in rodent faecal samples, with a mean \pm SD number of 35.3 \pm 38.2 seeds per sample (Table 2). The distribution of seed abundance in samples by plant species was significantly different (Kruskal–Wallis test, $\chi^2 = 24.2$, df = 5, P < 0.05). The Ericaceae (n = 6 species of rodent), Melastomataceae (n = 3) and Rosaceae (n = 3) were the best represented families consumed by rodent species, followed by Myrtaceae and Solanaceae (n = 2), and Brassicaceae and Bromeliaceae (n = 1). *Gaultheria* sp. 1 (Ericaceae) not only had the highest total number of seeds in faecal samples, but also

the highest mean number of seeds per faecal sample; in addition seeds were also present in all six rodent species examined (Table 2). *Miconia* sp. 1 (Melastomataceae) had the second highest abundance and mean number per sample, while *Gaultheria* sp. 2 had considerably lower total and mean abundance values (Table 2). *Miconia* sp. 1 and *Gaultheria* sp. 2 occurred in faecal samples from three species of rodent. *Gaultheria* sp. 2 and the remaining morphospecies have mean values of less than three seeds per sample and are found in one to two species of rodent.

Seed viability

We found that all plant species tested (except for *Myrteola* sp.) had viable seeds in faecal samples. Differences in proportion seed viability among plant species (excluding *Myrteola* sp., Solanaceae sp. 2 and Rubiaceae sp. 1 from

Table 3. Total intact seeds found in faecal samples, relative abundance of rodent species, proportion relative abundance of intact seeds, proportion species richness found in samples and proportion of viable seeds (total number of seeds tested) for each rodent species at Chiquintirca, Ayacucho, Peru 2011–2012. The disperser effectiveness index is the relative contribution of each rodent species to effective seed dispersal and is the product of the relative abundance of each rodent species \times proportion abundance of seeds \times proportion species richness of seeds \times proportions of viable seeds \times 100.

Rodent species	Total intact seeds in 12 faecal samples per individual	Relative abundance rodent species	Proportion abundance of seeds	Proportion species richness of seeds	Proportion of viable seeds	Disperser effectiveness index
<i>Akodon torques</i> n = 49	1096	0.37	0.24	0.38	0.14 (394)	0.47
<i>Calomys sorellus</i> n = 20	1099	0.15	0.24	0.15	0.57 (130)	0.31
<i>Microroryzomys minutus</i> n = 5	29	0.04	0.006	0.08	0 (15)	0
<i>Oligoryzomys andinus</i> n = 3	36	0.02	0.007	0.08	0.2 (20)	0.0003
<i>Thomasomys kalinowskii</i> n = 34	1723	0.25	0.37	0.92	0.43 (467)	3.8
<i>Thomasomys oreas</i> n = 21	671	0.16	0.14	0.38	0.12 (210)	0.10

the analysis due to $n < 10$) were significant ($\chi^2 = 229$, $n = 1231$, $df = 9$, $P < 0.001$). *Greigia* sp. ($n = 110$) and *Guatteria* sp. ($n = 10$), only found in *T. kalinowskii*, had the highest viability values, 80% to 84% respectively. *Gaultheria* sp. 1 was found in samples from every rodent species except for *M. minutus*. Overall viability was 30% ($n = 535$), with 21% ($n = 200$) viability for seeds found in *A. torques*, 70% ($n = 110$) for *C. sorellus*, 0% ($n = 15$) for *M. minutus*, 20% ($n = 20$) for *O. andinus*, 32% ($n = 90$) for *T. kalinowskii*, and 14% ($n = 100$) for *T. oreas*. *Gaultheria* sp. 2 seeds had a total viability of 27% ($n = 90$) with viability values of 27% ($n = 30$) for *A. torques*, 25% ($n = 20$) for *C. sorellus*, and 28% ($n = 40$) for *T. kalinowskii*. Seeds of this species were not found in samples from *M. minutus*, *O. andinus* or *T. oreas*. *Miconia* sp. 1 had a total seed viability of 15% ($n = 374$), with 4% viability ($n = 164$) for *A. torques*, 27% ($n = 150$) for *T. kalinowskii*, and 13% ($n = 60$) for *T. oreas*. Seeds of this species were not found in *C. sorellus*, *M. minutus* or *O. andinus*. *Miconia* sp. 2 were found only in *T. kalinowskii* and *T. oreas*, and had an overall viability of 7.5% ($n = 40$) with a viability of 0% ($n = 10$) for *T. kalinowskii*, and 10% ($n = 30$) for *T. oreas*. *Rubus* sp. had a total viability of 55% ($n = 20$), and seeds were found only for *T. kalinowskii*. *Myrteola* sp. had 0% viability but our very small sample size ($n = 1$) for *T. kalinowskii* precludes us from making reliable viability estimates. Seeds belonging to the Brassicaceae sp. 1 were found only in *T. kalinowskii* and had a total viability of 20% ($n = 30$). Rubiaceae sp. 2 seeds had a total viability of 9% ($n = 11$), with 1 seed out of 1 viable for *T. kalinowskii* and 0 seeds out of 10 for *T. oreas*. Solanaceae sp. 1 also had a total viability of 9% ($n = 11$), with 1 seed of 1 viable for *T. kalinowskii* and 0 seeds out of 10 viable for *T. oreas*.

Solanaceae sp. 2 was found only in *T. kalinowskii* and had a total viability of 75% ($n = 4$). We were unable to conduct a viability test for Rubiaceae sp. 1.

Rodent species and seed disperser effectiveness

We found that the distributions of plant species in faecal samples varied significantly across rodent species (Kruskal–Wallis test, $\chi^2 = 24.2$, $df = 12$, $P < 0.01$). Total seed abundance in faecal samples was greatest for *T. kalinowskii* ($\bar{x} \pm SD = 50.7 \pm 57.8$), followed by *C. sorellus* ($\bar{x} \pm SD = 55.0 \pm 36.5$), *A. torques* ($\bar{x} \pm SD = 22.4 \pm 18.7$), *T. oreas* ($\bar{x} \pm SD = 32.0 \pm 20.1$), *O. andinus* ($\bar{x} \pm SD = 12.0 \pm 4.0$) and *M. minutus* ($\bar{x} \pm SD = 5.8 \pm 1.8$) in descending order (Table 3). *Thomasomys kalinowskii* had the highest proportion plant species richness represented in faecal samples with 12 species of plants occurring in faecal samples (Table 3). *Thomasomys oreas* faecal samples contained five species of plants, followed by *A. torques* (3 species), *C. sorellus* (2 species), *M. minutus* and *O. andinus* (1 species each).

Although containing a relatively low seed species diversity in samples, *C. sorellus* had a relatively high seed abundance, and the greatest percentage of viable seeds in faecal samples (57%) followed closely by *T. kalinowskii* (43% viability; Table 3). The remaining species of rodents had from 12% to 20% viable seeds, except for *M. minutus*, which had no viable seeds in faecal samples. Differences in total seed viability among rodent species were statistically significant ($\chi^2 = 177$, $n = 1236$, $df = 5$, $P < 0.001$).

An index for seed disperser effectiveness for each rodent species, calculated using relative rodent abundance,

proportional seed abundance, plant species diversity and seed viability, showed that the combination of these variables indicates that *T. kalinowskii* is the most effective seed disperser at this montane-forest site. *Akodon torques* and *C. sorellus* are the second and third most effective seed dispersers. *Thomasomys oreas* and *O. andinus* are the fourth and fifth most effective seed dispersers whereas *M. minutus* did not disperse viable seeds (Table 3).

DISCUSSION

We found that small sigmodontine rodents (<100 g) are primary seed dispersers in the high-elevation tropical montane forest studied. Five of six species of rodents passed intact and viable seeds of 13 morphospecies, eight families and nine genera of plants. Our estimate of primary seed dispersal occurrence is likely conservative because a longer-term study examining diet found seeds from 17 morphospecies and nine families in faecal samples of all seven species at the same study site (Sahley et al. 2015). Primary seed dispersal for small rodents of the cricetid family has been noted only once, for *Necomys lasiurus*, which passed viable *Miconia albicans* seeds through its digestive tract (Brewer & Rejmánek 1999). Consumption of fruit and/or passage of intact seeds by small sigmodontine rodents has been noted for these and other species in various habitats such as the Brazilian Atlantic forest (Vieira et al. 2006), Chilean temperate rain forest (Meserve et al. 1988) and montane forest in Peru (Noblecilla & Pacheco 2012, Sahley et al. 2015), however except for the *N. lasiurus* study (Brewer & Rejmánek 1999) seed viability and/or contribution to seedling establishment was not examined.

Our study site is comprised of approximately 172 species and morphospecies in 94 genera and 54 families of plants that comprise a mosaic of forest and shrub habitat near the upper limit of montane forest (Sahley et al. 2015, Servat et al. 2013). The families identified in faecal samples are known to produce berries and in one case, capsules. Small-seeded berries are produced by the Bromeliaceae (Benzing 2000, Will & Zizka 1999), Melastomataceae (Renner 1989), Rubiaceae (Bremer & Eriksson 2008), Myrtaceae (Pizo 2002), Ericaceae (Eriksson 2008, Stiles 1980), Rosaceae (Stiles 1980) and Solanaceae (Barbosa-Albuquerque et al. 2006) while the Brassicaceae produce capsules (Hall et al. 2011). Krebs et al. (2010) found that berries are important food resources for North American small rodents and influence their population dynamics; thus it is not surprising that small neotropical rodents would also feed on small-seeded fruits (Sahley et al. 2015).

Seed disperser effectiveness

Our study shows the genera *Thomasomys*, *Akodon* and *Calomys* as important seed dispersers in the tropical montane forest studied. In accord with our hypothesis, the genus *Thomasomys* was responsible for most seed dispersal, with *T. kalinowskii* being the most effective disperser for the studied plant community. *Thomasomys* spp. may exhibit semi-arboreal habits; nests for *T. aureus* have been found in trees (Brito et al. 2012), and evidence of arboreal activity for *T. oreas* have been recorded (Pacheco unpubl. data), although such data do not exist as of yet for *T. kalinowskii*. Further research on the genus *Thomasomys* including effects of gut passage on seed viability, foraging behaviour and comparative dispersal effectiveness among species is warranted.

Akodon torques, reported as insectivorous (Noblecilla & Pacheco 2012, Solari 2007), consumed fruit and passed intact seeds at our study site, including a diverse and large quantity of insects. While it consumes fruits of fewer species than the genus *Thomasomys*, because of its high relative abundance and passage of viable seeds for *Gaultheria* spp. and *Miconia* sp. 1, it had the second highest effective disperser index of this rodent assemblage.

Calomys sorellus, a rodent often considered to be insectivorous and commonly found in high Andean grassland habitat (Pizzimenti & de Salle 1980) was found to include fruit in its diet at our study site (Sahley et al. 2015). The proportion of intact seeds (belonging to the genus *Gaultheria*) and seed viability in faecal samples was relatively high. This is significant as we found that *C. sorellus* was the only rodent to cross the 25-m-wide area cleared during pipeline construction during early restoration efforts before taller shrubs were re-established (Sahley unpubl. data). Thus, *C. sorellus* may have contributed to dispersing seeds to the 25-m-wide pipeline right of way during early stages of vegetation restoration.

Oligoryzomys andinus and *M. minutus* both had intact *Gaultheria* sp. 1 seeds in faecal samples. The relative abundance of both species was low in this rodent assemblage. For *O. andinus* seed viability was low to medium while for *M. minutus* seed viability was zero. Overall, these two species contribute the least to seed dispersal compared with others in this rodent assemblage.

In summary, *T. kalinowskii* was the most effective disperser in montane forest and shrub areas because of high seed abundance, diversity, and viability values; it also disperses seeds of two genera that are not found in other rodent species at our site. *Akodon torques* was important primarily because of its high abundance, and *C. sorellus* because of its high viability for one plant genus and its ability to cross the recovering pipeline right of way prior to the re-establishment of vegetation cover.

Fruit consumption and seed dispersal of plant families at the study site

The rodent assemblage at our site consumed fruits and dispersed seeds from families and genera that are also consumed and dispersed by other taxonomic groups, but these overlapped more with terrestrial mammals and birds than with bats. For example, *Greigia* sp. (Bromeliaceae) is a bromeliad that grows near the ground; its fruits are consumed by the Andean bear (*Tremarctos ornatus*; Troya *et al.* 2004) as well as by *T. kalinowskii*. *Greigia* fruits are also utilized for human consumption (Hornung-Leoni 2006, Will & Zizka 1999). Seed viability of *Greigia* sp. was high for *T. kalinowskii* (84%), but we did not record *Greigia* sp. in faecal samples of other rodent genera.

Gaultheria spp. (Ericaceae) are shrubs that produce berries that are consumed by birds, the spectacled bear (*Tremarctos ornatus*) and Andean fox (*Lycalopex culpaeus*); Rivadeira-Canedo (2008) showed that seeds of this genus were viable after bird and mammal consumption. We found *Gaultheria* sp. 1 seeds in all species of rodents studied and found viable seeds in four of the six rodent species examined, while *Gaultheria* sp. 2 was consumed by four of six rodent species examined.

Miconia spp. are primarily known for being consumed and dispersed by birds (Levey 1990, Loiselle & Blake 1999, Wheelwright *et al.* 1984). *Miconia* spp. seeds were relatively abundant in samples from this rodent assemblage, with three of six rodent species found to pass viable seeds. The *Miconia* spp. have previously been reported to pass as viable through the digestive tract of the sigmodontine rodent *Necomys lasiurus* (Magnusson & Sanaïotti 1987).

Gutteria spp. are generally found as small- to medium-sized trees and produce berries. These are consumed by birds (Snow 1981, Wheelwright *et al.* 1984) as well as spider monkeys (*Ateles* spp.) and the woolly monkey, *Lagothrix lagotricha* (Link & Di Fiore 2006, Stevenson 2000). We found *Gutteria* sp. (Annonaceae) seeds in relatively low abundance and only in *T. kalinowskii*. However, viability of these seeds was high.

Species belonging to the Rubiaceae in the neotropics have fruits that have been recorded as being consumed by small passerines (Loiselle *et al.* 1995, Snow 1981, Tabarelli & Peres 2002). We recorded two unidentified morphospecies in the Rubiaceae samples from the genus *Thomasomys*.

Rubus spp. have been recorded as being consumed and dispersed by birds (Wheelwright *et al.* 1984), as have other species within the Rosaceae (Herrera & Jordano 1981). One species belonging to the genus *Rubus* (Rosaceae) was found in samples, although relative seed abundance was low. While *Rubus* sp. seeds were viable in *T. kalinowskii* samples, sample size was too low to make

any firm conclusion on the importance of *T. kalinowskii* to its reproductive ecology.

Both bats and birds are reported to consume and/or disperse fruits and seeds belonging to the family Solanaceae (Caceres & Moura 2003, Galindo-Gonzales *et al.* 2000, Loayza *et al.* 2006, Snow 1981, Wheelwright *et al.* 1984). Seeds belonging to Solanaceae sp. 1 and sp. 2 were found only in samples belonging to the genus *Thomasomys*.

The Brassicaceae were represented by one morphospecies found in faecal samples belonging to *T. kalinowskii*; viability of seeds was 20%, suggesting a role for *T. kalinowskii* as a seed disperser. The Brassicaceae, unlike the other families identified in samples, form two-valved jointed and non-jointed capsules instead of berries (Hall *et al.* 2011) and have been reported to primarily utilize passive dispersal modes such as wind and water (Willis *et al.* 2014).

Implications for seed-dispersal ecology

In many studies of neotropical forests, primary or secondary seed-disperser taxa have been identified as bats, birds or medium to large rodents primarily belonging to the Dasyproctidae and Echimyidae. Our study suggests that in habitats where sigmodontine rodents consume small-seeded fruits in areas with shrubs or small to medium-sized trees, it is likely that they are serving as primary seed dispersers in montane forests, transition zones, as well as tropical montane habitats in early successional stages, and areas that are being restored or recovering from deforestation. Thus, we recommend that for a more complete understanding of plant reproductive ecology in montane forests, sigmodontine rodents should be included in frugivore and seed-dispersal studies.

While we identified the presence of intact seeds and seed viability in faecal samples of sigmodontine rodents, we recognize that additional components of seed dispersal, such as quality of deposition sites, germination rates and seedling establishment are necessary to gather a more complete picture of small-rodent contributions to seedling recruitment. We hope that additional studies will continue to elucidate the relationships between sigmodontine rodents, their food plants, and their role as seed dispersers in neotropical forests.

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