

Effects of manakin gut passage on germination of a neotropical melastome shrub (Melastomataceae)

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Abstract

Gut passage is an important but understudied component of animal-mediated seed dispersal that can impact germination and survival. Melastomataceae plants are abundant and ecologically important throughout the tropics, but studies have obtained contrasting results regarding effects of avian gut passage on melastome germination. We conducted a paired germination experiment to test how gut passage by four species of manakins—key avian dispersers of melastomes—affects germination of the pioneer melastome shrub *Miconia rubescens*. Manakin gut passage accelerated *M. rubescens* germination, with gut-passed seeds germinating an average of 5.1 days earlier than controls, and percent germination of gut-passed seeds was significantly higher at 20 and 40 days post-planting. Interestingly, manakin species varied in their gut passage effects, with *L. velutina* having stronger overall germination effects than *M. manacus*. Within species, greater body mass was correlated with higher percent germination and shorter times to first germination. Within *M. manacus*, seeds passed by females had significantly shorter times to first germination than seeds passed by males. Because control seeds were manually depulped in the experiment, the observed gut passage effects are likely attributable to minor scarification of the seed coat during gut transit. Our results suggest manakin gut passage can have biologically meaningful impacts on melastome germination, and the magnitude of these effects can vary based on manakin species, mass, and sex. This study refines our understanding of the “quality” component of seed disperser effectiveness in an iconic dispersal mutualism, with implications for plant community composition and recovery of deforested neotropical ecosystems.

Abstract in Spanish is available with online material.

KEYWORDS

frugivory, germination, gut passage, Melastomataceae, *Miconia*, Pipridae, seed dispersal, seed dispersal quality

1 | INTRODUCTION

Seed dispersal can benefit plants by reducing intraspecific competition and increasing escape from predators and pathogens that concentrate near parental plants (Connell, 1971; Janzen, 1970). In many systems,

frugivorous birds act as ecosystem engineers by influencing plant recruitment at multiple levels. For example, birds may increase plant establishment by moving seeds away from parent plants into areas more favorable to their germination and recruitment (Wenny & Levey, 1998). Additionally, digestive processing and handling of a seed in the gut

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following ingestion can enhance, have no effect, or completely inhibit germination of defecated seeds (Levey, 1987; Traveset et al., 2007). In the neotropics, where there is now more secondary forest than primary forest due to human disturbance (Chazdon et al., 2009), frugivorous birds can play a particularly important role in recovery dynamics via their seed dispersal services (Blendinger et al., 2011; Campagnoli et al., 2023; Loiselle & Blake, 1993; Murray, 1988; Pejchar et al., 2008; Sekercioglu, 2012). As such, investigating how avian digestive processing impacts seed fate is an important step toward refining our understanding of seed disperser effectiveness (Schupp et al., 1993; Schupp et al., 2010) such as the “quality” of the dispersal services provided by different frugivores. By extension, this information also has consequences for our understanding of plant community composition and forest successional dynamics.

Fruit and seed manipulation and processing in the gut by a frugivore can affect seed fate via several important mechanisms. First, gut passage may enhance seed germination via depulping (i.e., the removal of fruit pulp from around the seed during digestion), which separates the seed from germination-inhibiting compounds present in fruit pulp and significantly reduces the likelihood of pathogen infestation (i.e., the “deinhibition effect”; Traveset & Verdú, 2002; Samuels & Levey, 2005; Robertson et al., 2005; Silveira et al., 2012; Ribeiro et al., 2016; Messeder et al., 2022). Second, gut passage may increase germination success if the surrounding fecal matter provides nutrients to the defecated seed (i.e., the “fertilization effect”; Traveset & Verdú, 2002; Robertson et al., 2005). Third, the handling of a seed prior to or during ingestion has the potential to damage a seed as it enters the alimentary canal, thereby impacting germination success (Levey, 1987; Moermond & Denslow, 1985). For instance, birds referred to as “gulers” (e.g., manakins, thrushes, and toucans) swallow fruits whole with minimal handling, while “mashers” (e.g., tanagers, finches, and parrots) more thoroughly manipulate or entirely crush fruits in the bill, the latter being associated with seed death (Janzen, 1981; Levey, 1987; Murray, 1988). Finally, abrasion of the seed coat through the mechanical and chemical handling in the gut can positively or negatively affect germination (i.e., the “scarification effect”; Barnea et al., 1990; Barnea et al., 1991; Traveset, 1998). The scarification effect may be one of the more complex gut-passage effects, as a large number of factors—including gut-passage time and morphology of the frugivore (Ellison et al., 1993; Moermond & Denslow, 1985; Traveset, 1998; Worthington, 1982), as well as seed size and morphology (Levey, 1987; Howe, 1993; Stiles & Rosselli, 1993; Jordano, 2000; Traveset & Verdú, 2002; Silveira et al., 2012)—can influence the amount of scarification that occurs and whether this scarification is beneficial or inhibitory to germination. Resolving the impact of gut passage on seed fate in a greater number of plant-frugivore interactions will help us better understand the complex factors shaping dispersal dynamics, particularly the “quality” component of seed disperser effectiveness (in this case, impacts on germination rate and success) that is often understudied relative to the “quantity” component (e.g., how many seeds are ingested and dispersed) (Schupp et al., 1993; Schupp et al., 2010).

Melastomataceae is a highly diverse, pantropical fruiting plant family (nearly 5000 described species) that is ecologically important for frugivorous birds and plays a key role in recolonizing disturbed habitats in neotropical regions (Ellison et al., 1993; Pearson et al., 2002; Renner et al., 2001; Silveira et al., 2013). Plants in the hyper-diverse genus *Miconia* (over 1900 species) are particularly important in the neotropics, as they produce a large amount of small, fleshy fruits year-round, which provides a reliable food source for frugivores, especially birds, when fruits are scarce during the dry season (Messeder et al., 2021, 2022; Michelangeli et al., 2019; Silveira et al., 2013). *Miconia* species have been suggested to play a keystone role in the neotropics due to their relationship with a great variety of frugivores. In addition, their positively photoblastic germination allows them to have higher germination success in gaps and regenerating areas (Putz, 1983; Ellison et al., 1993; Pearson et al., 2002), leading them to be potentially advantageous for reforestation efforts (Messeder et al., 2021). Prior studies of gut passage effects in melastomes have yielded widely variable results (Silveira et al., 2013), with some finding negative (Alves et al., 2008; Messeder et al., 2021), null (Gomes et al., 2008; Ribeiro et al., 2016), positive (Lessa et al., 2013, 2019), or a combination (Ellison et al., 1993; Silveira et al., 2012) of effects on germination success (which is not consistently defined). Importantly, many of these germination experiments have shown that gut passage tends to have a greater effect on the timing of germination than the germinability of seeds, although these effects vary between species and lifeforms (Ellison et al., 1993; Lessa et al., 2013; Silveira et al., 2013).

The ecological relationship between manakins (Aves: Pipridae) and Melastomataceae represents a classic plant-frugivore relationship in the neotropics. Manakins and other prominent avian dispersers of melastomes in Neotropical forests are hypothesized to play significant roles in the recruitment and population dynamics of several melastome species, particularly those in the *Miconia* genus (Blendinger et al., 2011; Campagnoli et al., 2023). Despite this, the quality of endozoochorous seed dispersal provided by manakins to ecologically important *Miconia* species is unclear. Ellison et al. (1993) investigated effects of gut-passage by red-capped manakins (*Ceratotipira mentalis*) in Costa Rica, finding that in some *Miconia* species, such as *M. affinis*, gut-passage resulted in earlier germination, while in others, like *M. simplex*, seeds of the gut-passed treatment germinated later (Ellison et al., 1993). It is also possible that manakins differ in the quality of their seed dispersal services within and between species, although this remains virtually unknown. A recent study in thrushes (*Turdus leucomelas*) found that gut passage by larger individuals was associated with higher germination success (Campagnoli et al., 2023), indicating that intraspecific variation within frugivores can influence seed processing in the gut (e.g., due to differences in gut retention times), which can affect germination outcomes of digested seeds (Levey, 1987; Campagnoli et al., 2023; Schupp et al., 1993; Schupp et al., 2010). Better understanding the seed dispersal quality manakins provide to *Miconia* species in the context of regenerating forest is essential, given the important role of *Miconia* as a keystone and pioneer genus in regenerating habitat and the near ubiquity of manakins in secondary forests across the neotropics.

We investigated the influence of manakin gut passage on the germination of a common and geographically widespread shrub, *Miconia rubescens*, in a highly threatened and understudied region of northwestern Ecuador (Myers et al., 2000). We conducted a paired germination experiment to compare the germination of gut-passed seeds to non-digested control seeds from the same plant using four species of manakins: *Ceratopipra mentalis*, *Cryptopipo litae*, *Lepidothrix velutina*, and *Manacus manacus*. To investigate the role of interspecific and intraspecific variation on dispersal quality, we also examined how species, mass, and sex influenced germination timing and success. Because manakins are “gulpers” with rapid gut transit times (Blake & Loiselle, 2002; Snow, 2004; Worthington, 1982), we hypothesized that manakin gut passage would increase percent germination (i.e., proportion of seeds germinated) and accelerate germination times of *Miconia* seeds, consistent with a positive impact of mild-to-moderate scarification of the seed coat. Given the relatively similar body sizes and digestive morphologies across manakins (Worthington, 1982), we did not hypothesize that there would be differences in gut-passage effects according to manakin species, mass, or sex.

2 | METHODS

2.1 | Study area

This study took place in the Chocó biogeographic zone of northwestern Ecuador, a global hotspot for biodiversity experiencing extreme habitat loss and declining species abundance due to deforestation and other anthropogenic activity (Myers et al., 2000). Field work was conducted at Reserva FCAT (Fundación para la Conservación de los Andes Tropicales; 00° 23' 28" N, 79° 41' 05" W), a 700-ha private reserve within the Mache-Chindul Ecological Reserve in Esmeraldas Province. The average temperature in the area ranges between 23 and 25°C and annual precipitation is approximately 2500–3000 mm, with the wet-season occurring from late December to June (Clark et al., 2006). At our site, agricultural crops (e.g., cacao and plantain) and pasturelands are prevalent and increasing, although intact and successional forests also remain relatively common (Van der Hoek, 2017). However, heavy deforestation and fragmentation has occurred in the Mache Chindul Reserve, disrupting connectivity and species interactions (Van der Hoek, 2017).

2.2 | Study system

Our study species, *Miconia rubescens* (Gamba & Almeda, 2018; formerly *M. neomicrantha* (Judd & Skee, 1991) and *Octopleura rubescens* (Triana, 1872)), is a woody shrub producing fruits that are small (mean height × width: 6.04 × 2.99 mm; mean weight = 0.11 g), round, watery, and white when ripe (mean Brix = 4.88%). This species is the most geographically widespread species in the Octopleura clade, occurring in 13 countries over Central and South America (Gamba & Almeda, 2014, 2018). Fruit produced by *M. rubescens* are consumed by numerous neotropical

frugivorous birds, particularly manakins, tanagers, thrushes, and brush-finches (Kessler-Rios & Kattan, 2012; Loiselle & Blake, 1999; Stiles & Rosselli, 1993; Wheelwright et al., 1984).

Manakins are small passerines that constitute some of the most abundant frugivores in South and Central American rainforests, making them prominent agents of endozoochorous seed dispersal in these habitats (Cestari & Pizo, 2012, 2013). In this study, the following manakin species were used in gut passage trials: *Manacus manacus*, *Lepidothrix velutina*, *Ceratopipra mentalis*, and *Cryptopipo litae*. Manakins at our field site are regularly observed eating whole fruits of *M. rubescens*. This is especially true of *M. manacus*, which tend to situate their lek sites in disturbed secondary forest and along forest edges where *M. rubescens* is relatively abundant.

2.3 | Gut passage trials

Gut passage trials were performed on wild-caught birds over the course of 8 weeks, from early June to late July 2022. Passive mist netting took place in regenerating forest surrounding known lek sites of *M. manacus* using 2–7 nets, each 12 m in length, that remained open in the morning hours until manakins were captured; we paused netting for subsequent stages of the trials. Birds were fasted for 45 min after capture to ensure that the majority of previously consumed seeds had left the bird's digestive tract (Levey, 1986; Worthington, 1989). During the fasting period, manakins were extracted from nets, weighed, processed, and banded for identification. Once processing was complete, they were placed back into a fabric mist netting bag in the shade until the fasting period was complete.

Ripe fruits (determined by color and softness) were collected from the field <24 h prior to use in gut passage trials and stored in dry and dark conditions. Each paired trial in the experiment corresponded to fruits collected from a different *M. rubescens* individual ($n=41$), which were marked to avoid resampling. Following the fasting period, birds were hand fed 1–4 whole *M. rubescens* fruits that had been previously collected from a single plant. The number of fruits fed to a given bird varied depending on the individual's cooperation and condition. Immediately after feeding, birds were placed into a small pet carrier with a perch, covered for 45–60 min, then released. Fecal samples containing gut-passed seeds were collected from a piece of white printer paper at the bottom of the carrier, placed in sterilized marked containers, and processed for the experimental germination procedure later the same day (below).

2.4 | Germination experiment

We compared percent germination of gut-passed and non-digested (control) seeds using a paired experimental design. For a given experimental trial, gut-passed and control fruits were sourced from the same plant to account for potential individual variation in germination rate or success among plants. To minimize handling effects during

extraction from feces (gut-passed treatment) or fruits (non-digested treatment), seeds were suspended in a small amount of sterile water and gently removed with a sterile metal spatula. Extracted seeds were then placed on sterile germination paper inside plastic petri dishes. For each paired trial, the same number of seeds were placed in control and gut-passed petri dishes. However, due to variation in the number of seeds that were recovered following gut passage, the number of seeds obtained varied among trials (mean: 31.83 ± 1.72 SEM, range=6–42). Petri dish pairs were placed immediately adjacent to one another indoors where temperatures ranged from 13 to 22°C and situated near a window to allow exposure to indirect natural sunlight on a natural 12 h light/12 h dark cycle. Germination paper was kept damp as needed using a spray bottle filled with sterile water. Control seeds received the same amount of water as paired gut-passed seeds and were watered at the same times. All petri dishes were monitored together at least 1–2 times per week to record the number of germinated seeds.

2.5 | Statistical analysis

To compare the effect of gut passage on germination times across all seeds, we fit a linear mixed-effects model using the *nlme* package in R (Pinheiro et al., 2017). The model included time elapsed until germination as a response variable (square root transformed to improve residual normality), treatment (i.e., gut-passed vs. non-digested) as a predictor variable, and dish within trial as a nested random effect. This nested random effect structure accounted for the fact that seeds belonging to the same trial (i.e., paired gut-passed and non-digested seeds) were derived from the same *M. rubescens* plant, and seeds in the same dish (in the case of the gut-passed treatment) passed through the same manakin. To test whether gut passage influenced variation in seed germination time, we calculated the within-dish variance (σ^2) in time to germination for all gut-passed and non-digested seeds in each trial separately. We then conducted paired *t*-tests to compare the variances in germination times between treatments for all manakins, for *L. velutina* only, and for *M. manacus* only; variable transformations were applied as necessary to meet normality assumptions. To test whether gut passage influenced percent germination, we fit a model in *lme4* (Bates et al., 2015) with final percent germination at the end of data collection as a response variable, treatment as a fixed effect, and bird ID and species as random intercepts.

To examine germination success at various timepoints throughout the experiment, we conducted Wilcoxon signed-rank tests comparing the percent of gut-passed (GP) versus non-digested (ND) seeds that germinated at 20, 40, 60, and 80 days after planting. Because seeds were not checked for germination on a daily basis, we used the percent germination recorded closest to the desired 20-day interval for analyses (20-day timepoint mean \pm SD: 20.17 ± 1.14 days; 40-day timepoint: 40.32 ± 1.60 days; 60-day timepoint: 60.80 ± 2.01 days; 80-day timepoint: 80.20 ± 2.69 days). All seeds were checked for germination on the same days, so the distance from a given 20-day

interval did not differ within an experimental-control pair. We compared percent germination of gut-passed seeds relative to paired controls for each of the following groups: all manakin species together, *L. velutina* only, and *M. manacus* only. Gut passage by *C. mentalis* and *C. litae* was not analyzed separately due to small sample sizes.

We fit additional linear mixed-effects models in *nlme* to investigate how bird mass and sex influenced germination parameters. Due to the small sample sizes of *C. mentalis* and *C. litae*, only *L. velutina* and *M. manacus* were included in these analyses, and only trials that reached 80 days post-planting ($n=30$) were considered. To investigate the effects of mass, sex, and species on germination success, we fit a model that included the difference in percent germination between gut-passed and control seeds (Δ percent germination) as a response variable; mass, sex, and species as fixed effects; and individual bird ID as a random intercept. To investigate the effects of bird mass, sex, and species on germination rate, we fit a second model with the same fixed and random effects as the first, but a response variable of Δ days until first germination (i.e., the difference between gut-passed and control treatments in days elapsed prior to the first occurrence of germination). This model also included a fixed variance structure to account for heteroskedasticity. Finally, within *M. manacus* (the species for which we had the greatest number of known-sex individuals), we used a Wilcoxon test to compare Δ days until first germination between known males and females. Data was managed in Microsoft Excel Version 16.88 (Microsoft Corporation, 2018). Statistical tests and figures were conducted and generated in RStudio Version 4.4.1 (RStudio Team, 2020) and JMP Version 17.00 (JMP, 2021). All descriptive statistics are presented as means \pm SEM.

3 | RESULTS

We conducted a total of 41 gut passage trials across the four manakin species: *Manacus manacus* ($n=29$ trials on 26 individuals), *Lepidothrix velutina* ($n=9$ trials on eight individuals), *Ceratopipra mentalis* ($n=2$ trials on two individuals), and *Cryptopipo litae* ($n=1$ trial). While it would have been ideal to have equal sample sizes for each species, these differences in numbers of individuals per species were attributable to differences in capture rate and local abundance at our field site.

3.1 | Time to germination

Among the subset of seeds that germinated during the experimental period ($n=4521$ gut-passed seeds and $n=3868$ non-digested seeds across 39 trials), gut-passed seeds had significantly shorter times to germination than non-digested seeds (46.73 ± 0.58 vs. 51.83 ± 0.63 days, respectively; linear mixed-effects model: $t=3.33$, $df=35$, $p=0.002$; Figure 1a). In addition to assessing the overall effects of manakin gut passage, we separately analyzed the effects of gut

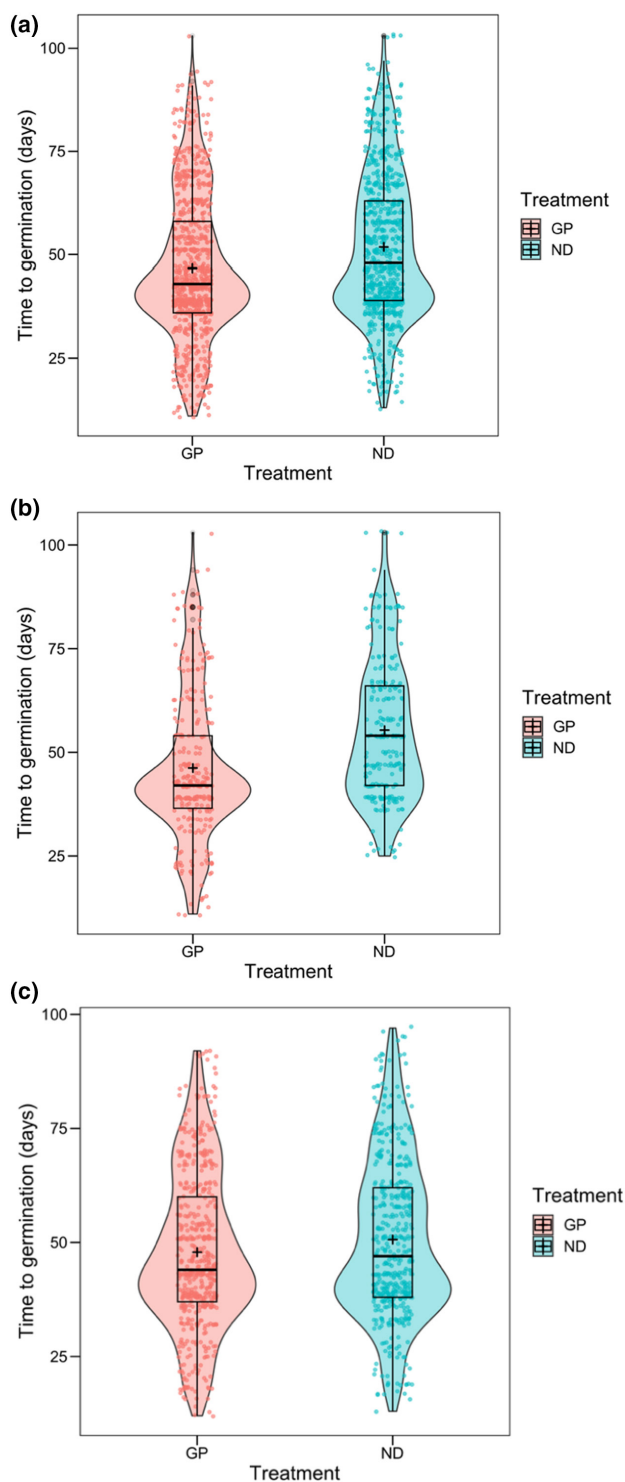


FIGURE 1 Effects of manakin gut passage on seed germination times. (a) Across all trials where germination occurred during the experimental period ($n=39$), gut passage by manakins significantly accelerated seed germination times (linear mixed-effects model: $T=3.33$, $df=35$, $p=.002$). (b) Gut passage by *L. velutina* ($n=9$ trials) had an especially strong effect on seed germination time ($t=4.05$, $df=7.91$, $p=.004$). (c) The effect of gut passage by *M. manacus* ($n=27$ trials) was not significant ($t=1.55$, $df=19.22$, $p=0.14$). Violin plots represent the shape of the germination time distributions, and boxplots depict medians (bold lines) and quartiles. Crosses denote treatment means. Treatments: GP, gut passed seeds; ND, non-digested seeds.

passage for the two species for which we had the largest sample sizes. Gut passage by *L. velutina* significantly accelerated seed germination times (46.19 ± 1.07 vs. 55.35 ± 1.12 days; $t=4.05$, $df=7.91$, $p=.004$; Figure 1b), whereas gut passage by *M. manacus* did not (47.88 ± 0.74 vs. 50.63 ± 0.78 days; $t=1.55$, $df=19.22$, $p=.14$; Figure 1c).

3.2 | Variance in germination time

We also assessed whether gut passage influenced plate-level variance in seed germination times (i.e., within-trial dispersion in time elapsed prior to germination; σ^2). Variance in germination times did not significantly differ between gut-passed and non-digested treatments (paired t -test: $t=1.12$, $df=30$, $p=.27$; Figure 2). We also observed no effect of gut passage on germination time variance when *L. velutina* and *M. manacus* trials were analyzed separately (*L. velutina*: $t=1.71$, $df=7$, p -value=.13; *M. manacus*: $t=1.37$, $df=19$, p -value=.19).

3.3 | Percent germination

Across all manakin species, we did not observe an effect of gut passage on the overall proportion of seeds germinating within a given trial over the course of the data collection period (66.32 ± 4.64 vs. 62.04 ± 4.50 percent for gut-passed and non-digested seeds, respectively; LMM: $t=1.00$, $df=43.61$, $p=.32$). However, we did observe timepoint-specific effects throughout the experiment, with gut-passed seeds exhibiting significantly higher percent germination than non-digested seeds at 20 days (4.13 vs. 0.89%, respectively;

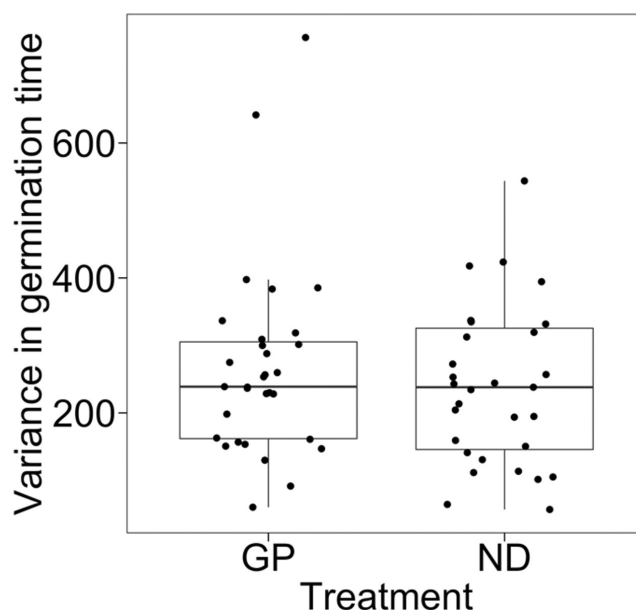


FIGURE 2 No effect of manakin gut passage on germination time variance. There was no significant difference in the within-trial variance in seed germination times between gut-passed and non-digested treatments (paired t -test: $T=1.12$, $df=30$, $p=.27$).

Wilcoxon signed-rank test: $V=29, p=.01$, 40 days (31.83 vs. 22.01%, respectively; $V=169.5, p=.02$), and 60 days post-planting (52.51 vs. 45.65%, respectively; $V=206, p=.047$; Figure 3a). Although this trend was apparent throughout most of the experiment, differences in percent germination between gut-passed and non-digested seeds were not significant at the final 80-day timepoint (69.09 vs. 64.03%, respectively; $V=201, p=.16$; Figure 3a). Looking within species, seeds passed by *L. velutina* had significantly higher percent germination at 40 and 60 days post-planting (Figure 3b), while seeds passed by *M. manacus* did not have higher percent germination at any of the timepoints examined (Figure 3c).

3.4 | Effects of mass, sex, and species

Based on a linear mixed-effects model, manakin mass had a significant positive effect on Δ percent germination (i.e., the difference in percent germination between gut-passed and non-digested seeds), with heavier individuals having greater effects ($t=2.49, df=23, p=.02$; Figure 4a, Table 1). This positive correlation between frugivore body mass and percent germination was present in both *L. velutina* and *M. manacus*, although gut passage by *L. velutina* had significantly greater overall effects on percent germination than *M. manacus* ($t=3.07, df=23, p=.005$; Figure 4b, Table 1). We did not detect an effect of sex on percent germination, with seeds passed by known females exhibiting no significant difference in percent germination relative to known males ($t=0.79, df=23, p=.44$) or individuals of unknown sex ($t=1.36, df=23, p=.19$; Table 1).

We observed similar effects of mass and species on Δ time to first germination (i.e., the difference in days elapsed prior to the first occurrence of germination in gut-passed versus non-digested seeds), with seeds passed by heavier individuals having significantly shorter times to first germination ($t=-2.48, df=22, p=.02$; Figure 5a) and gut passage by *L. velutina* having shorter times to first germination time than *M. manacus* ($t=-2.88, df=22, p=.009$; Figure 5b, Table 2). In addition, seeds passed by known females had significantly earlier times to first germination than seeds passed by known males ($t=-2.26, df=22, p=.03$) or individuals of unknown sex ($t=-2.50,$

FIGURE 3 Timepoint-specific percent germination effects of manakin gut passage. Mean percent germination of seeds gut-passed by manakins (GP) vs. non-digested control seeds (ND) at different timepoints. (a). Data for all manakin trials ($n=41$) at 20 days ($V=29, p=.01^*$), 40 days ($V=169.5, p=.02^*$), 60 days ($V=206, p=.047^*$), and 80 days ($V=201, p=.16$). (b). Data for *Lepidothrix velutina* trials ($n=9$) at 20 days ($V=0, p=.10$), 40 days ($V=0, p=.01^*$), 60 days ($V=0, p=.01^*$), and 80 days ($V=6, p=.11$). (c) Data for *Manacus manacus* trials ($n=29$) at 20 days ($V=17.5, p=.10$), 40 days ($V=117.5, p=.36$), 60 days ($V=141, p=.57$), and 80 days ($V=122.5, p=.91$). Asterisks denote significance by Wilcoxon signed-rank tests ($*=p<.05$). Error bars represent ± 1 SE.

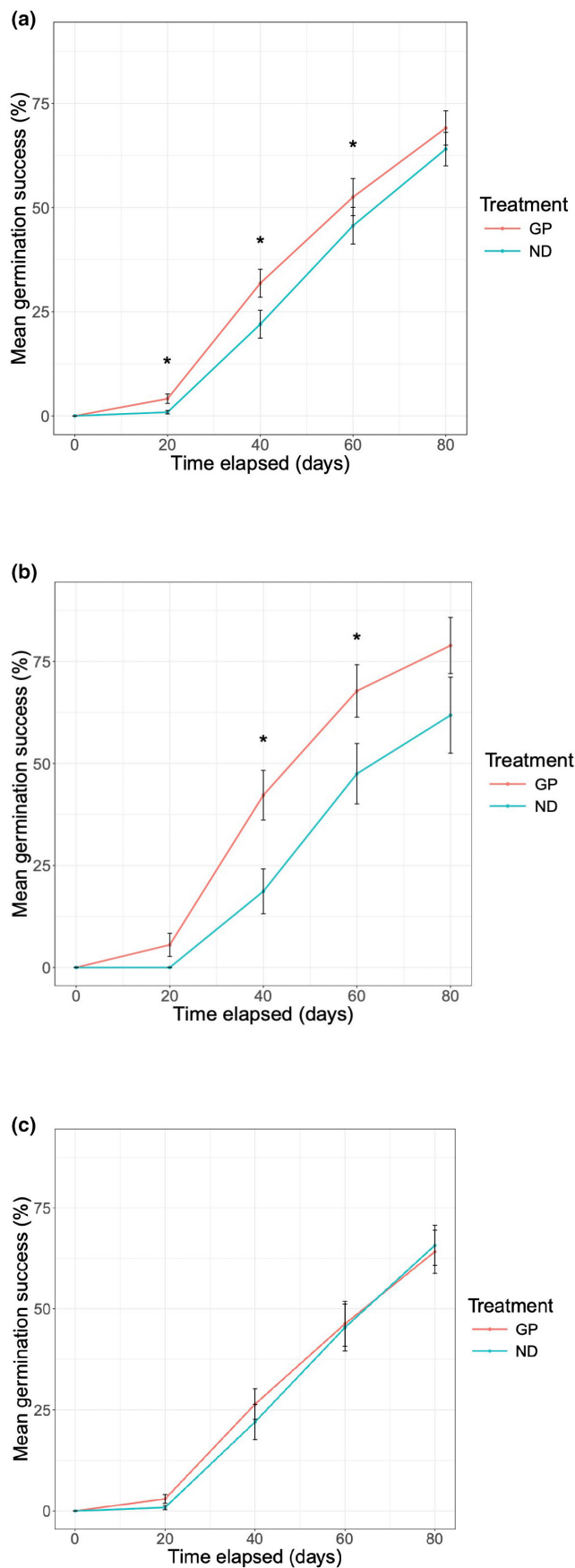


FIGURE 4 Effects of manakin mass and species on germination success. (a) Mass and species had significant effects on percent germination (i.e., Δ percent germination, the difference between gut-passed (GP) and non-digested (ND) seeds). (b) There was a significant difference between *L. velutina* and *M. manacus* in Δ percent germination.

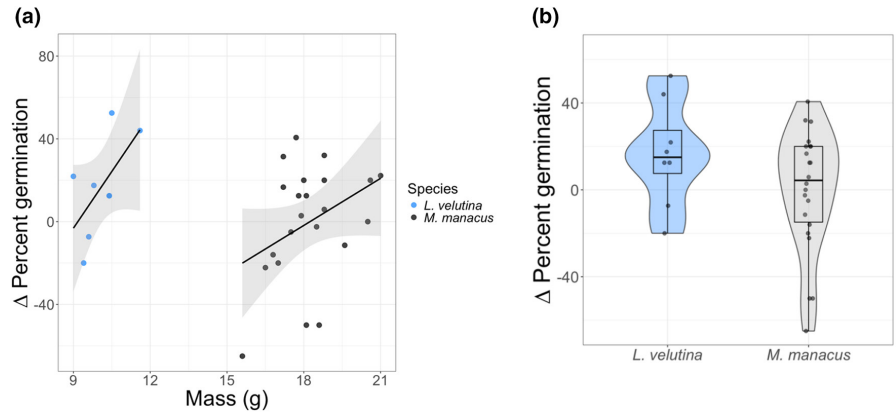
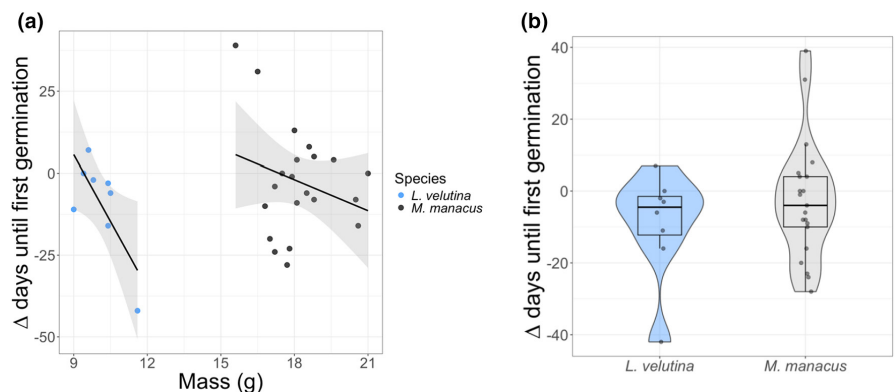


TABLE 1 Effects of manakin mass, species, and sex on percent germination.

	Estimate	SE	Df	t	p
Intercept	-70.74	42.41	23	-1.67	.11
Mass	10.13	4.06	23	2.49	.02
Species (<i>M. manacus</i>)	-106.09	34.53	23	-3.07	.005
Sex (Male)	-11.07	14.04	23	-0.79	.44
Sex (Unknown)	-16.94	12.46	23	-1.36	.19

Note: "Species (*M. manacus*)" output indicates effects of *M. manacus* relative to *L. velutina*. 'Sex (Male)' indicates effects of male gut passage relative to females, while 'Sex (Unknown)' indicates effects of unknown sex individuals relative to females. Model includes a random effect of bird ID and a fixed variance structure. Significant effects are bolded.

FIGURE 5 Effects of manakin mass and species on germination time. (a) Manakin mass and species had significant effects on time to first germination (i.e., the difference in time elapsed until the first occurrence of germination (Δ days until germination) between gut-passed (GP) and non-digested (ND) seed treatments). (b) There was a significant difference between *L. velutina* and *M. manacus* in Δ days until first germination.



df=22, $p=.02$; Table 2). When gut passage effects of males and females were compared within *M. manacus*, the species with the largest sample of known-sex individuals, females had significantly greater effects on time to first germination than males ($W=3$, $p=.007$; Figure 6).

4 | DISCUSSION

This study used a field-based experiment to document effects of gut passage by manakins, an iconic family of Neotropical frugivorous birds, on the germination of a widespread neotropical melastome, *Miconia rubescens*. Our results supported the hypothesis that gut passage by manakins facilitates earlier germination of *M. rubescens* seeds, although we found no overall effects of manakin gut passage

on germination time variance or germination success (i.e., proportion of seeds germinated). Interestingly, the magnitude of gut passage effects varied across manakin species, with *L. velutina* having greater overall gut passage effects than *M. manacus*. Within species, we also observed significant effects of mass and sex: gut passage by heavier individuals yielded higher percent germination and shorter times until first germination, and, within *M. manacus*, gut passage by females more strongly accelerated time to first germination compared to males.

Our finding that gut-passed seeds germinated significantly earlier than controls is consistent with prior studies that have found stronger effects of gut passage on the timing of melastome germination than on germination success (Ellison et al., 1993; Silveira et al., 2012; Traveset & Verdú, 2002). More rapid germination is not always beneficial, and may even be fatal to seeds in conditions

	Estimate	SE	Df	t	p
Intercept	32.09	23.33	22	1.38	.18
Mass	-5.56	2.25	22	-2.48	.02
Species (<i>M. manacus</i>)	55.07	19.14	22	2.88	.009
Sex (Male)	17.23	7.63	22	2.26	.03
Sex (Unknown)	17.00	6.79	22	2.50	.02

Note: "Species (*M. manacus*)" output indicates effects of *M. manacus* relative to *L. velutina*. "Sex (Male)" indicates effects of male gut passage relative to females, while "Sex (Unknown)" indicates effects of unknown sex individuals relative to females. Significant effects are bolded.

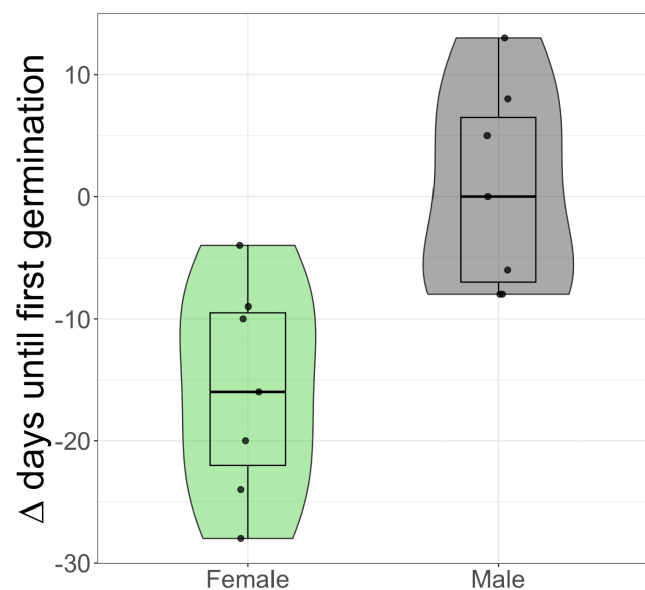


FIGURE 6 Effects of *Manacus manacus* sex on germination time. Gut passage by female *M. manacus* resulted in significantly shorter times to first germination (i.e., Δ germination time, the difference between the number of days until the first occurrence of germination between GP and ND treatment seeds) relative to gut passage by male *M. manacus* ($W = 3$, $p = .007$).

favoring dormancy (e.g., pathogen presence, water limitation, and unfavorable light conditions); however, in the hypercompetitive setting of a regenerating site, seeds of early-germinating pioneer species may benefit from early emergence and establishment by increasing seedlings' access to light, which becomes more limited as seedling density increases (Janzen, 1981; Miller et al., 1994; Murray, 1988; Robertson et al., 2005; Verdú & Traveset, 2005). Early germination tends to increase seedling growth and fecundity rather than survival (Verdú & Traveset, 2005). This may be a particularly important factor for light-sensitive *Miconia* species that establish as pioneers in regenerating areas. In contrast, we found no effect of gut passage on within-trial germination time variance. Greater variation in germination time may be evolutionarily favored to avoid synchronous emergence, which could be detrimental to seed fate if germination of all or most seeds is followed by unfavorable conditions (Murray, 1988; Izhaki & Safriel, 1990; Verdú & Traveset, 2005). Field experiments to determine how the timing of manakin-digested seedling emergence may influence the long-term success of the seedlings and resulting

TABLE 2 Effects of manakin mass, species, and sex on germination time.

successional plant community are required to better understand the ecological implications of our findings.

Because our experimental design involved removing the pulp from non-digested seeds and the feces surrounding gut-passed seeds, the gut-passage effects we observed are expected to be primarily attributable to micro-scarification of the seed coat (rather than deinhibition or fertilization effects). While scarification remains one of the more poorly understood gut-passage effects following endozoochory, the primary mechanism by which it is thought to enhance germination is by increasing a seed's permeability to water and nutrients (Barnea et al., 1990; Traveset et al., 2001) or ability to detect light (Murray, 1988; Traveset et al., 2001). The latter effect may be particularly important for species with light-dependent germination, as is the case for our study species and most other melastomes (Silveira et al., 2013). It may at first be surprising that manakin gut passage could have significant impacts on seed coats integrity during gut transit: manakins are gulpers (Levey, 1987), have rapid gut-passage times (Levey, 1986; Worthington, 1982), and lack a crop and grinding gizzard (Ellison et al., 1993; Worthington, 1982), and thus direct scarification of the seed coat from the digestive tract is likely to be relatively minor (Moermond & Denslow, 1985). However, longer gut retention times have sometimes been shown to produce detrimental levels of scarification, resulting in excessive seed deterioration and embryo death (Charalambidou et al., 2003; Murray et al., 1994). This raises the possibility that minor, more beneficial scarification may occur during rapid gut transit.

Overall, studies investigating the scarification effect have yielded mixed results, and therefore the effects of scarification on seed fate are likely highly dependent on the morphology of the seed being consumed and the digestive anatomy of the bird consuming it (Traveset, 1998). Interestingly, *M. rubescens* seeds are sharply pointed, and scanning electron microscopy (SEM) images demonstrate that the anticlinal boundaries of some cells are raised inconsistently throughout the corpus of the seed (Gamba & Almeda, 2014). Could it be that the shape and texture of the seed coat increases scarification in the otherwise gentle digestive processes of small avian frugivores such as manakins? Or that seed passage in birds with longer or shorter digestive tracts than manakins may result in too much or too little scarification? Regardless, the combination of morphological traits that characterize manakin digestion may be ideal for the tiny seeds typical of most melastomes, which have high surface-area-to-volume ratios and may only require minimal scarification to elicit

germination. It should also be considered that less well-understood gut passage effects (e.g., microbiome interactions in the digestive tract) may also have influenced results. Further investigation, perhaps by comparing the cellular structure of the seed coat between SEM images of digested and non-digested *M. rubescens* seeds, is required to determine if scarification is the mechanism resulting in the earlier germination of gut-passed seeds. Additional research determining how scarification affects light sensitivity within the seed and the time elapsed until germination would also be helpful.

Birds are the most frequent frugivores attending *Miconia* plants (Messeder et al., 2021) and seed-dispersal effectiveness can vary depending on both the avian and *Miconia* species involved (Ellison et al., 1993; Silveira et al., 2012; Messeder et al., 2021). We found a significant difference among manakin species in the magnitude of gut passage effects, with seeds passed by *L. velutina* exhibiting more accelerated germination relative to controls than those passed by *M. manacus*. A recent study in thrushes found that body mass positively predicted the germination success of gut-passed *Miconia rubiginosa* seeds (Campagnoli et al., 2023). We also found intraspecific differences in gut passage effects within both *M. manacus* and *L. velutina*, with heavier individuals conferring greater germination success on gut-passed seeds. This may be attributable to longer gut-retention times in larger individuals, likely leading to greater scarification of the seed coat that stimulates or promotes germination (Barnea et al., 1990; Barnea et al., 1991; Campagnoli et al., 2023; Traveset et al., 2001). Paradoxically, although mass positively predicted the magnitude of gut passage effects within species, the effects of gut passage by *L. velutina*—the smaller species—were greater than those of *M. manacus*. This could be due to yet-unknown differences in digestive morphology, enzymatic activity, or gut retention time between the species requiring further study. Within *M. manacus*, seeds passed by females had shorter times to first occurrence of germination than those passed by males. Given that male manakins perform energetically costly lekking behaviors, females may have slower metabolic and digestive rates, leading to longer processing of the seed in the gut, greater scarification of the seed coat, and earlier germination. Our results suggest that seemingly subtle morphological or physiological differences between avian frugivores, both interspecific and intraspecific, may have important influences on melastome seed germination.

Overall, our study adds to our understanding of the “quality” component of seed disperser effectiveness (Schupp, 1993; Schupp et al., 2010), suggesting that manakins can have biologically meaningful effects on melastome germination, although the magnitude of these effects can depend on manakin mass, sex, and species. Given that *Miconia* species provide year-round food for diverse animals, *M. rubescens* establishment facilitated by manakin dispersal may have important cascading ecological effects on the recovery of disturbed areas. *Miconia* has been proposed to constitute a keystone group of pioneer plants, and thus our findings also highlight the potential importance of manakins as seed dispersers in regenerating areas. Variations of this manakin–melastome relationship are present throughout the neotropics, and further investigation into these

dynamics will provide important insights into the forces shaping plant community structure and composition in threatened and regenerating tropical rainforests.

AUTHOR CONTRIBUTIONS

KR designed the experiment with support from HLA and input from JK, who supervised the project. KR and HLA implemented the experiment, collected data, and analyzed the data. HLA led formal analyses for the study. KR led the writing of the manuscript with input from HLA and further editing by JK. All authors contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at: <https://doi.org/10.5061/dryad.2bvq83c0b>.

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