Title: Variation in ant-mediated seed dispersal along elevation gradients.

Authors: Israel Del Toro[1*], Relena Ribbons[1]

Affiliations: [1]Lawrence University, Biology Department, 711 E. Boldt Way, Appleton WI, 54911, USA.

*corresponding author: Israel Del Toro Israel.deltoro@lawrence.edu

Israel Del Toro: ORCID: 0000-0002-3901-8713

Relena Ribbons ORCID: 0000-0002-9566-3813

Author Contributions: IDT and RRR designed the study, completed fieldwork, data analyses and wrote the manuscript.

Abstract

Ant-mediated seed dispersal, also known as myrmecochory, is a widespread and important mutualism that structures both plant and ant communities. However, ~~-~~the extent to which ant functional types gradients (e.g granivorous generalists vs myrmecochorous ants) across environment affect seed removal rates is not fully understood. We used a replicated, standardized seed removal experiment along elevation gradients in four mountain ranges in the southwestern United States to test predictions that: (1) seed removal rates would be greater at lower elevations, and (2) seed species identity influences seed removal rates, (i.e. seeds from their native elevation range would be removed at higher rates than seeds outside of their range). Both predictions were supported. Seed removal rates were ~25% higher at lower elevation sites than at higher elevation sites. The low elevation *Datura* and high elevation *Iris* were removed at higher rates in their respective native ranges. We attribute observed differences in dispersal rates to changes in ant community composition, functional diversity, and abundance. We~~, and~~ also suggest that temperature variation along the elevation gradient may explain these differences.

Keywords: mountain, biodiversity, myrmecochory, community ecology

Introduction

~~The geographic variation in ant-plant mutualistic relationships can shed light on plant and arthropod community structure and how they may respond to changing environmental conditions. In the temperate deciduous forests of North America, ants disperse up to 50% of all herbaceous species (Zelikova et al. 2008(Zelikova, Sanders & Dunn, 2011)).~~ Myrmecochory– ant-mediated seed dispersal – is an ecologically important and ubiquitous mutualistic interaction that exists between ants and plants (Ness and Bressmer 2005), occurring in over 11,000 species, and across 70 plant families (Lengyel et al. 2010). Seeds of myrmecochorous plants contain lipid-rich appendages called elaiosomes, which serve as nutritional rewards for ants (Warren and Giladi 2014; Gomez and Espadaler 2013, Ness 2005). ~~Myrmecochory is an important and widespread ecological phenomenon, and variation~~ Variation in seed removal rates can be explained by ant morphological traits (Fokuhl et al. 2012) and seed traits like eliaosome and plant size (Leal et al. 2015; Peters et al. 2003). Ants also influence the dispersal capacity of a seed by making seeds unavailable to other potential seed predators (Leal et al. 2015) and also disperse non-elaiosome bearing seeds through seed harvesting or granivory (Christianini et al. 2007; Taber 1999). In both cases, ant-mediated seed dispersal plays a key role as an ecosystem ~~service~~ process by shaping vegetation community structure (Del Toro et al. 2012; Ghobadi et al. 2015).

~~Seed dispersal distance has been studied on a global scale (Lengyel et al. 2010; Gomez and Espadaler 2013), but the variation in seed dispersal rates along environmental gradients on a landscape scale remains to be studied and can clarify the mechanisms~~

Commented [JZ1]: spelling

Formatted: Highlight

Formatted: Highlight

Commented [JZ2]: So are ants dispersers or seed predators – this needs to be made really clear here. Ants that disperse non-elaiosome seeds can also be eating those seeds and if they are not eating them, they are caching them (which may remove seeds from predation by others but may also create unfavorable germination conditions)

Formatted: Highlight

Commented [JZ3]: No, ant seed dispersal is not considered a key ecosystem process.

Formatted: Highlight

~~behind seed dispersal.~~ "Sky islands" are individual mountains isolated from larger continuous ranges by vastly different habitat types, in this case the Chihuahuan and Sonoran deserts at the lower elevations. The sky islands of the southwestern United States provide an excellent system for studying how myrmecochory varies along a continuous elevation and habitat gradient. This gradient extends from desert scrub to subalpine coniferous forest (Brusca and Moore 2013), which is an excellent natural experiment as both plant and arthropod communities tend to change systematically along gradients (Del Toro 2012).

Ant-mediated seed dispersal shapes vegetative communities ~~(Zelikova et al. 2008)~~ and this important mutualism is potentially resilient to increased temperatures in temperate forests in the eastern U.S. (Stuble et al. 2014). However, less is known about the potential breakdown of ant-mediated seed dispersal in a desert to forest mountain gradient ~~gradient due to changes in climate~~. We suspect strong mutualisms within desert communities, due to their extreme climates and rapidly changing environmental gradients (for example, intense deluges of rain and dramatic shifts in temperatures in a single day). Thus, we predict that myrmecochory may play a strong role in shaping vegetation communities in desert environments and expect tightly coupled ant-plant mutualisms that are species-specific.

Adding to the threats to ant-mediated seed dispersal include shifts in ant community composition, potentially either in response to a changing climate or being displaced by invasive competitor species (Rodriguez-Cabal 2011). We documented seed removal rates, and the effect of seed species identity on seed removal rates along this gradient. We predicted that: 1) rates of seed removal would be higher at lower elevations,

Formatted: Highlight

Commented [JZ4]: By this rationale, all mountains are isolated from other ecosystems – if "sky islands" are truly unique for ant seed dispersal, need to make that case here. Them being different is not enough of a context to justify the framing for this study.

Commented [JZ5]: Citations?

Formatted: Line spacing: Double

Formatted: Font: (Default) Times New Roman, 12 pt, Highlight

Commented [JZ6]: This doesn't seem like enough of a reason – are there other studies that show that mutualisms are stronger or more frequent in desert ecosystems?

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Font: (Default) Times New Roman, 12 pt

possibly associated with higher ant abundances and known different ant communities (Andersen 1997), and 2) individual rates of seed removal for each seed species would be highest at a seeds' native elevation range.

Commented [JZ7]: What does that mean?

Commented [JZ8]: What is a seed's native range? Why is that a factor in this study? Doesn't match the framing.

Materials and Methods

a) Study Site and Organisms

We conducted this study on four sky islands in the southwestern United States of America in June and July 2015 (see supporting data file for site details; S1, Table 1). At each elevation band we deployed 10 seed depots, each containing 100 seeds, with 25 seeds from four different plant species (Table 1). To test whether seed removal rates were dependent on species identity, we selected seeds from plants native to different habitats along the elevation gradient. We built seed depots using laminated white index cards covered with an overturned, reinforced, disposable plastic plate (Dixie Co. Atlanta GA, USA) held in place with lawn staples (Easy Gardener Inc. Waco TX, USA) to prevent seeds from being blown by wind or being removed by larger granivores. Ants were allowed to enter and exit the depot through 1cm openings, cut out around the covering plate. Each seed depot contained 25 seeds of the four study species (detailed below). We counted the remaining seeds every 12 hours over a 48-hour period. Each depot was deployed and counted within hours of each other, within a single mountain site.

Formatted: Highlight

Commented [JZ9]: This is already stated above

Formatted: Highlight

We selected seeds from four different plants (Datura, Iris, Oat, and Sumac) to test our second ~~objective~~prediction, that seeds would be removed at greater rates in their native elvation range. *Datura wrightii* is the only species with an eliaosome-bearing seed and is common in desert scrub habitat (typically found at elevations <1800 m.a.s.l.)

Commented [JZ10]: Again misspelled

(Carter 1997)(Carter, 1997)(Carter, 1997)(Carter, 1997)[1]. We collected seeds within one week of deploying the depots to account for phenological emergence. Based on our field observations, this seed was typically removed by Harvester ants (*Pogonomyrmex* spp). Little Leaf Sumac (*Rhus microphylla*) fruits were observed in the field being harvested by various ant genera (*Pogonomyrmex*, *Aphaenogaster* and *Pheidole*) at mid elevations from 1800 m.a.s.l to 2400 m.a.s.l. The Rocky Mountain Iris (*Iris missouriensis*) normally occurs only in habitat above 2400 m.a.s.l.(`Brusca & Moore, 2013), and ants in the genera *Formica* and *Myrmica* were observed actively removing seeds from the plants. Lastly, we used an oat seed (*Avena sativa*) that served as our control group, as it is not native to the study region nor does it contain an eliasome, but may be a source of nutrients for opportunistic and granivorous ants.

To assess ant community composition and abundances, we used a16 pitfall quadrant array at each sampling location. Pitfall traps were deployed for the same 48 hours when seed removal rates were observed. We report ant incidence (i.e. number of pitfalls that captured an individual genus) as a conservative measure of ant abundance.

b) Statistical analyses

We used a generalized linear mixed model (GLMM) to test for an additive ~~interaction~~ effect between elevation and seed species, and to test our first prediction that seed removal would vary across elevation and site. We treated time, elevation, and seed identity as fixed effects, and specified a Poisson distribution for the count data. The total number of seeds removed over time was compared between seed species and elevation bands using repeated-measures analysis of variance (RMANOVA). To test our second prediction (that seed identity influences seed removal across elevations) we used a

Commented [JZ11]: Be more specific

Commented [JZ12]: Which seed?

Formatted: Highlight

Formatted: Highlight

Commented [JZ13]: Again spelling

Formatted: Highlight

Formatted: Highlight

Commented [JZ14]: Then this is not an appropriate experimental control

Formatted: Highlight

Commented [JZ15]: Not presented in the results section

Commented [JZ16]: Its actually not at all a measure of abundance, it is its own metric and usually referred to as "occurrence" which has its own suite of analyses associated with it (as well as assessment of whether this method misses rare species or species that do not respond to pitfall traps)

Formatted: Highlight

Formatted: Indent: First line: 0.5", Line spacing: Double

Formatted: Highlight

Commented [JZ17]: What does "additive effect" mean?

Commented [JZ18]: As far as I understand, these are one in the same

Formatted: Highlight

Commented [JZ19]: Count of what?

Formatted: Highlight

Commented [JZ20]: Among since you have more than 2

Formatted: Highlight

GLMM and Chi square tests for each species separately, and included site as a random factor.

We conducted an overdispersion test, modified from Ben Bolker (overdisp_fun; see Supplementary material lines 24-32). This function was applied to all glmer models and results are reported in the supplementary materials. Overdispersion was not detected in the global model M1, but was present in the individual models of Iris and Sumac. For Iris and Sumac, overdispersed models were fitted using a quasi-Poisson distribution, which allowed us to estimate which sites and elevations are driving the primary detected patterns. For Iris- the significant difference in high elevations is driven by site MOG. For Sumac- variable responses at high elevation sites (2800 m) may be dampening any possible trends.

See the supporting information file (S1) for the detailed code and dataset used in the analyses. All analyses including GLMMs were implemented in R statistical program version 3.2.3 (R Development Core Team 2014) using the "lme4" package (Bates et al. 2015)(Douglas Bates et al., 2014)(Douglas Bates et al., 2014)(Douglas Bates et al., 2014)[3] and Chi square tests in the "car" package (Fox and Weisberg 2011)(Fox & Weisberg, 2011)(Fox & Weisberg, 2011)(Fox & Weisberg, 2011)[4]. To identify differences in ant community composition we used Principal Component Analysis (PCA) implemented in the "FactoMineR" package and visually inspected PCA biplots.

Results

Total seed removal rates were similar among sites at 1600 m and those at 2200 m, but seed removal rates were 23.8% lower at 2800 m than at the lower elevations (Figure

Commented [JZ21]: Give a reason why

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Font: (Default) Times New Roman, 12 pt

Commented [JZ22]: Global model? This was followed by individual species modeled singularly? Need to give those kinds of details

Formatted: Font: (Default) Times New Roman, 12 pt

Commented [JZ23]: What does a result like this mean if anything? This tells me there is no pattern.

Formatted: Font: (Default) Times New Roman, 12 pt, Highlight

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Font: (Default) Times New Roman, 12 pt, Highlight

Commented [JZ24]: Also have no idea what this means.

Formatted: Highlight

Formatted: Font: (Default) Times New Roman, 12 pt, Highlight

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Font:

Formatted: Highlight

Commented [JZ25]: This is a weird way to present the elevation gradient results – if there is no elevation gradient, as expected, start with that.

1, Figure S1), a pattern consistent with our first prediction. Our repeated measures analyses suggested a strong ~~interaction~~ additive effect between elevation and seed species (Table 2, $p < 0.001$). In all analyses (global model and seed specific models), time influenced the number of seeds removed. This suggests that the longer the depots are active, the more seeds are removed, ranging from 25% to 58% over the 48-hour time period.

Datura and oat seeds accounted for most of the seed removal (Figure 2A, 2C, (13% and 18% respectively)), whereas Iris and Sumac seeds were removed at lower rates (2B, 2D (~5% for either species)). Datura seed removal was highest at the low elevation sites, with no differences between the mid and high elevation sites. Oat seed removal tended to be greater at mid elevations and approximately the same at low and high elevations (Figure 2C), compared to the other seed species. Iris and Sumac seeds were removed less frequently from our depots, with Iris seeds having greater removal rates (Figure 2B) while Sumac had the lowest removal rates between these two species (Figure 2D), at high elevation sites after 48 hours. Our repeated measures analyses suggest that elevation was an important factor in explaining seed removal rates for all four species, and site level effects were important for Datura ~~, Iris~~ and Oats, but Iris ~~not~~ or Sumac.

Discussion

Our findings highlight that while ~~granivory~~ seed removal may be widespread across environmental gradients, it may be more pronounced in arid low-elevation compared with mesic high-elevation habitats. Observed seed removal rates were greater in lower elevations than in higher elevations. Seed removal was strongly dependent on seed species identity and its native elevation range, which was consistent with our predictions.

Commented [JZ26]: I again don't know what this additive effect means, its not a parametric statistical result

Formatted: Highlight

Commented [JZ27]: This seems obvious to me, not sure it's a big result to present. I guess it would be interesting and unexpected if seeds were not removed?

Formatted: Highlight

Commented [JZ28]: A result like this worries me – elevation cannot in and of itself remove seeds but is being involved as a driving thing when in actually, variation in seed removal rates is likely driven by shifts in ant community composition and/or activity and those aspects were not presented or invoked.

Commented [IDT29]: The geographic variation in ant-plant mutualistic relationships can shed light on plant and arthropod community structure and how they may respond to changing environmental conditions. In the temperate deciduous forests of North America, ants disperse up to 50% of all herbaceous species (Zelikova et al. 2008(Zelikova, Sanders & Dunn, 2011)).

Commented [JZ30]: I find it puzzling that the study did not include any observation of which ants were interacting with the seeds and no link made between the ant communities and seed removal. This is a fetal flaw for this study that keeps it from (1) addressing the actual research goals, (2) drawing any conclusions whatsoever about the mechanisms that are structuring seed movement and I would venture, resultant plant communities. As a result, this study misses the mark and does not bring any new knowledge or understanding. If the authors can find a way to reshift their focus and think about the biological interactions rather than using elevation as a proxy for everything, this study can be made relevant.

The pattern of total seed removal may be attributable to higher abundance of seed dispersing ants, especially Harvester ants (*Pogonomyrmex* spp., *Novomessor* spp.). These two species are more common at lower elevations (Taber, 1998)(Taber, 1998)(Taber, 1998)[5](Taber 1998) and have multiple traits which make these ants ideal dispersers of seeds that are dropped while foraging and not consumed (Warren and Giladi 2014; Zelikova et al. 2008), including a specialized dietary preference for seeds (Taber 1999). These harvester ants were observed removing seeds of Datura and Sumac, as well as the control Oat, but never dispersing the Iris. This observation may be a fruitful line of inquiry in future work.

In other temperate region studies, ant abundance is correlated with unimodal species richness and abundance patterns with low ant diversity/abundance at high elevations, with a peak of diversity/abundance in mid to lower elevations (Bharti et al 2013; Lessard et al. 2011). Our results suggest a similar pattern of ant abundance could be driving seed removal rates, as both seed removal and ant abundances were higher at low elevation sites. Myrmecochory may be more prevalent in ecosystems where high ant abundances can be advantageous for dispersing seeds, (e.g. Datura in low-elevations). The mutualistic relationship of harvester ants (*Pogonomyrmex*) and *Datura wrightti* has been carefully documented and the effects of Datura seed diets on ant reproductive output have been experimentally tested (Marussich, 2006). ~~(Zelikova et al. 2008).~~ Ant community composition also changes along these elevation gradients, with the lower elevations having high abundances of hot-climate specialist and generalized Myrmicinae species, and high elevation sites tend to have lower abundances of ants which were mainly cold climate specialist and opportunistic species (Andersen 1997) (S1). The observed ant community differences

Formatted: u-mb-2, Indent: Left: -0.25", Space After: 0 pt, Outline numbered + Level: 1 + Numbering Style: Bullet + Aligned at: 0.25" + Tab after: 0.5" + Indent at: 0.5", Font Alignment: Center, Pattern: Clear (Custom Color(RGB(252,252,252)))

may explain the patterns of seed removal along this gradient. Behaviorally dominant and abundant genera may remove more seeds at low elevations, while opportunistic genera may remove fewer seeds at high elevation sites. Higher rates of seed removal at lower elevations may also correlate with higher temperatures, which leads to increased activity such as removal rates (Stuble et al. 2014).

Seed species identity also influenced observed seed removal patterns. Datura and Iris seeds were removed at higher rates in their native elevation ranges (1600 m and 2800 m, respectively). The pattern detected in our study suggests that at low elevations, ant communities have highly active and abundant, seed-dispersing species (S1). Mid-elevation sites tend to have preferentially granivorous ant communities (as indicated by the higher removal of oat seeds at mid-elevations). High-elevation sites have relatively lower ant abundances (S1) largely comprised of opportunistic species. Our results may reflect an unequal distribution of functional ant diversity along these elevation gradients. This uneven distribution of functional diversity places concern on seed-dispersing ant species that may be sensitive to climate change, especially in temperate (high elevation) ecosystems (Del Toro et al. 2015) or instances where climate-driven ecological mismatches between seed drop and ant activity occur (Warren and Bradford 2014).

Future work should explore the network of ants interacting with various seed species being dispersed along environmental gradients. This would help identify major seed dispersing ant species and the total influence they have on structuring vegetation communities. We recognize the potential for the influence of seed-drop phenology influencing the seeds being dispersed, a pattern that was documented in eastern North American forests (Warren and Bradford 2014). This may partially explain low rates of

231 Sumac removal, since it tends to drop its seeds earlier in summer than the other seeds
232 (Cater 1997).

233

234 **Conclusions**

235 Although myrmecochory is widespread and important in structuring plant and
236 animal communities (Warren and Giladi 2014; Del Toro et al. 2012), this relationship is
237 not equally distributed along elevation and habitat gradients. Furthermore, a single ant
238 species can perform a majority of seed dispersal, such as *Pogonomyrmex* spp. and
239 *Novomessor* spp. in this study or *Aphaenogaster rudis* in the Great Smoky Mountains
240 (Zelikova et al. 2008). We highlight that for some species (Datura and Iris) their ant-
241 mediated dispersal rate is highest in their native elevation range, which may suggest
242 strong mutualistic links between ants and these plant species. The work on seed dispersal
243 along elevation gradients allows us to explore how key ant-mediated ecosystem processes
244 respond to environmental cues and help us predict how communities might respond to
245 future climatic and habitat change.

246

247 **Acknowledgements:**

248 Sampling permits were obtained from the United States Forest Service. We thank
249 Christian Rodriguez and Bill McKay for data collection and genera identification
250 assistance, Sara Baqla and Julie Schlicte for data collection assistance, and the Sanders
251 lab group and Brandon Bestelmeyer for input on previous drafts of this manuscript.

252 Funding was provided by a National Science Foundation postdoctoral research fellowship
253 awarded to IDT, and UTEP REU and Jornada LTER REU programs.

254

255 **Conflict of Interest:** The authors declare that they have no conflict of interest.

256

257 **References:**

258 Andersen, A. N. (1997). Functional groups and patterns of organization in North
259 American ant communities: a comparison with Australia. *Journal of Biogeography*,
260 *24*(4), 433–460. http://doi.org/doi:10.1046/j.1365-2699.1997.00137.x

261 Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-
262 effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.
263 http://doi.org/10.18637/jss.v067.i01

264 Bharti, H., Sharma, Y. P., Bharti, M., & Pfeiffer, M. (2013). Ant species richness,
265 endemicity and functional groups, along an elevational gradient in the himalayas.
266 *Asian Myrmecology*, *5*(1), 79–101. http://doi.org/10.1111/j.1600-0706.2010.18772.x

267 Brusca, R. C., & Moore, W. (2013). *A natural history of the Santa Catalina Mountains,*
268 *Arizona, with an introduction to the Madrean sky islands*. Arizona-Sonora Desert
269 Museum Press.

270 Carter, J. L., Dennis, B., Leggitt, M. C., & Underwood, W. J. (1997). *Trees and shrubs of*
271 *New Mexico*. Mimbres Pub.

Formatted: Line spacing: Double

Christianini, A. V., Mayh, J., Oliveira, P. S., Mayhé-Nunes, A. J., Oliveira, P. S., Mayh, J., Mayhé-Nunes, A. J. (2007). The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a neotropical savanna. *Journal of Tropical Ecology*, *23*(3), 343. http://doi.org/10.1017/S0266467407004087

Del Toro, I., Ribbons, R. R., & Pelini, S. L. (2012). The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News*.

Del Toro, I., Silva, R. R., & Ellison, A. M. (2015). Predicted impacts of climatic change on ant functional diversity and distributions in eastern North American forests. *Diversity and Distributions*, *21*(7), 781–791. http://doi.org/10.1111/ddi.12331

Fokuhl, G., Heinze, J., & Poschlod, P. (2012). Myrmecochory by small ants - Beneficial effects through elaiosome nutrition and seed dispersal. *Acta Oecologica*, *38*, 71–76. http://doi.org/10.1016/j.actao.2011.09.007

Fox, J., & Weisberg, S. (2011). An ~~{~~R~~}~~ Companion to Applied Regression, Second Edition. *Sage*, (September 2012), 2016. ~~Retrieved from~~ http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Ghobadi, M., Agosti, D., Mahdavi, M., & Jouri, M. H. (2015). Effects of Harvester Ants' Nest Activity (Messor spp.) on Structure and Function of Plant Community in a Steppe Rangeland (Case Study: Roodshoor, Saveh, Iran). *Journal of Rangeland Science*, *5*(4), 269–283. ~~Retrieved from~~ ~~http://www.rangeland.ir/article_516635_110095.html%5Cnhttp://www.rangeland.ir/pdf_516635_3a47b7f56ebd5c39ddb668e6579733cc.html~~

293 Gómez, C., & Espadaler, X. (2013). An update of the world survey of myrmecochorous
294 dispersal distances. *Ecography*, *36*(11), 1193–1201. http://doi.org/10.1111/j.1600-
295 0587.2013.00289.x

296 Leal, I. R., Leal, L. C., & Andersen, A. N. (2015). The benefits of myrmecochory: A
297 matter of stature. *Biotropica*, *47*(3), 281–285. http://doi.org/10.1111/btp.12213

298 Lengyel, S., Gove, A. D., Latimer, A. M., Majer, J. D., & Dunn, R. R. (2010).
299 Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in
300 flowering plants: A global survey. *Perspectives in Plant Ecology, Evolution and*
301 *Systematics*. http://doi.org/10.1016/j.ppees.2009.08.001

302 Lessard, J.-P., Sackett, T. E., Reynolds, W. N., Fowler, D. A., & Sanders, N. J. (2011).
303 Determinants of the detrital arthropod community structure: the effects of
304 temperature and resources along an environmental gradient. *Oikos*, *120*(3), 333–343.
305 http://doi.org/10.1111/j.1600-0706.2010.18772.x

306 Marussic, W.A. (2006). Testing myrmecochory from the ant's perspective: The effects
307 **of *Datura wrightii* and *D. discolor* on queen survival and brood production**
308 **in *Pogonomyrmex californicus*. *Insectes Sociaux* 53(4), 403-**
309 **411.**

310 Ness, J. H., & Bressmer, K. (2005). Abiotic influences on the behaviour of rodents, ants,
311 and plants affect an ant-seed mutualism. *Ecoscience*, *12*(1), 76–81.
312 http://doi.org/10.2980/i1195-6860-12-1-76.1

Formatted: Font: Times New Roman, 12 pt, Not Bold
Formatted: Font: Times New Roman, 12 pt
Formatted: Line spacing: Double
Formatted: Font: Times New Roman, 12 pt
Formatted: Indent: Left: 0.33", Line spacing: Double
Formatted: Font: Italic
Formatted: Font: Times New Roman, 12 pt
Formatted: Line spacing: Double

313 Peters, M., Oberrath, R., & Bohning-Gaese, K. (2003). Seed dispersal by ants: are seed
314 preferences influenced by foraging strategies or historical constraints? *Flora*,
315 *198*(6), 413–420. http://doi.org/10.1078/0367-2530-1210114

316 R Development Core Team. (2016). R: A Language and Environment for Statistical
317 Computing. *R Foundation for Statistical Computing Vienna Austria*, *0*, {ISBN} 3-
318 900051-07-0. http://doi.org/10.1038/sj.hdy.6800737

319 Stuble, K. L., Andrew, N., Patterson, C. M., Rodriguez-Cabal, M. A., Ribbons, R. R.,
320 Dunn, R. R., & Sanders, N. J. (2014). Ant-mediated seed dispersal in a warmed
321 world. http://doi.org/10.7717/peerj.286

322 Taber, S. W. (1999). *The world of the harvester ants.* Texas A & M University Press.
323 Warren, R. J., & Giladi, I. (2014). Ant-mediated seed dispersal: A few ant species
324 (Hymenoptera: Formicidae) benefit many plants. *Myrmecological News*.

325 Zelikova, T. J., Dunn, R. R., & Sanders, N. J. (2008). Variation in seed dispersal along an
326 elevational gradient in Great Smoky Mountains National Park. *Acta Oecologica*,
327 *34*(2), 155–162. http://doi.org/10.1016/j.actao.2008.05.002

328

329

Formatted: Line spacing: Double

Figure legends

Figure 1. Mean seed removal rates per ~~bait station~~seed depot along the elevation gradient over a 48-hour period. Squares=1600 m.a.s.l., circles= 2200 m.a.s.l. and triangles= 2800 m.a.s.l. Bars indicate standard error about means.

Figure 2. Mean species-specific seed removal rates per station along the elevation gradient over a 48-hour period. Squares=1600 m.a.s.l., circles= 2200 m.a.s.l., triangles= 2800 m.a.s.l. Bars indicate standard error about means.