

University of Nevada, Reno

**Seed Dispersal and Dispersal Syndromes in Manzanitas,
and Other Higher Plants**

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in
Ecology, Evolution, and Conservation Biology

By

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THE GRADUATE SCHOOL

We recommend that the dissertation
prepared under our supervision by

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Entitled

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And Other Higher Plants**

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INTRODUCTION

Dispersal is an emergent property of biological systems existing in a spatial world. Specifically, if rules governing autonomous biological agents are to (i) acquire and utilize resources to respectively (ii) metabolize and reproduce, then space is a limiting factor in areas with finite resources. Further, if parents have a greater ability to acquire resources than filial generations, only offspring of the ultimate reproduction event would have a survival probability greater than zero. Therefore, we observe movement away from parents (dispersal) as a ubiquitous phenomenon observed in all biological systems that increases the ability of biological agents to acquire resources and reproduce.

From a perspective of multiple parents reproducing over time in a finite area (*i.e.*, an ecological population) dispersal is a collective property that is generally relative to two factors: (i) population turnover (*i.e.*, availability of previously used resources [occupied patches]) and (ii) environmental heterogeneity (*i.e.*, availability of new resources [new patches]). If fecundity is normalized, dispersal distributions (frequency or density distribution as a function of distance expressed in one or two dimensions) are examined as the kurtosis of the sum of all parents' offspring individually or collectively. Further, dispersal metrics (kurtosis of individuals or populations) can be measured demographically where individuals are the unit or genetically where genes from an individual contribute to the gene pool.

To disperse, organic life has evolved an array of mechanisms (*e.g.*, structures like flagella, fins; behaviors like density dependent dispersal) at all life stages (*e.g.*, diploid zygotes or diaspores, haploid gametes, reproductive adults, non-reproductive juveniles). In the seed plants (spermatophytes) that macroscopically dominate and energetically

support virtually all terrestrial ecosystems through primary productivity, dispersal can occur at two life stages: haploid pollen dispersal and diploid seed dispersal. The outcome of each type of dispersal is different, with pollen being of uniparental (paternal) origin and strictly contributing to genetic (gene flow) but not demographic dispersal, and seeds being of biparental origin and contributing to demographic and likely genetic dispersal if ecological establishment is achieved.

Plants have evolved different means of dispersing seeds, generally by adaptation to abiotic and biotic vectors. Abiotic vectors include fluids like air and water, and biotic vectors include a wide variety of animal taxa. Animals generally disperse seeds through digestion, through incomplete recovery of stored food, and through discarding seeds after they have been dispersed intentionally or incidentally by attachment. Adaptations to various modes of dispersal by plants result in suites of traits that match the behavior, physiology, or morphology of the vectors, and referred to as dispersal syndromes.

This core of this dissertation examines dispersal syndromes across different scales of biological organization. The first chapter attempted to determine how a single species of plant with an ambiguous dispersal syndrome is dispersed. I conducted a series of experiments to determine how the species' seeds are dispersed and the consequences of that particular mode of dispersal. This is mainly because this mode of dispersal may illuminate how other seeds in fire-prone ecosystems can form seedbanks that can escape the lethal temperatures of fire. The second chapter expands beyond the single-species perspective and I used a morphometric analysis to compare the focal species of chapter 1 to other species in the same genus. Because I had studied one species in depth, I could conclude with high certainty that a number of species in the same genus are very likely to

have the same mode of dispersal. Additionally, I examined seed and fruit characteristics to find patterns of morphological differences across environmental gradients that are known to affect these characteristics. Lastly, in chapter 3, I scaled-out further and examined patterns of seed dispersal syndromes across a continent, with specific foci on patterns of distribution of all plant species, plant species without mutualist seed dispersers, plant species with mutualist seed dispersers, plant species distributions of the three major modes of animal dispersal (frugivory, scatter-hoarding, myrmecochory), and the differences between species and interactions across several environmental gradients at a large spatial scale. I found patterns of seed dispersal syndromes that differed than patterns of species richness, a strong latitudinal gradient, and interaction richness. I hope that this dissertation contributes to ever-growing body on literature on animal-mediated seed dispersal. There is still much more to learn about, with respect to determining boundaries of seed dispersal syndromes, the ecology of animal-mediated seed dispersal, and large-scale patterns of animal-mediated seed dispersal. This is a first attempt into some previously unexplored areas into these aspects of seed dispersal, and I hope it proves to be fruitful.

DEDICATION

This dissertation is dedicated to my immediate family, grandparents George and Rose Moore, grandparents Abel and Lydia "Lily" Bedoya, parents George and Laura Moore, and brother Aaron Moore. It is secondarily dedicated all other family and friends who nourished and encouraged my wonderment with the natural world. Lastly, this dissertation is dedicated to other teachers and educators who inspired throughout my life. A non-exhaustive list includes Mrs. Giokaris for her special assemblies on geodes and mammals, Mr. Craig from Granada Middle School for his love for "creepy-crawlies," Peck from La Habra pets, Dr. Glenn R. Stewart for knowing everything about organismal biology and the natural history of California, Greg McConnell for his passion for Lissamphibia and being a caring teacher, and Sarah Millus for her laugh and knowledge of small mammals.

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Chapter 1: Seed dispersal of a fire-adapted shrub by seed-caching rodents

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Abstract. Seed dispersal is the demographic process whereby plants disperse seeds through space and time to escape negative density dependent effects and colonize available sites. In fire-prone ecosystems, very little is known about how dispersal occurs and seed banks establish, yet some seeds seemingly persist fires with temperatures that area lethal to some seeds. This study examined seed dispersal of a fire-adapted plant that is putatively dispersed by omnivorous mammals in the order Carnivora to understand how its seeds are dispersed and how they are incorporated into the soil seedbank. The focal organism in this study was greenleaf manzanita (*Arctostaphylos patula*), a widespread and abundant fire-adapted shrub in the western United States. To determine the seed dispersal process, full-shrub exclosures and motion-sensor cameras were used to determine if and what animals removed seeds, seeds were radiolabeled and followed to determine seed deposition, and patterns of post-fire recruitment were observed. Seed-caching rodents removed the majority of fruits from manzanita shrubs, dispersed the majority of seeds to microsites that were not significantly different than from where they were found to germinate (mean cache depth = 23.0 mm, mean germination depth = 24.1 mm), and most seedlings germinated in clumps. These findings implicate scatter-

hoarding rodents as the effective dispersers of manzanitas, a plant previously thought to be dispersed by omnivorous carnivores or frugivorous birds. Additionally, dispersal kernels were used to infer aspects of seed-caching behavior and showed that the rate at which rodents cache decreased at a decreasing rate with distance. It is concluded that seed-caching acts as a "burial syndrome" because seed-caching rodents deposit seeds in microsites that protect some seeds from lethal fire temperatures. In fire-prone ecosystems, depending on the fire regime, it is imperative that seeds escape fire-based mortality, and future studies should investigate these processes to better understand recruitment in these ecosystems.

Keywords: Arctostaphylos; *caching; dispersal syndrome; food hoarding; frugivory; manzanita; mutualism; optimal cache spacing theory; seed dispersal;* Tamias

INTRODUCTION

To understand plant population dynamics, entire plant lifecycles need to be understood (Wang and Smith 2002, Forget et al. 2005). Notwithstanding, our understanding of plant population patterns and processes is predominately based on adult demographic studies (Harper 1977). What has empirically been relatively understudied—yet is inexorably linked to adult recruitment in sedentary plants—is the seed dispersal phase. Seed dispersal is critical to understand in this sense because, for instance, it links the end of the reproductive cycle to seedling establishment, is the only part of the plant lifecycle when migration occurs, and is part of the plant lifecycle with the highest mortality rates. Closing the gap between reproduction and recruitment will

help better understand plant population dynamics (Wang and Smith 2002) and help us make more accurate predictions about range dynamics, say, in the light of a changing climate (Travis et al. 2013).

Plant recruitment can be continuous or regularly intraannual (seasonal) through time, or it can be interannually episodic with plant populations recruiting in pulses ("event-driven dynamics," *sensu* Walker 1993). In arid-to-semi-arid areas, episodic recruitment often seems to be the rule rather than the exception (Grime 1977, Fowler 1986), especially with long-lived plants (e.g., *Carnegiea gigantea*, Pierson and Turner 1998; *Acacia* sp., Wiegand et al. 2004; *Larrea tridentata*, Allen et al. 2008; *Pinus ponderosa*, Taylor 2010). Theory contends that in high-stress environments—like arid and semi-arid regions—processes that shape the structure and functioning of plant communities are environmental constraints (Grime 1977), thus minimizing the importance of intraguild biotic interactions that can be understood as density-dependent, like competition. Taken a step further, the argument could be made that because intraguild biotic interactions between adult plants have a reduced role in structuring plant communities in high-stress environments, seed dispersal (arrival to high-quality microsites) is a limiting factor in these environments. Incidentally, intraguild interactions have been proposed as playing a lesser role in shaping species-rich plant communities than dispersal under certain conditions. Janzen (1970) and Connell (1971) state that specialist pests and pathogens keep plant species rare enough or reduce their competitive ability enough so as to make space available for many other species. The corollary to this individual-parent view of density dependence processes of removing nearby offspring and conspecifics is that it suggests that highly vagile taxa are an evolutionary outcome,

which increases rates of diversification. Hubbell (2006) took this concept a step further and demonstrated that highly vagile taxa within species-rich communities create conditions that are unfavorable for pairwise interspecific interactions to evolve between species within a guild. In Hubbell's model, dispersal dynamics determines the rate of pairwise interactions that would lead to specific coevolution between species within a guild, which does not happen in the species-rich forests that the model describes and further suggests that dispersal plays an integral role in ecological and evolutionary dynamics even in taxonomically-rich areas.

One type of episodic recruitment in high-stress, taxonomically-rich areas for which seed dispersal is designated important is post-fire recruitment. Many plants have adapted to fire regimes (Keeley et al. 2011) that can be categorized into two strategies (*sensu stricto* Turner et al. 1998): colonizing or residing. Residual taxa represent individuals that have the ability to survive through a fire event and resprout; whereas colonizing taxa persist via seeds, usually in a below-ground seedbank. Of the types of seed recruitment that can occur, persistent seed banks are the cornerstone of fire-prone ecosystems. Transient seeds are generally short-lived and fire does not induce germination (non-refractory), whereas persistent seeds are long-lived and refractory (Keeley 1991). It is these persistent rather than transient seed banks that overwhelmingly contribute to post-fire recruitment and establishment (Keeley et al. 2005).

Despite the importance of seed-based recruitment in fire-prone ecosystems, seed bank dynamics is understudied and poorly understood. For instance, most literature on life-history or the ecology of plants in fire-prone ecosystems will include discussions on obligate and facultative seeding, yet fail to address or simply disregard seed dispersal

(Keeley and Zedler 1978, Keeley 1987a). Few studies have addressed critical aspects of seed dispersal in fire-prone ecosystems (e.g., Peart 1984, Garnier and Dajoz 2001), for example: How are seeds deposited into soil seed banks? At what rates are seeds dispersed into the soil to survive fire events that are otherwise lethal?

The aim of this study was to investigate seed dispersal processes and patterns in a fire-adapted plant that is putatively dispersed by omnivorous medium-to-large mammals belonging to the family Carnivora in a fire-prone ecosystem. I have chosen a ubiquitous, abundant, and often ecologically dominant member of the most taxonomically-rich genus in the fire-prone California Floristic Province, greenleaf manzanita, *Arctostaphylos patula* (Greene, Ericaceae), with documented persistent soil seed banks. Manzanita (*Arctostaphylos* Adans.) fruits and seeds ostensibly do not conform well to known dispersal syndromes and our understanding of seed bank dynamics are based on few studies that were equivocal in their findings (Keeley and Hays 1976, Keeley 1987b, Kelly and Parker 1990). To date, no study has exclusively focused on examining seed dispersal in any manzanitas.

Our current understanding of dispersal in manzanita is based on the following anecdotal evidence of three guilds of animals (frugivorous birds, rodents, omnivorous carnivores) as candidates for dispersers of manzanita. One reference to birds as frugivores was by Cipollini and Stiles (1993), where American Robins (*Turdus migratorius*) consumed manzanita fruit when given a two-choice fruit selection experiment using low-preference food items, *A. uva-ursi* and blue huckleberry (*Vaccinium macrocarpon*). Hauser (2007) also mentions manzanita as being bird-dispersed; however, when investigating the citations, I could find no references with explicit

examples of birds consuming or dispersing manzanita fruit or seeds. Some studies have found evidence of scatter-hoarding rodents as predators or dispersers of manzanita seeds (Tevis 1953, Keeley and Hays 1976, Keeley 1977, 1987b, Kelly and Parker 1990). Tevis (1953) found evidence of greenleaf manzanita (*A. patula*) seeds in the cheekpouches, and endosperm in the stomachs of long-eared chipmunks (*Tamias quadrimaculatus*). Tevis (1953) also noted that, after fire, seedlings emerged in clumps from what appeared to be rodent caches. In two other studies, Vander Wall et al. (2005) observed yellow pine chipmunks (*Tamias amoenus*) foraging on greenleaf manzanita seeds, and Kuhn and Vander Wall (2009) found seeds in chipmunks' winter larders. Tevis (1953) considered rodents as dispersers of manzanita seeds, and others consider rodents as important seed predators (Keeley and Hays 1976). The last, and most cited candidate as dispersers of manzanita fruits are omnivorous carnivores (Bowyer et al. 1983, Delibes et al. 1989, Wilson and Thomas 1999, Nielsen et al. 2004, Silverstein 2005). Ants have never been reported as handling manzanita fruits or seeds, and the three-year duration of this study shared a similar lack of observation despite careful and thorough observation in the field. Lastly, carnivorous mammals have been shown to consume manzanita fruits, such as gray foxes (*Urocyon cinereoargenteus*), coatis (*Nasua narica*), coyotes (*Canis latrans*), American black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*). One study (Silverstein 2005) examined germination from scat (coyote), and found germination rates of only 0.2–1.6 %, suggesting that consumption by carnivorous mammals may not increase germination.

The main question asked in this study is: How are *Arcostaphylos patula* seeds dispersed? To answer this question (i) whole-shrub exclosures were erected to allow

access to certain guilds of potential animal dispersers, (ii) radiolabeled seeds were placed in front of motion-censored cameras to determine what animal species remove the seeds, (iii) radiolabeled seeds were relocated to look for patterns of dispersal and deposition, and (iv) observed patterns of deposition were compared to natural patterns of emergence. The *a priori* hypothesis was (H_0) omnivorous carnivores are the effective dispersers of greenleaf manzanita seeds. Alternative hypotheses were that (H_1) that small, scatter-hoarding rodents, (H_2) frugivorous birds, or (H_3) abiotic burial are the effective mean by which greenleaf manzanita seeds are dispersed.

METHODOLOGY

Field site

The study was conducted in the University of Nevada's George Whittell Forest and Wildlife Area, located in Little Valley, 5-km west of Washoe Valley and northeast of the Lake Tahoe basin ($39^{\circ} 14' - 17' N$, $119^{\circ} 52' - 53' W$), with an average elevation of 1,975 m. Little Valley is characterized by a Mediterranean climate, with hot, dry summers, and cool, wet winters in the California Floristic Province. Most (~75%) precipitation in Little Valley occurs in the winter months (November–May) from westerly airflows over the Sierra Nevada in the form of snow. Mean annual precipitation is 87.5 cm, with interannual variation ranging approximately from 50–200% of the mean. Mean monthly temperatures range from 11–16°C in the summer, and -4–0°C in the winter. Large-scale disturbances that occur in Little Valley are primarily from fires. Low severity surface fires have historically occurred approximately every 9–14 years in Little Valley prior to European settlement around 1850 (Taylor 2004), and there is no

evidence of subsequent fires because of fire suppression of nearby woodlands, extensive logging until the 1870s, and grazing until the 1970s (Vander Wall 2005).

Soils of Little Valley are primarily granitic in origin with little organic matter. Major vegetation types consist of Jeffrey pine (*Pinus jeffreyi*)-white fir (*Abies concolor*) forest, lodgepole pine (*P. contorta*) forest, red fir (*Ab. magnifica*)-mixed subalpine forest, aspen (*Populus tremuloides*), riparian, montane shrub, and meadows. Greenleaf manzanita (*A. patula*) is common throughout Little Valley; it is only absent from meadows, riparian, and red fir-mixed subalpine forests. It is often found in associations with tobbacobrush ceanothus (*Ceanothus velutinus*). At higher elevations (c. 2,500 m), in the red fir-mixed subalpine forests, greenleaf manzanita is replaced by pinemat manzanita (*A. nevadensis*).

Fruit removal

To examine removal of manzanita fruits, wire-mesh vertebrate exclosures were constructed around individual shrubs to estimate fruit removal in the absence of specific seed dispersers. Each exclosure was a $2 \times 2 \times 1.3$ -m cuboid placed around an individual shrub with a 5 × 5-cm-thick wooden frame, wrapped with 12 × 12-mm galvanized steel wire-mesh. Shrubs were arbitrarily selected throughout the valley, with the criteria that shrubs (i) were producing fruit, (ii) were small enough to be enclosed and (iii) could be separate from other shrubs, trees, and boulders. The base of each exclosure was buried at least 0.15 m to discourage rodents from burrowing underneath the exclosure and removing seeds. Although traps were not set in exclosures where rodents were excluded, there was no observed evidence that rodents accessed the shrubs. There were a total of

four treatments, each replicated five times and repeated for two years. One treatment was a full enclosure (hereafter, full enclosure), to keep out all vertebrates (e.g., mammals, birds). A second treatment was an enclosure with eight 8 × 8-cm holes along the ground to exclude birds and large mammals, and allow rodents access (hereafter, rodent access). A third treatment had no top, and aluminum flashing (0.5-m height) was placed along the top of the sides of the enclosure to prevent rodents from climbing in the enclosure, but potentially allow birds and large mammals known to eat manzanita fruit, such as black bears and coyotes, to access the shrub (hereafter, rodent enclosure). The controls were shrubs that were measured the same way as the seed removal treated shrubs (hereafter, control). Exclosures were erected while fruits were immature (late August through September) in the summers of 2010 and 2011.

Because manzanitas often have hundreds of fruit per individual, counting all fruits multiple times was impractical; I therefore chose to measure removal from five arbitrarily sampled branches, each with 10–40 fruits, several times throughout the fruiting period and averaged for each shrub. Fruiting branches were labeled with discreet individually numbered plastic poultry bandettes (National Band and Tag Co., Newport, KY, US) and fruits were counted on each visit. Once fruit removal began, counts occurred approximately once per week and counting was terminated when all fruits were removed from the shrubs or snow prevented access to the field site, at which time potential seed dispersers are in hibernation.

Categorical predictor variables (enclosure treatment) and a continuous univariate response variable (fruit count) in the experiment lent itself to an analysis of variance design. A randomized complete block design was used because it was more biological

meaningful to have all of the treatments in spatial proximity to minimize heterogeneity of disperser communities between treatments rather than using a complete randomized design. The final design included each of the four treatments within five blocks across two years. Because data were heteroscedastic with no mean-variance relationship that would conform to parametric analyses (e.g., general or generalized linear models), a Kruskal-Wallis nonparametric rank test was performed with multiple comparisons to control for the Familywise error rate of making a type I error using the Holm-Bonferroni method.

Seed dispersal

To examine seed dispersal patterns in greenleaf manzanita, a Lagrangian approach was taken (*sensu* Turchin 1998), whereby seeds are tracked from a point source and the direction and magnitude of individual paths can be determined. Thirteen trials of approximately 300 seeds were labeled with radioactive scandium-46 (2009, 2010) and iron-59 (2011) underneath manzanita shrubs in late summer when the fruits begin to ripen, and I monitored displacement from source shrubs. (The nuclide supplier discontinued production of scandium-46 in 2011.) Scandium-46 is a γ -emitting radioisotope with an 84.5-day half life and iron-59 is a γ -emitting radioisotope with a 45-day half life. The seeds were separated from the fruits by removing the thin, coriaceous exocarp and dry, mealy mesocarp and dried for 24 hr at 30°C for better nuclide absorption. The nuclide was mixed with water and the seeds were wetted in the solution for 1 hr until all of the isotope was absorbed, then dried 48 hr until the water evaporated. Seeds were deployed once fruits were mature at the field site and the caches

were monitored for re-removal until snowfall (September–November). Seeds were taken to the field and approximately 300 were placed under source shrubs for animals to discover and remove. After a substantial amount of seeds were removed (generally > 75%) they were relocated with a Geiger counter by walking in concentric circles until a 50-meter radius is reached from the original location of the seeds. When caches were discovered, the distance to the source, depth of the top and bottom of the cache, number of seeds, and microsite conditions (placement relative to woody shrub canopy: interior, edge \pm 10 cm, or open; leaf litter: heavy, medium, light, bare soil) were recorded. Additionally, at several of the seed sources, infrared cameras (HCO ScoutGuard SG550 Camo, 5 megapixel IR game camera) were set at seeds under shrubs to determine which species of animals remove seeds and examine disperser behavior when collecting seeds from a seed source in 2009 and 2010.

To analyze the seed dispersal data, the dispersal probability density function was estimated, known as the dispersal kernel. The use of "dispersal kernel" has historically been conflated in depicting two discrete phenomena: (i) the probability of the end location of a seed relative to the source, known as the "dispersal location kernel" denoted by k_L and (ii) the probability that a dispersal event ends at a distance away from the source, known as "dispersal distance kernel" denoted by k_D (Peart 1985, Cousens et al. 2008, Nathan et al. 2012). k_L takes into account that as a seed moves away from its source, the area of the annuli that it traverses non-linearly increases by a constant (π) and to the second power, whereas k_D is simply the distance moved from the source. A simple example might be 5 seeds that are 1 cm in diameter that disperse 1, 2, 3, 4, and 5 m from a source. The probability that a seed will disperse 1, 2, 3, 4, and 5 m as k_D would all be

0.20. Because the seed has area and traverses two dimensions, however, the probability that a seed will found at radii 1, 2, 3, 4, and 5 m from the source after adjusting for area (k_L) would respectively be 0.44, 0.22, 0.15, 0.11, and 0.09—a stark contrast to k_D . Mathematically, using polar coordinates, assuming radial symmetry for radius r , k_L and k_D relate:

$$k_D(r) = k_{R,\theta}(r, 0) + k_{R,\theta}(r, \pi) = 2k_L(r), \quad (\text{eqn. 1})$$

$$k_D(r) = \int_0^{2\pi} k_{R,\theta}(r, \theta) r d\theta = 2\pi r k_L(r) \quad (\text{eqn. 2})$$

in one- (eqn. 1) and two-dimensional (eqn. 2) space. Because the scope of the study includes the patterns of dispersal of seeds from the parent plant and the patterns of dispersal of seeds by seed-caching animals, both types of kernels are reported.

For the sake of balancing model overfitting (*sensu* Mayer et al. 2010), biological meaningfulness, and inferences about the data (deductive rather than inductive) considering the type of data (recovery of seeds ranged from 75–100%, right truncated), model selection was limited to two exponential functions that have been shown to have biologically meaningful parameters (see Wichmann et al. 2009):

$$k_D(r) = a \exp(-br), \quad (\text{simple exponential; eqn. 3})$$

$$k_D(r) = a \exp(-r^b). \quad (\text{power exponential; eqn. 4})$$

In these models, the area under the function is $\int_0^\infty k_D(r) dr = 1.0$. Eqns. 3 and 4 are both shaped by the first term, a , which describes the proportion of un-cached seeds at radius r (also interpreted as Cartesian distance $d = \sqrt{x^2 + y^2}$ from the x,y -point source 0,0). Within the exponent, for eqn. 3, the caching rate is constant. Within the exponent for eqn. 4, the caching rate can be interpreted as bd^{b-1} . For that term, if $b > 1$, then the

caching rate is increasing as a function of distance; if $b < 1$, then the caching rate is decreasing as a function of distance. Each eqn. was fit to a probability density estimation based on a Gaussian kernel estimate with a bandwidth of 3.44 (Venables and Ripley 2002) over histogram or nearest-neighbor estimation, but they give qualitatively similar results. The two response variables corresponded to (i) the density of caches and (ii) the density of seeds.

Eqns. 3 and 4 were qualitatively compared as they relate to underlying biological processes based on the residual sum of squares of each model using on the nonlinear least-squares method in the R stats package (R Core Team 2013). The particular biologically relevant context lies in optimal cache spacing theory (OCST). OCST posits that scatter-hoarding animals space their caches in a manner that balances the cost of carrying food items to caches and cache-robbery risk (Stapanian and Smith 1978, Clarkson et al. 1986, Dally et al. 2006). Constant (eqn. 3) and non-constant (eqn. 4) caching rates were chosen because OCST can respectively predict that animals cache more heavily weighted by travel cost (constant linear distance from the food source) or food density (non-constant decaying function of distance from the food source).

Seedling emergence

Seed germination in manzanitas is reported to only occur after fire, stimulated by charred wood (otherwise known as 'charate'; e.g., Rogers 1950, Parker 1987, Keeley 1991). Because the first two parts of this study examined proximate patterns of seed dispersal, I then addressed ultimate patterns of dispersal. Specifically, two burned sites were investigated in the springs following fall burns. The first was a natural fire, the

Crystal Fire, in 1995, which burned 2,500 hectares in eastern California, about 30 km NNW of Little Valley. Two 10 × 10-m plots over 500 m apart were established in the interior of the burn and all seedlings were mapped and counted, specifically paying attention to the number of seedlings per germination site (e.g., singletons versus groups of seedlings). The second site was in Little Valley, where management implemented fuel-reducing treatments and mechanically hand-thinned small-to-medium trees, placed them into burn piles, and prescribed fire by the Nevada Division of Forestry (NDF). In November 2010, NDF burned piles, including 18 piles in a manzanita-Ceanothus shrubland. Pile burns are by no means similar to natural fires because of the unnaturally high temperatures and duration that can volatilize essential nutrients and sterilize soils (Korb et al. 2004). Nevertheless, the periphery of the piles do resemble natural-occurring fires based on the number of refractory seedling recruits and resprouting plants that emerge (personal observation). It is from the periphery of the pile burns that data were gathered on the number of seedlings that emerged singly and in groups.

RESULTS

Fruit removal

Fruit removal was found to be different between the four treatments of animal exclosures (Kruskal-Wallis rank sum test, $N = 40$, $\chi^2 = 10.01$, $P = 0.018$). No fruits were removed from experimental exclosures where rodents had no access. Mean ranks (and median removed fruits) per infructescence for each treatment were rodent enclosure = 14.95 (2.5), full enclosure = 14.90 (2.5), rodent access = 23.70 (7.0), and control = 28.45 (8.0) (Figure 1). Pairwise multiple comparisons revealed two statistically significant

differences with confidence intervals that did not overlap zero; these were between the control-rodent exclosure ($P = 0.038$) and the control-full exclosure ($P = 0.038$) treatments. No parametric or nonparametric analyses found block or year effects. Although qualitative differences were observed between years and with a year-treatment interaction in some analyses, because there the study was only over two years there was no power to detect differences. Additionally, between-year effects were not in the purview of the study.

Seed dispersal

Seeds that were radiolabeled and relocated in the field appeared to be removed, cached, and eaten exclusively by rodents. Thirteen trials of approximately 300 radiolabeled seeds each were placed in the field resulted in accounting for 1,856 seeds, 360 of which were not removed. The lack of removal was likely due to the seeds being non-viable, as this was visually determined for 200 of the remaining seeds. For five of the trials I detected larders (many seeds deep in burrow), and excavation was not attempted. Of the approximately 300 seeds set in each trial where a larder was detected, 53, 55, 197, 58, and 248 seeds were recovered, so there were no trails with strictly larder-hoarded seeds. There were 779 seeds in 122 caches that were scatter-hoarded (depth 1.0–40. mm). These seeds were vertically dispersed under 23.0 ± 0.6 mm of soil ($\bar{x} \pm s$; Figure 2, Cache), and there was no relationship found between the distance dispersed and the depth of the cache ($R^2 = -0.01$, $F_{1,87} = 0.11$, $P = 0.729$). Horizontal dispersal was leptokurtic, with most of the seeds dispersed near the seed station. The median dispersal distance was 9.6 m, the mean was 12.7 m, and the maximum measured dispersal distance

by a scatter-caching animal was 38.4 m. The litter conditions at the majority of microsites where seeds were cached were bare soil (85 caches), with 34 caches in light (< 10 mm) litter, 12 caches in medium (10–30 mm) litter, and 9 caches were found in heavy (> 30 mm) litter. With respect to the canopy of woody shrubs, 95 caches were made > 10 cm from the edge of a woody shrub, 28 cm on the edge (\pm 10 cm), and 16 > 10 cm under the woody shrubs. Although not tested, cache sites did not appear different than what was available for the local area.

Motion-sensor cameras revealed that diurnal rodents were the only animals removing radiolabeled seeds from stations. The cameras only detected three species of rodents removing seeds: yellow-pine chipmunk (*Tamias amoenus*), long-eared chipmunk (*T. quadrimaculatus*), and golden-mantled ground squirrel (*Callospermophilus lateralis*). Only one species (*T. amoenus*) exclusively visited a seed station, which happened in two of the 13 trials, where cache characteristics were similar to those previously reported for this species (e.g., Vander Wall 1993a, 1993b), and appeared to be responsible for most of the observed caching (e.g., Figure 2, cache). Of the 31 caches known to be exclusively made by yellow-pine chipmunks, however, 11 relocations of groups of seeds were on the surface and not cached under soil. When comparing the last footage of a day against the first footage the following morning, all seeds appeared to remain for all trials, suggesting that the known common nocturnal granivore in the area, deer mice (*Peromyscus maniculatus*), was likely not involved in seed removal. Although, in 2011, deer mice appeared to remove some radiolabeled manzanita seeds that were placed in one of ten carnivore scats and the seeds were never relocated.

Fitting dispersal kernels was not different when modeling cache or seed distributions, but the type of kernel (k_D or k_L) mattered. Both distance, k_D , and location kernels, k_L , were generated for (i) caches made by animals and (ii) the number of seeds present, for given radii, r , from the seed source. The two *a priori* models used to fit the kernels based on animal behavior showed similar fits using number of caches or number of seeds as response variables (Table 1; Figures 3 and 4). Between the two models (eqns. 3 and 4), for both caches and seeds as response variables, the residual sum of squares of the simple exponential (eqn. 3) was lower for the dispersal distance kernel (k_D) and higher for the dispersal location kernel (k_L). The b parameter in the power exponential function was < 1.0 in all cases, which corresponds to a caching rate that decreases as a function of distance. The caching rate and of the number of seeds being dispersed decreased with distance from the kernel modeling, and corroborated a weak, statistically significant positive relationship found between the number of seeds per cache and dispersal distance ($R^2 = 0.038$, $F_{1,87} = 4.45$, $P = 0.038$; Figure 5).

Seedling emergence

Most seedlings appeared to have germinated from rodent caches. The number of seedlings that emerge after an artificial burn and two sites in the same natural fire, 87% of the seedlings germinated in pairs or clumps greater than two ($N = 2,828$ seedlings). Manzanita nutlets can often be fused and rodents generally cache seeds in clumps larger than two, so looking at the ratio of clumps to singletons may overestimate the number of seeds that germinated following scatter-caching rodent deposition. To use the mode number of nutlets per fruit (5) as more indicative of clumps formed by abiotic burial, the

number of seedlings that putatively emerged from caches was 60%, or 1,693 from 97 germination sites compared to 1,135 from 848 germination sites by abiotic burial.

Graphical examination of the distribution of the three log-log plots shows what appears to be a break in the number of seedlings around 10 at the three sites (Figure 6) that also approximates the average seeds per cache found in this study ($\bar{x} = 11.13, s = 5.7$). Using 10 as a break point, the number of seedlings that putatively emerged from caches was 53%, or 1,497 from 70 germination sites compared to 1,295 from 861 germination sites.

For 30 seedlings across the fires, the depth of germination was estimated by excavating the area around the seedling to locate the seed coat that fractures in the soil at the depth from which it germinates. The mean minimum germination depth was 24.1 ± 5.9 mm ($\bar{x} \pm s$; Figure 2, Germination). This is not statistically different than the depths of caches ($\bar{x} = 23.0$ mm, $s = 0.6$ mm) that were measured by following radiolabeled seeds (Mann-Whitney $U = 396, P = 0.348$).

DISCUSSION

The aim of the study was to determine how greenleaf manzanita (*Arctostaphylos patula*) seeds are dispersed, testing the four hypotheses of seed dispersal by three guilds of animals (birds, scatter-hoarding rodents, or omnivorous carnivores) or abiotic burial. Our main findings show strong support for scatter-hoarding rodents as the primary disperser of greenleaf manzanita because full-shrub exclosures that allowed rodents access had the most fruits removed, recovered radiolabeled seeds were found in caches, motion-sensor cameras only captured rodents removing seeds from seed stations, and the depth of seedling emergence was not statistically different than the depth in which

rodents cache seeds. From this study, frugivorous carnivores or birds do not appear to consume or disperse fruit or seeds. Abiotic burial was not completely ruled out as a means of recruitment for greenleaf manzanita, although it seems unlikely to account for patterns of seedlings establishment observed and is elaborated upon below.

Schupp (1993, and Schupp et al. 2010) devised the concept of seed dispersal effectiveness (SDE) as the most pertinent framework in which to put seed dispersal studies that examine multiple modes of dispersal to estimate individual dispersers' contributions to plant fitness. Components of SDE require the investigation of both the quantity and quality of seed dispersal that respectively reflect the number of seeds dispersed and the probability that a dispersed seed produces a new adult. In greenleaf manzanita, the quantitative component of SDE was overwhelmingly rodents. Compared to the controls, in the two treatments where rodents had access, 68.7% of fruits were removed, compared to 12.5% where rodents did not have access to the shrubs. This means that rodents removed 5.5 times the number of fruits compared to other animals. We know from observations and previous studies that omnivorous carnivores are responsible for consuming fruits and dispersing some manzanita seeds (e.g., Bowyer et al. 1983, Delibes et al. 1989, Wilson and Thomas 1999, Nielsen et al. 2004, Silverstein 2005), however, there was no evidence found for this mode of dispersal in the exclosure experiment. Similarly, there was a lack of fruit removal where frugivorous birds were allowed access to shrubs where rodents were excluded. The lack of removal coupled with a lab study where American Robins would not eat greenleaf manzanita fruits (unpublished data) suggest that frugivorous birds do not disperse their seeds.

Within the SDE framework, the quality of seed dispersal among rodents and between rodents and other dispersers must also be considered. First, among rodent species present in this study, SDE was not directly tested but it ostensibly varied. In camera traps where yellow-pine chipmunks were the sole seed removers, most manzanita seeds were scatter-hoarded. Throughout the duration of the study, we observed yellow-pine chipmunks foraging in the canopy of manzanita shrubs, removing seeds from the fruit pulp, filling their cheekpouches, and making seed caches. When the camera traps detected seed removal by > 1 rodent species, some seeds were scatter-hoarded and others were larder-hoarded. None of the camera traps detected deer mice removing seeds, nor did it appear that the number of seeds at seed stations changed overnight, when deer mice are actively foraging. Yellow-pine chipmunks are likely responsible for scatter-hoarding seeds within this rodent assemblage, as this has been studied in other plants at this field site using indirect (determining relative abundance through trapping) and direct (enclosure trials) methods (e.g., Vander Wall et al. 1994, Roth and Vander Wall 2005, Briggs et al. 2009, Barga and Vander Wall 2013). If seeds are larder-hoarded, then there is a low probability that a seed will germinate based on (i) the inability of the leached charate stimulus to reach the seed and break dormancy and (ii) the physical inability the shoot to reach the surface for photosynthesis. At one seed station, the camera only detected long-eared chipmunks and golden-mantled ground squirrels removing seeds, and all of the seeds were stored in deep (> 50 mm) caches with many more seeds per cache (>75). The caches made by these two rodents likely have a lower probability of germination based on our emergence finding of seedlings germinate after fire, which were not statistically different than where scatter-caches were found (Figure 2). Second,

the other potential group of dispersers is the omnivorous carnivores, and the quality of their dispersal is difficult to ascertain. Previous studies have shown that the quality of gut passage does not significantly increase or decrease germination rates of manzanita (Kauffman and Martin 1991, Silverstein 2005), and the quality of seed deposition is questionable. Unfortunately, attempts to germinate manzanita seeds in field experiments that examined burial depth as a treatment that would have differentiated the probability of germination on the surface (omnivorous carnivore deposition) and below ground (rodent deposition) were unsuccessful, as manzanitas are notoriously difficult to germinate in the field or greenhouse (e.g., Carlson and Sharp 1975). Although, Keeley (1991) documented germination of another species of manzanita, *A. glandulosa*, that showed that charate and dark over light conditions enhanced germination, which further suggests that the quality of dispersal provided by the omnivorous carnivores is relatively poor if seeds are exposed to light. Although not fully in the purview of this study, diplochory (*sensu* Vander Wall and Longland 2004) could possibly occur in manzanita dispersal, which could warrant omnivorous carnivores as an effective component of long-distance dispersal followed by rodent scatter-hoarding of seeds removed from feces. In a recent study, Enders and Vander Wall (2012) demonstrated that rodents could be effective dispersers of two species' (*Cornus stolonifera*, *Prunus virginiana*) seeds that rodents removed from bear scat by radiolabeling seeds and following their fate and by conducting a germination experiment. The germination experiment showed that seeds treated through the guts of American robins or black bears had a significantly lower proportion of seeds germinate compared to seeds that were cached by rodents. This could be occurring in greenleaf and other manzanitas, but the lack of any seed removal from bear

and coyote scats in a pilot study of 10 feces with manzanita seeds in addition to the lack of dispersal documented by the primary rodent in that study (*Peromyscs maniculatus*) suggests that it may not be very often if it occurs.

Greenleaf manzanita has a relatively large geographic range, from the Sierra San Pedro Martir in Baja California at the southern end, north to the central Cascades in southern Washington State; and from the California and Oregon coast-ranges at the western end, east to the southwestern Rocky mountains. With such a broad geographic range, greenleaf manzanita often occurs with communities of rodents composed of different species (Reid 2006, International Union for the Conservation of Nature 2012) in different areas. To evaluate scatter-hoarding rodents as effective dispersers of greenleaf manzanita across its range, examining both (i) the plant community composition and (ii) the prevalence of scatter-hoarding rodents can be informative. First, to examine the plant community composition across greenleaf manzanita's geographic range, patterns of plants that have seed dispersal mutualisms across North America were analyzed in Chapter 3 of this dissertation. Within the geographic range of greenleaf manzanita our sample included 40 communities, which had a mean of 3.2%, or 16 seed plants (quartile, $Q_1 = 10.0$, $Q_3 = 21.3$) that were dispersed by scatter-hoarding animals. This minimally demonstrates that other species of plants that have a scatter-hoarding dispersal syndrome are present in the same communities where greenleaf manzanita is found. Second, scatter-hoarding rodents are abundant across greenleaf manzanita's range. Arid western North America contains abundant and diverse rodent communities that scatter-hoard seeds. Storing food (including scatter-hoarding) confers advantages to individuals to

provision energy in these environmentally heterogeneous areas, in addition as a possible mechanism of coexistence within each community.

One aim of the study was to take a plant species with an ambiguous seed dispersal syndrome that had been misattributed to frugivorous birds and mammals and study it to further our understanding of how plants are dispersed, thereby more clearly delimiting dispersal syndromes. This is, by no means, trivial, as any examination of the seed dispersal literature will reveal that further studies are needed to delimit dispersal syndromes. The main suite of informative studies on correlates of seed mass and dispersal at a global scale (Moles et al. 2005a, 2005b, 2007), for instance, label 61% of the plant species in their dataset as having an "unknown" dispersal syndrome (specifically, Moles et al. 2007, Figure 3(c)), which doesn't include "unassisted" dispersal syndromes. (Lack of close examination often leads to researchers passively claiming that a plant is "unassisted" in its dispersal, meaning that any reasonable level of gene flow and migration would happen over improbable time scales.) Another study collected information on dispersal syndromes for the Greater Sydney region, Australia, and 63% of the plants had no identified dispersal syndrome (Thomson et al. 2010). If ecologists aim to accurately predict population dynamics, the effects of disperser abundance on population dynamics, range dynamics in the face of climate change, or genetic connectivity between populations, then a thorough understanding of dispersal modes is needed. This study took a previously "unknown" mode of dispersal and extended the breadth of what we understood to be rodent dispersed. Only one other study has added this much to our understanding of rodent-dispersed seeds, in Longland et al. (2001). In this study, they demonstrated that dispersal by seed-caching rodents confers a fitness

advantage to a grass, which has a seed that had a much smaller energetic reward than what was normally thought necessary of for rodent-dispersed seeds (e.g., oaks, hickories, walnuts).

The use of Wichmann et al.'s (2009) approach to fit the dispersal data with a semi-mechanistic model with biological interpretable parameters is an improvement in the utilization of dispersal kernels, whereas curve fitting can sometimes misattribute or lose sight of the underlying biological mechanisms (see McGill 2003, Frank 2009). In Wichmann et al.'s (2009) approach, they examined shoe-mediated seed dispersal, and the b parameter was the dropping rate of seeds from shoes. In this study, it was analogized that the dropping rate of seeds was equivalent to the caching rate of an animal. An examination of models overlying the data (Figures 3 and 4, especially the bottom row) demonstrates the trade-off in fit. This trade-off is in the heads ($r \rightarrow 0$) and tails ($r \rightarrow \infty$) of the curves, in that the power exponential deviates from the observed data as $r \rightarrow 0$, and, because $b < 1.0$, the tail is deviating from the observed data by decreasing at an decreasing rate as $r \rightarrow \infty$ (i.e., it has a fatter tail).

This study also considered models in an optimal cache spacing theoretic context, which could potentially provide a useful way of analyzing dispersal data in the future by incorporating animal behavior into dispersal studies (*sensu* Cousens et al. 2010). Because the simple exponential model fit the observed data better for the dispersal distance kernel k_D , it can be concluded that caching rate decreases as a constant function of distance from the source. Because space does not shrink nor do animals grow as a function of distance from the source, however, it is more appropriate to adjust for distance in the dispersal kernels and use the dispersal location kernel, k_L . In this case, the

caching rate was decreasing at a decreasing rate. If the caching rate decreased constantly, then that would suggest animals were caching as a constant function of distance. Because the caching rate was decreasing at an increasing rate, it suggests that animals that had traveled farther from the source were caching less. Possible mechanisms to explain this result could be (i) that it is more energetically costly to travel with the food reward a farther distance or (ii) that the probability of recovery of a cache is higher at farther distances if pilferage is positively related to cache density; hence the more time-consuming, secretive behavior (Clarkson et al. 1986).

Which of the two models best fit the data was dependent on the type of dispersal kernel generated, either k_D or k_L . This study finds that the implications of using one or the other needs to be explicitly stated in future studies, and it echoes the call of other dispersal biologists (Nathan and Muller-Landau 2000, Cousens et al. 2008, Nathan et al. 2012). Here, it is demonstrated that the ultimate biological interpretation of the data can vary. Even though most dispersal data are collected and interpreted as k_D , it may not be the most appropriate for the questions and analyses of the researchers. For instance, given the tumult on climate change and range expansions (Corlett and Westcott 2013, Travis et al. 2013), being transparent and using the most appropriate kernel is tantamount to making accurate predictions, whether for a seed or any other organism. Similar to other interpretations of dispersal kernels (e.g., Nathan and Muller-Landau 2000, Higgins et al. 2003), I posit that k_D should be used if a researcher wants to know the distance that a dispersing unit will travel (i.e., spatially implicit), and that k_L should be used for all spatially explicit estimates of dispersal because k_L is area-adjusted (e.g., range expansions, species distribution modeling).

This study is limited primarily because seed germination and seedling survival were not experimentally shown to be greater for seeds that have been cached by rodents compared to other potential seed fates; namely, abiotic burial. At most, there is indirect evidence that rodents disperse seeds to microsites that would be suitable for germination that would allow the seeds to both experience the charate germination stimulant and avoid the lethal temperatures of a fire event. To fully follow the seed fate pathway and demonstrate this would be the best, direct evidence for rodents as effective seed dispersers. Another limitation of the study is that the abiotic burial of seeds was not completely discounted. The main problem with setting out seeds that animals are attracted to is that they remove the seeds, so the animals would need to be excluded. To exclude animals, a structure would need to be erected that would alter the abiotic conditions that the seeds would otherwise experience (e.g., wind, precipitation, or temperature affecting cryoturbation). We attempted to assess abiotic burial without excluding animals, but too few seeds were moved vertically into the soil before they were removed by animals to determine abiotic burial rates of viable seeds with any confidence.

One potential line of future investigation could include the role of scatter-hoarders or other "burial syndromes" (*sensu* Humphreys et al. 2011) in fire-prone ecosystems. Most investigations thus far have looked within grasses with hygroscopic awns (Pearl 1984, Garnier and Dajoz 2001, but see Chambers et al. 1991), the relative abundance of which varies considerably. Nevertheless, a mechanistic understanding of recruitment is imperative for understanding population and community dynamics in these ecosystems. Another area that warrants further investigation is the melding of animal behavior with dispersal biology. Cousens et al. (2010) call for the integration of these two fields, but

with respect to a better understanding of animals that disperse seeds through ingestion (endozoochory) and attachment (ectozoochory). There is already a rich literature on hoarding of food by animals (Stapanian and Smith 1978, Clarkson et al. 1986, Vander Wall 1990, Sunyer et al. 2013) and seed dispersal biology (Levin et al. 2003, Cousens et al. 2008, Clobert et al. 2012), and bringing these two fields together could indeed be very fruitful. Levin et al. (2003) and others argue that phenomenological models of seed dispersal need to converge with mechanistic models to be able to make sound predictions and that, aside from passive fluid-based dispersal, the animal models are considerably underdeveloped. Given that about 16% of seed plants in temperate North American (Chapter 3 of this dissertation) are dispersed by animals and 70–90% of woody tropical plants are dispersed by frugivores (see Jordano 2000), if we want a comprehensive understanding of seed dispersal, then the time is ripe to integrate the fields of seed dispersal biology and animal behavior.

The seed dispersal process is complex and stochastic. In this study, we take steps to understand and highlight the necessity to further study seed dispersal in fire-prone areas, seed dispersal syndromes, and the integration of seed dispersal biology and animal behavior. It is concluded that scatter-hoarding rodents are dispersers of manzanita, an ecologically dominant species in the fire-prone California Floristic Province. Given that seeds in fire-prone ecosystems often need to escape lethal temperatures to survive, it is suggested that burial processes should be further investigated, especially in the light of dynamically changing fire regimes across the world.

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Chapter 1, Table 1. Parameter values from dispersal estimation functions for caches or seeds as the response variable. Each had a dispersal distance and location kernel generated and were fit to two exponential models with biological meaningful parameters. Parameters a and b are nonlinear least-squares estimates, with the residual sum of squares bolded for the best fit model for each response variable \times kernel type. The simple exponential model fit better for the dispersal distance kernel and the power exponential model fit better for the dispersal location kernel for both response variables.

Data	Kernel type	Model	<i>a</i>	<i>b</i>	Residual sum of squares
Caches	Distance kernel (k_D)	eqn. 3 Simple exponential	0.0060	0.0579	0.000226
		eqn. 4 Power exponential	0.0047	0.3042	0.000999
	Location kernel (k_L)	eqn. 3 Simple exponential	0.1394	3.1877	0.004015
		eqn. 4 Power exponential	0.0145	0.8951	0.000234
	Seeds	Distance kernel (k_D)	0.0047	0.0410	0.000212
		eqn. 4 Power exponential	0.0039	0.2441	0.000694
Seeds	Location kernel (k_L)	eqn. 3 Simple exponential	0.1280	3.1424	0.003565
		eqn. 4 Power exponential	0.0139	0.8800	0.000174

Chapter 1, Figure 1. The number of fruits removed from greenleaf manzanita (*Arctostaphylos patula*) infructescences across different treatments of entire-shrub exclosures. Treatments that allowed rodents (clear) and excluded rodents (shaded) had similar central tendencies, but nonparametric post-hoc pairwise multiple comparisons concluded that the only two statistically different treatments were the control when compared to the rodent and full exclosures (horizontal bars). Each treatment was replicated 10 times.

Chapter 1, Figure 2. A comparison of the minimum depth at which greenleaf manzanita (*Arctostaphylos patula*) seeds germinate in a natural fire (left) and the depth at which they are cached by scatter-hoarding rodents (right). The mean depth of germinated seeds and cached-seed depth are statistically not different.

Chapter 1, Figure 3. Fit dispersal kernel functions of caches for the dispersal distance kernels (left column), and dispersal location kernel (right column) for true values (top) and log-log axes (bottom) to visualize differences found between the two models. Plotted is the observed dispersal kernel with a bandwidth of 3.44 (dotted line), simple exponential function (solid line), and power exponential function (dashed line). The simple exponential model fit better for the dispersal distance kernel and the power exponential model fit better for the dispersal location kernel for both response variables. The ticks inside of the plot on the x axis corresponds to the raw data.

Chapter 1, Figure 4. Fit dispersal kernel functions of seeds for the dispersal distance kernels (left column), and dispersal location kernel (right column) for true values (top) and log-log axes (bottom) to visualize differences found between the two models. Plotted is the observed dispersal kernel with a bandwidth of 3.44 (dotted line), simple

exponential function (solid line), and power exponential function (dashed line). The simple exponential model fit better for the dispersal distance kernel and the power exponential model fit better for the dispersal location kernel for both response variables.

The ticks inside of the plot on the x axis corresponds to the raw data.

Chapter 1, Figure 5. The distance that a scatter-caching animal traveled (m) as a function of the number of seeds it is carrying. There is a weak statistically significant relationship, which suggests that the cumulative quality of the foraging bout and the associated traveling cost bout may determine the caching placement with respect to the distance from the seed source.

Chapter 1, Figure 6. The distribution of post-fire seedling clumps of greenleaf manzanita (*Arctostaphylos patula*) at one artificial burn (Brushfire) and two plots in a natural fire (Crystal Fire). The x -axis corresponds to the ranked seedling clump and the y -axis corresponds to the number of seedlings in each clump. The log-log relationship is linear with roughly the same slope on the right side of the graphs and there appears to be a break around 10 clumps. This break was used to delimit abiotically buried and cached seeds.

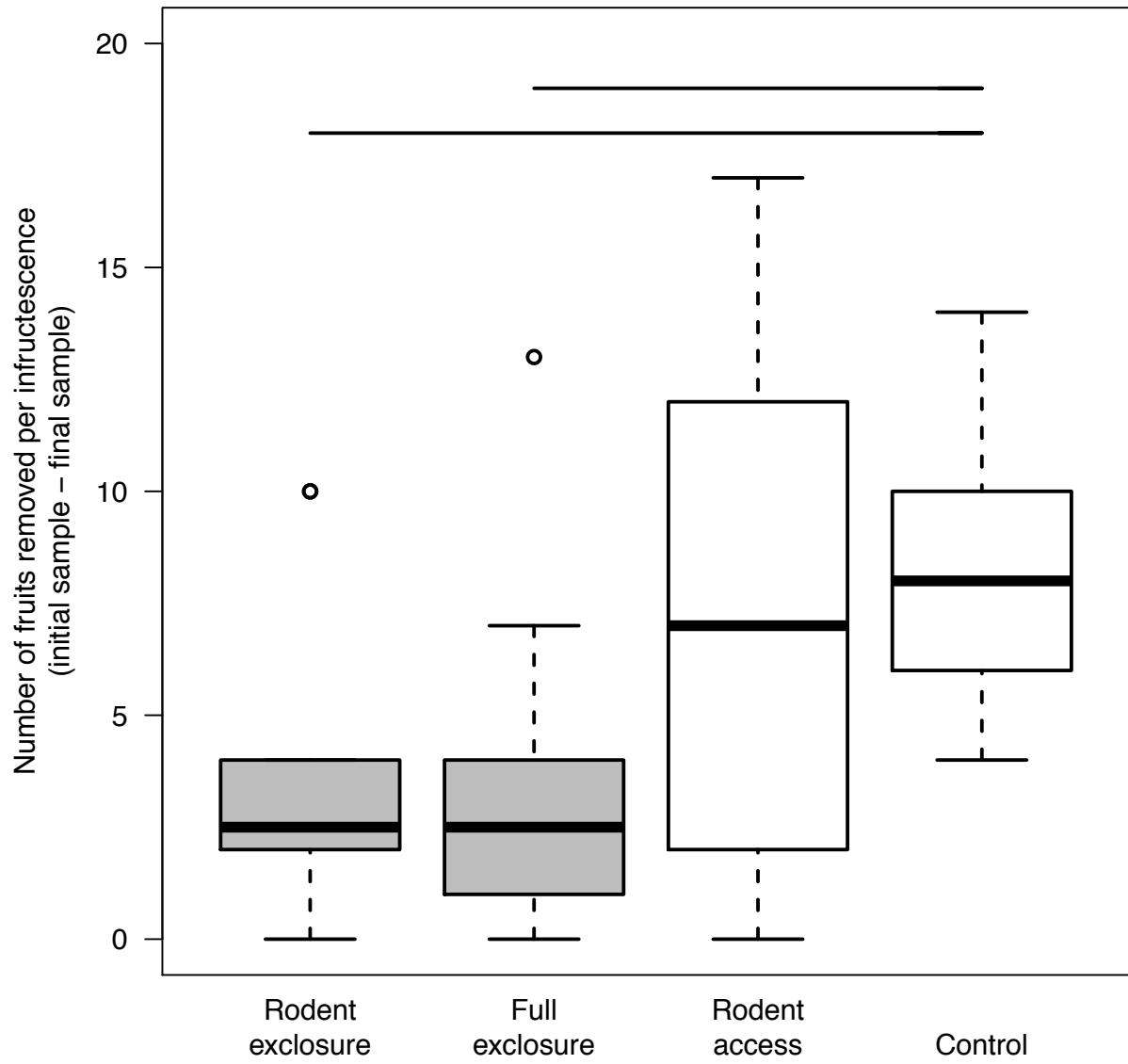


Figure 1.

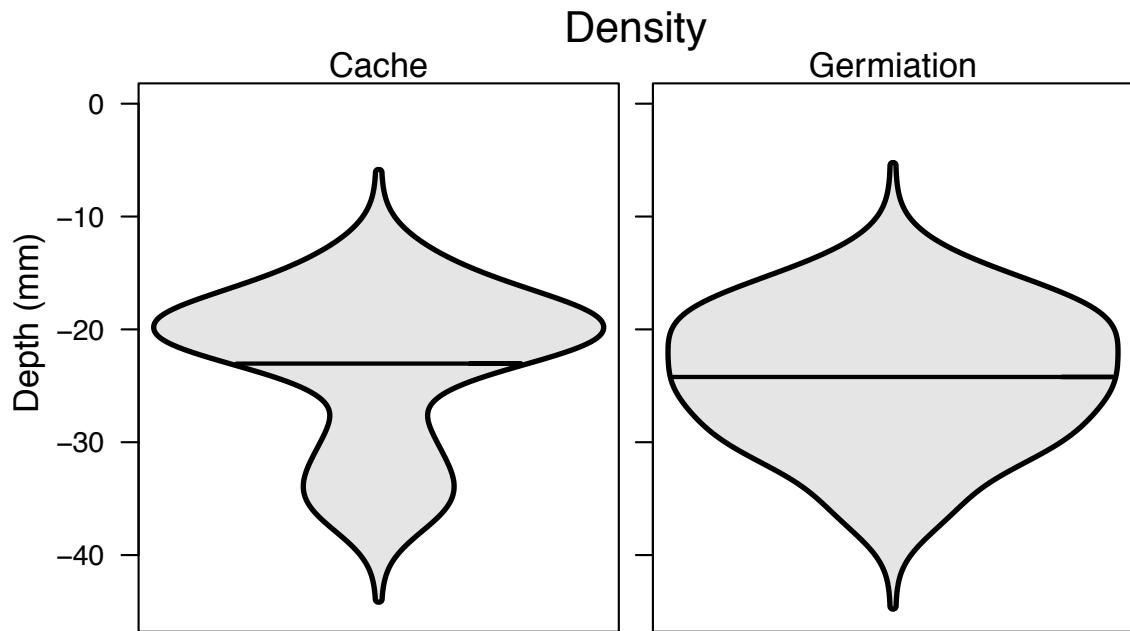


Figure 2.

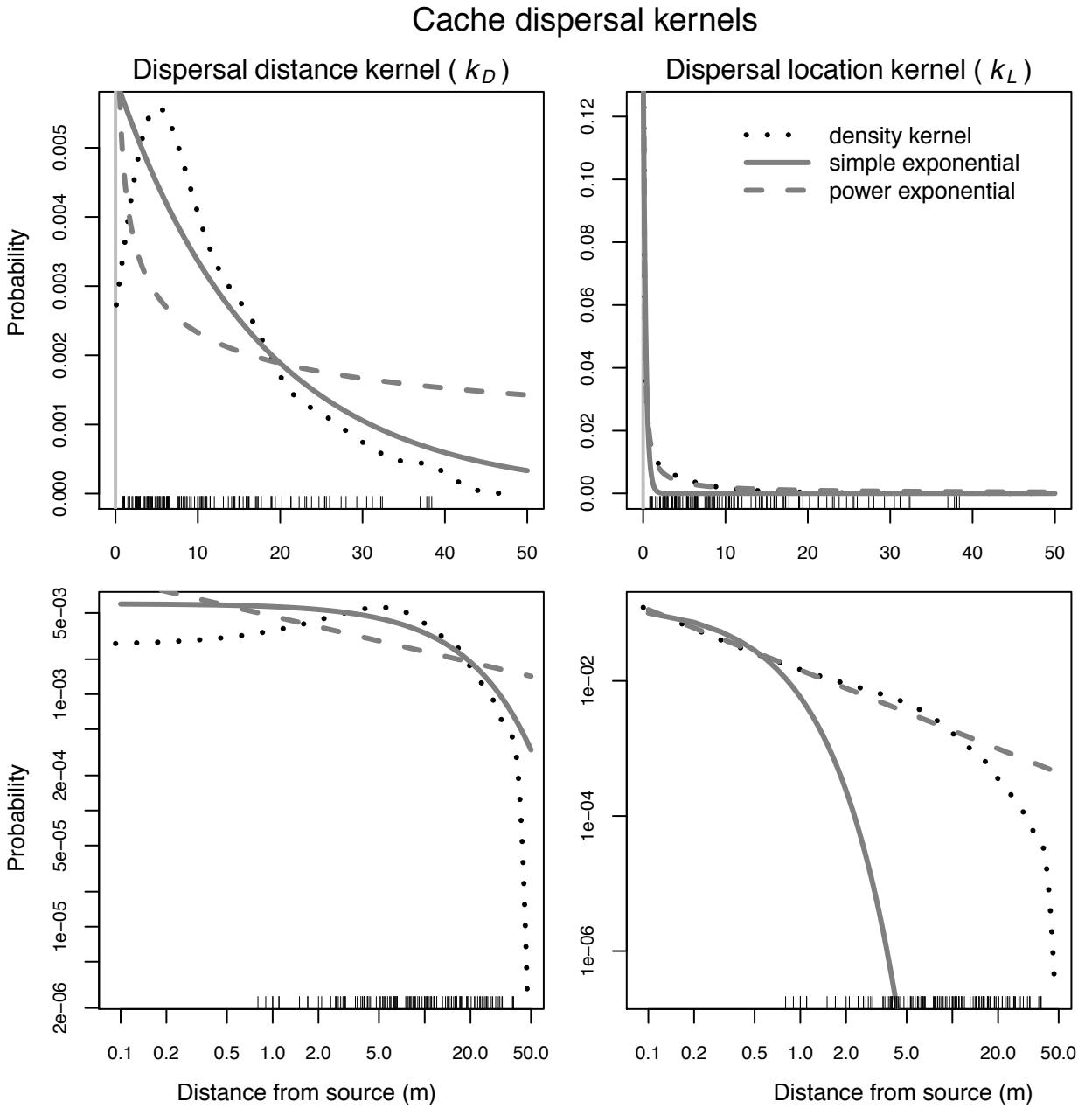


Figure 3.

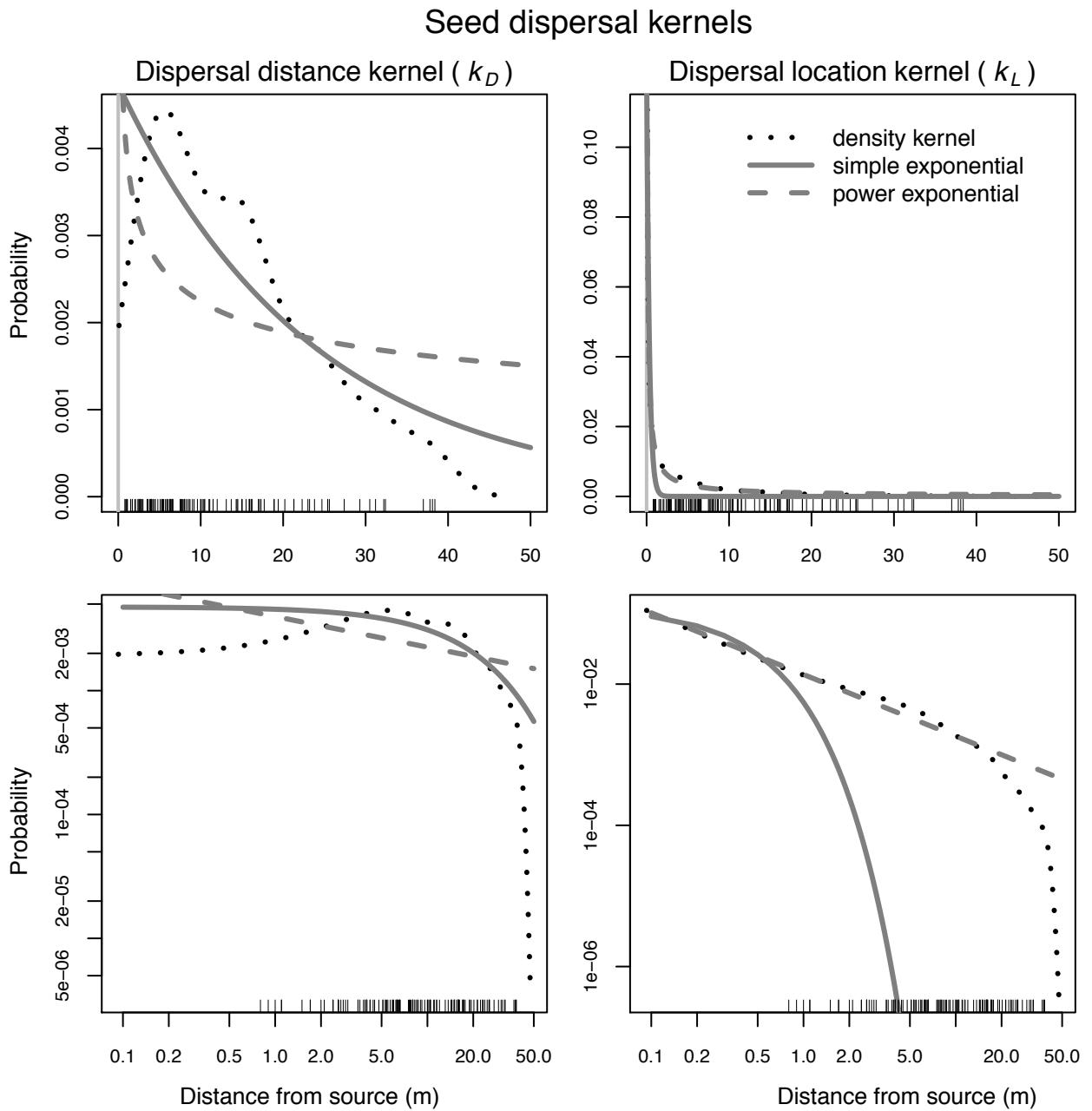


Figure 4.

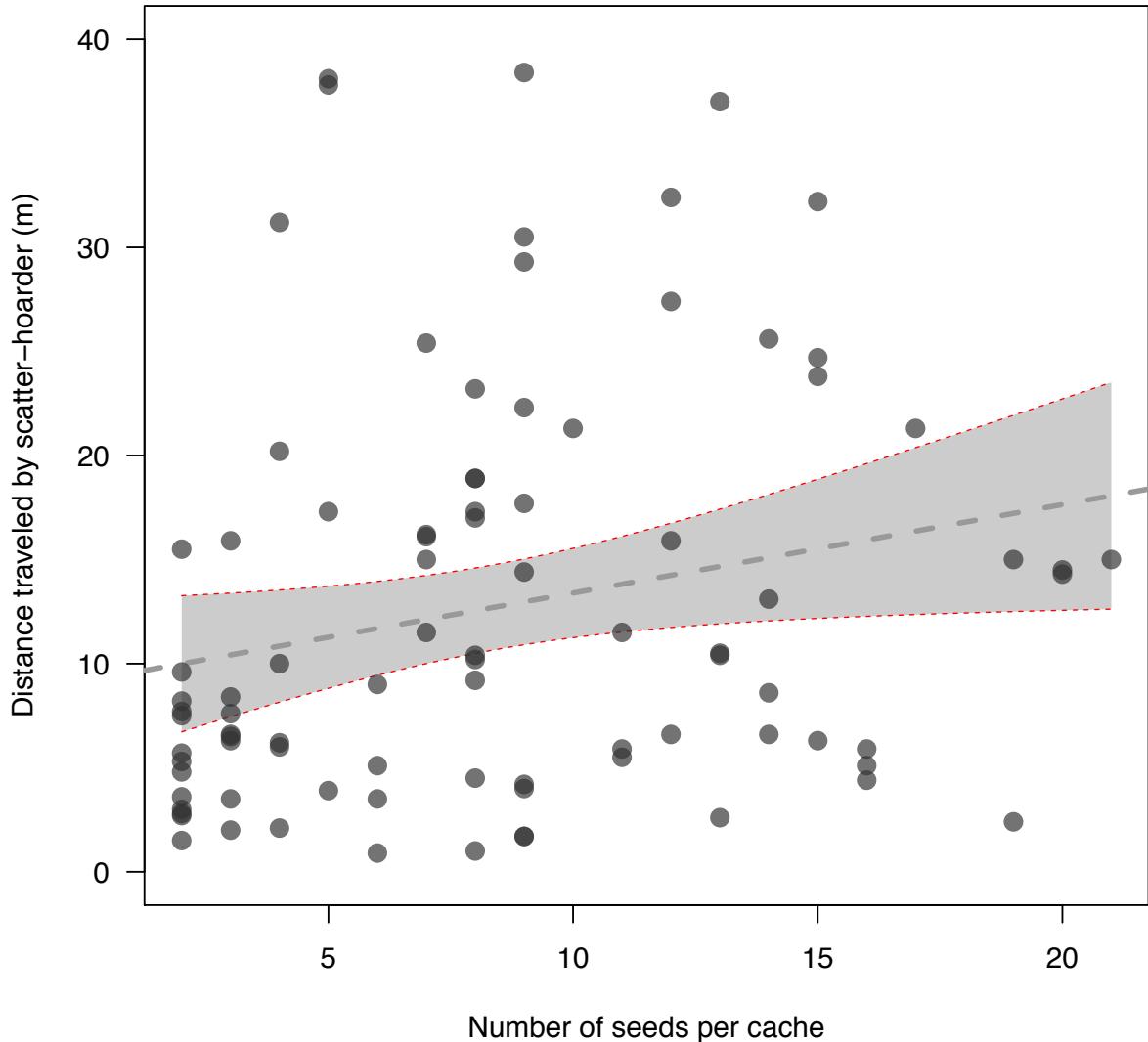


Figure 5.

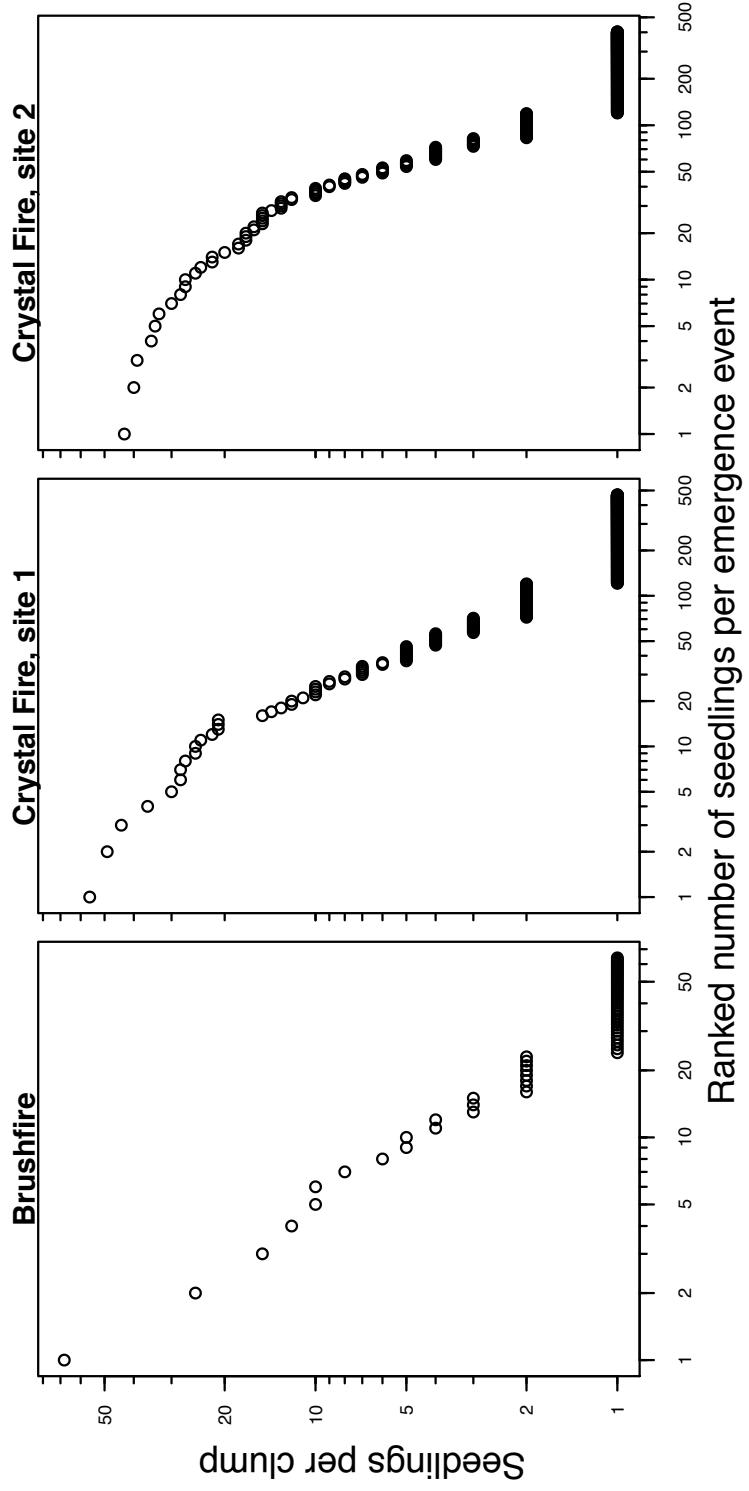


Figure 6.

Chapter 2: Seed dispersal syndromes in manzanitas

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Abstract. The ability for plants to disperse is a key factor in plant ecology and evolution. Many plants have coevolved with animals through mutualistic interactions where animals provide a dispersal service at the expense of plants providing animals with a nutrient reward. Different guilds of animals treat the dispersing unit including the plant embryo, the diaspore, differently, and therefore have different consequences for the ecology and evolution of plants. The goal of the study was to delimit seed dispersal syndromes in an ecologically and taxonomically diverse group of plants, manzanitas (*Arctostaphylos* sp.) to determine how they are dispersed and what factors could contribute to diaspore morphology within this group. To do this, I conducted a morphometric analysis, investigated diaspore traits in relation to other life-history traits and along environmental gradients, and compared these results to a sympatric, ecological analog, *Ceanothus*. I found great variation in diaspore traits in manzanita, many species of which were nut-like in morphology. However, the majority of these traits did not correlate with other life-history traits or environmental gradients that have been shown to strongly affect diaspore morphology, but I found expected patterns in *Ceanothus*. I conclude that a scatter-cached nut syndrome is present in most manzanitas and that detailed studies should be conducted

on the species that morphologically deviate from a nut syndrome to more clarify exactly how they are dispersed .

Keywords: Arctostaphylos; Ceanothus; frugivory; life history; manzanita; mutualism; scatter-hoarding; seed dispersal; seed dispersal syndrome

INTRODUCTION

Dispersal is a process whereby biological agents, with the ability to establish, move to escape parent-offspring conflict and exploit unused resources most commonly in space (Howe and Smallwood 1982), but also in time (i.e., bet hedging; Cohen 1966, 1967, Venable and Brown 1988). In seed producing plants, this can occur at the gametic phase where paternal gametes move (e.g., flagellated pollen in Ginkophyta) or are moved by biotic (e.g., insects) or abiotic vectors (e.g., wind). Similarly, the movement of seeds can be achieved by biotic or abiotic means. The two main differences are that seeds inherit the biparental product of the pollen and ovules and disperse the embryo, and seeds have the potential to recruit and establish (Ennos 1994).

The processes of both gametic and embryonic dispersal can have significant genetic (Ennos 1994, Bacles et al. 2006, Grivet et al. 2009), ecological (Clark et al. 1998, Harms et al. 2000), and evolutionary consequences (Wright 1969, Richardson et al. 2014). Specifically considering seed dispersal, many researchers (Tiffney and Mazer 1995, Tiffney 2004, Lorts et al. 2008; but see Herrera 1989a and Eriksson et al. 2000) have attributed the early Tertiary radiation of angiosperms (Magnoliophyta) to coevolved animal-mediated dispersal (i.e., zochory). Ecologically, seed dispersal is effectively the

sole means by which seed plants can move from the natal habitat. Meaning, subsequent ecological interactions (e.g., competition, facilitation) and gametic gene flow are dependent upon where the seed settles. It is important to understand, however, that not all biotic vectors provide the same quality of dispersal service (Schupp 1993, Wenny and Levey 1998, Hollander and Vander Wall 2004, Schupp et al. 2010, Fedriani et al. 2010, García and Martínez 2012). As an example of biotic vectors dispersing seeds and providing different quality of dispersal distance, Jordano et al. (2007), in a study on *Prunus mahaleb* (Rosaceae), genotyped parents and seed coats of trapped seeds and found that small birds dispersed seeds short distances (50% < 51 m) and medium-sized birds (50% > 100 m) and mammals (50% > 495 m) moved seeds far distances. As an example of biotic vectors dispersing seeds providing different effectiveness, both combining the quantity and quality of dispersal, Calviño-Cancela and Martín-Herrero (2009) were able to combine simulation models with field-collected data to demonstrate that animals vary in the quality of their dispersal in a habitat-specific manner. As a consequence of differential seed dispersal effectiveness among guilds of animal dispersers, plants have evolved different means of attracting different types of animal disperses, known specifically as seed dispersal syndromes (van der Pijl 1969, Lomáscolo et al. 2008, Lomáscolo et al. 2010).

Seed dispersal syndromes are suites of correlated plant traits matched to the behavior, physiology, and morphology of different types of dispersers (van der Pijl 1969). Seed dispersal syndromes include all of the correlated plant traits, while diaspores are the actual units of dispersal. Diaspores are a part of the dispersal syndrome, and traits associated with syndromes and not the diaspore largely concern the presentation of the

diaspore (e.g., contrast color of the foliage, phenology, dehiscence). In this study, three types of vertebrate seed dispersal syndromes are considered: (i) frugivorous bird (hereafter, bird-dispersed), (ii) omnivorous medium-to-large-mammalian frugivore in the family Carnivora (hereafter, carnivores or carnivore-dispersed), and (iii) scatter-hoarding animal (hereafter, rodent-dispersed). Bird-dispersed diaspores are usually small drupes or berries with conspicuous, bright coloration with thin flesh that stay attached to the adult at maturity (Wheelwright 1985, Herrera 1989b, 2002). Carnivore-dispersed diaspores are often large, dull-colored, odorous, and have a tougher husk or rind. Herrera (1989b) showed that all bird-dispersed diaspores were eaten by carnivorous mammals, but the reverse was not true in a Mediterranean-type habitat. Rodent-dispersed diaspores are often large, drupaceous, nut-like, and dull in color (Vander Wall 2001). Lastly, these syndromes are not always easily delimited, as multiple-phased seed dispersal (i.e., diplochory; Vander Wall and Longland 2004, 2005) has been shown to occur in many plant species (Vander Wall et al. 2005, Enders and Vander Wall 2012). With different types of animals acting as different selective forces on diaspore morphology, diaspores with multiple dispersal phases can appear as an amalgam of syndromes.

Bird- and carnivore-dispersed diaspores are a form of endozoochory (ingested and most often defecated, but sometimes regurgitated), whereas rodent-dispersed diaspores are a form of dyszoochory (external form of energy storage where animals hoard food for later consumption). Simply deducing from the respective behaviors of each guild of dispersers, it is evident that the treatment of seeds by animals within each syndrome varies considerably (Vander Wall and Beck 2012). Birds are volant and can traverse large areas with ease, and therefore can potentially disperse seeds great distances. Birds

also have a short gut-retention time and sometimes roost, however, which respectively would lead to short dispersal distances and place seeds in high concentrations.

Carnivores can potentially disperse seeds long distances because they have large home ranges, some migrate, and they have a relatively long gut-retention time compared to frugivorous birds. The densities of conspecific seeds in carnivoran feces are often high and often contain seeds of heterospecifics, thereby eliminating the benefit of escaping negative density dependent benefits of dispersal and potentially increasing seedling-seedling competition. The density of seeds in carnivore feces may subject seeds and seedlings to high densities that, despite if seeds are dispersed to favorable microsites, could possibly reduce survival (Spiegel and Nathan 2010). Lastly, rodents that scatter-hoard often deliver seeds to suitable habitats in low concentrations, but it is often at the cost of high seed mortality and usually only short distances. Table 1 qualitatively compares these three dispersal modalities.

The California Floristic Province (CFP) is a floristic biodiversity hotspot (Mittermeier et al. 2000). Within the woody genera in the CFP, manzanita, *Arctostaphylos* sp. (Adans., Ericaceae), is the most taxonomically diverse, with estimates between 62–108+ species. The next most diverse are respectively *Ceanothus* sp. L. (Rhamnaceae) with approximately 75 species and oaks (*Quercus* sp. L., Fagaceae) with approximately 20 species. Within the high taxonomic diversity in *Arctostaphylos* there is high diversity in life-history traits, including high morphological variation in diaspores (i.e., fruits and seeds), suggesting that multiple seed dispersal syndromes may exist.

Figure 1, for example, shows the difference in sizes of the three species' seeds, which span three orders of magnitude in volume. Marked differences can additionally be found

in other morphological traits (e.g., color, nutlet fusion, seed weight). Lastly, *Arctostaphylos* display great diversity in ecological habits and understanding how they disperse may contribute to understanding their recent evolutionary radiation.

The main goal of the study is to delimit seed dispersal syndromes in *Arctostaphylos*. To achieve this end, I used diaspore morphology as a proximate indicator of dispersal syndromes and assessed: (i) morphological variation between species, (ii) how morphological variation between species covaries with life-history traits, (iii) how morphology changes along environmental gradients known to affect diaspore characteristics, and (iv) changes in diaspore morphology with an ecologically analogous clade with seeds that do not appear to be dispersed by animals.

METHODOLOGY

Diaspore collection and morphometrics

In the summer and fall of 2011 and 2012, ripe fruits were collected from *Arctostaphylos*. Fourteen species were chosen (Table 2) because they were accessible and were morphologically distinct. As *Arctostaphylos* fruits develop, they are first fleshy, with a light-colored exocarp (green-to-yellow) and a soft endocarp. As the embryos reach the end of development, the endocarp hardens and becomes fused or remains as distinct nutlets. The amount of mesocarp varies among species, and can be absent (e.g., *A. glauca*), mealy (e.g., *A. patula*), have higher water content (*A. nevadensis*), or be dry and hard (*A. catalinae*). It is at this time that the thin exocarp becomes a darker color; most species have a reddish-brown color, but some are more

orange, and *A. uva-ursi* is red. This is the point that fruits were considered ripe, and fruits were not collected before ripening.

Fruits were collected with the criteria that they were ripe, showed no evidence of parasitism (exit hole or was deformed), and had not been aborted (small and deformed) uniformly from each shrub. They were collected from one to five individuals of 14 species and placed in a sealable plastic bag to avoid water loss and returned to the laboratory for measurement. Five fruits were randomly selected for measurement, which included: (I) fruit polar diameter (mm), (II) fruit equatorial diameter (mm), (III) fruit wet mass (g), (IV) fruit dry mass (g), and (V) number of nutlets per fruit. Nutlets (hereafter, seeds) were then removed from the fruits and the following were recorded: (VI) individual seed mass (g), (VII) individual seed height of polar axis (hereafter, height; mm), (VIII) individual seed width as the maximum orthogonal distance from the polar axis (hereafter, width; mm), and (IX) the individual seed length as maximum orthogonal chord to the width (hereafter, length; mm). Derived traits included: (X) fruit volume calculated as the volume of an oblate spheroid ($\text{mm}^3 = \frac{4}{3}\pi a^2 c$, where a is the equatorial radius and c is the polar radius, and $a > c$), (XI) total seed mass (g), (XII) fruit dry:wet mass (g), and (XIII) seed:fruit mass (g). Dry mass was calculated after placing fruits in a drying oven at 30°C for 24 hr.

Life-history correlation

To determine the relationship between diasporule ecological and life-history traits, data on growth form, median shrub height (m), incidence of resprouting habit (i.e., presence of fire-resistant lignotuber), latitudinal range (degrees), and area (km^2) were

compiled. Growth form, median shrub height, and incidence of resprouting habit data were retrieved from Wells (2000) and Jepson Flora Project (eds.) (2014). Geographic ranges were estimated by calculating the areal extent of a minimum convex polygon from Jepson Flora Project (eds.) (2014) for species found within California, and The Biota of North American Program (Kartesz 2013) and “Encyclopedia of Life” (2014) for species found throughout the rest of North America. Minimum convex polygons were sufficient to use as a proxy over area occupied because one aim of the study is to correlate dispersal syndrome with life history characteristics, and latitudinal range is a proximate measure of the spatial extent with which *Arctostaphylos* species interacts.

Comparison with environmental variables and an ecological equivalent taxon

I sought to determine the relationship between *Arctostaphylos* diaspore morphology and several environmental variables. Records of 4,431 occurrences of manzanitas from within California, were obtained from the California Consortium of Herbaria (CCH 2014). Because I wished to include information on as many *Arctostaphylos* species as possible, I supplemented the data with publicly available data from Kew Botanic Garden Seed Information Database (Royal Botanic Gardens Kew 2014). It would be ideal to compare all diaspore characteristics, but seed mass was the only available trait for which I could compile sufficient data. It is important to note, however, that seed mass (i) explained more variation of the differences between diaspores than any other trait (see results) and (ii) is an important life-history trait that has been found to covary with other life-history traits and therefore has evolutionary and ecological significance (Moles et al. 2004, 2005b, 2005c, Grubb et al. 2005). I contrasted

diaspore morphology with six environmental variables that have been shown to correlate with various aspects of diaspore morphology by overlaying the occurrence records with GIS layers. The environmental data included including mean fire return interval (yrs), mean annual temperature (°C), mean annual precipitation (cm), and net primary productivity (NPP; Pg of carbon per 0.25 decimal degree), median elevation (km) and median latitude (degrees). Mean fire return interval data were extracted from LANDFIRE (LANDFIRE 1.1.0 2010) maps, mean annual temperature and precipitation were extracted from WorldClim climate layers (Hijmans et al. 2005), and NPP from NASA's Global Change Master Directory (Imhoff et al. 2004).

Because I was ultimately interested in selective pressures that shape diaspore morphology, I chose an ecologically similar clade to act as a control against which I would compare manzanita; specifically, *Ceanothus* sp. *Ceanothus* and *Arctostaphylos* are similar in that they are largely sympatric, sclerophyllous, very diverse in geographic range variation by spanning several orders of magnitude, mostly shrubs but vary in growth form from prostrate to arborescent, germinated by fire, found in similarly specific and general edaphic communities, found to respond to fire by resprouting and seeding, and taxonomically diverse. The main ecological differences between the two genera include *Arctostaphylos* readily hybridizing (about two-thirds being polyploid) while *Ceanothus* is diploid, and *Ceanothus* has nitrogen-fixing actinomycetes in most, if not all, species. The relevant difference for this study, however, is that *Ceanothus* does not appear to be dispersed biotically (small seeds, ballistically dispersed from a capsule) and does not vary in diaspore morphology as much as *Arctostaphylos*. Because there is little difference in *Ceanothus* diaspore morphology and larger differences in *Arctostaphylos*, if

there is a relationship between environmental characteristics and seed mass, then any difference in *Ceanothus* and *Arctostaphylos* should be indicative of other selective pressures acting on diaspore morphology that are not solely due to the abiotic environment, like dispersal vectors.

Data analysis

Morphometric analyses were performed using principal components analysis (PCA) for both the diaspore (fruit and seed characteristics) and seed traits to examine the interrelationship between diaspore traits between the 14 species of *Arctostaphylos*. PCA orthogonally decomposes data into axes that maximally explain variation in diaspore morphology between species, and axes that explained a substantial amount of variation in diaspore morphology (> 5%) were regressed using general linear modeling against both life-history traits and environmental variables. Diaspore morphology strictly address the goals of the paper, but the analyses of seed mass as an individual variable are reported because there has been a great deal of work performed on patterns of global seed mass in recent years from macroecological (Moles et al. 2007) and evolutionary (Moles et al. 2005a) perspectives (see discussion), and I was able to supplement the data on 14 species to include data on 23 species. Lastly, bivariate comparisons between *Ceanothus* seed mass and the same six environmental gradients using general linear modeling. All analyses were conducted in R (R Core Team 2013).

RESULTS

Morphometric analysis

Collected manzanita species varied considerably in diaspore traits (Table 2). The range of several traits spanned three orders of magnitude between species (i.e., fruit volume, dry and wet fruit mass, individual seed mass), while others showed very little variation (e.g., dry:wet mass). To examine multivariate associations and distributions of diaspore traits, PCA revealed several strong gradients among diaspores of manzanita species. Figure 2 shows a PCA biplot of *Arctostaphylos* species along the first three component axes, all of which explained more than 5% of the variance (Table 3, with *A. glauca*). The first component explained 74% of the variance (eigenvalue, $\lambda = 9.94$), second explained 13% of the variation ($\lambda = 1.75$), and the third, 5% ($\lambda = 0.66$). All of the loadings (eigenvectors) were strongly correlated with the first component (> 0.90) except for seed:fruit mass, fruit dry:wet mass, and number of seeds. All other traits were associated with fruit and seed size, and the number of seeds showed a negative correlation. This was largely driven by one species, *A. glauca*, with a component score of 10.3. The two loadings most highly correlated with the second component were the number of seeds ($w = 0.73$) and seed:fruit mass ($w = -0.85$). Lastly, the third component had one loading showing a strong correlation, and that was the fruit dry:wet mass. The first three components can be interpreted as PC1 = size-related traits, PC2 = nut-related traits, and PC3 = fruit-related traits.

Because *A. glauca* is an outlier, another PCA was conducted with the remaining species (Figure 3; Table 3, without *A. glauca*). The first two components explained 82% of the variance ($\lambda_{PC1} = 6.34$, 49%; $\lambda_{PC2} = 4.28$, 33%), and the third, 7% ($\lambda = 0.88$). The first component was similar to the PCA with *A. glauca*, with size-related traits overwhelmingly correlated with that component. Additionally, like the PCA including *A.*

glaуca, the first component was positively correlated with diaspore size and negatively correlated with the number of seed per fruit. One main difference is that fruit dry:wet mass was more strongly correlated with the first component. The second component was also similar to the analysis with *A. glauca*, except there was a relatively strong bimodality along the nut-like characteristics with a gradient of individual seed sizes negatively correlated with fruit sizes. This was reflected by the negative loading of seed:fruit mass (-0.71). The third component had no loading greater than ± 0.52 .

Life-history correlations

Many, but not all diaspore traits were correlated (Table 4). I used linear combinations of diaspore traits (i.e., axes from PCA) to determine their relationships with other life-history traits (i.e., height, seed fusion, resprouting, median latitude, area, and latitudinal range). Bivariate linear regression detected three significant relationships between principal components and life history traits (Table 5). In analyses including *A. glauca*, component 1, which was correlated with size-related traits, was positively correlated with the height of the species ($F_{1,12} = 7.55, P = 0.02$), and marginally significantly positively correlated when excluding *A. glauca* ($F_{1,11} = 3.22, P = 0.10$; Figure 4). The only other life-history characteristic found to show a statistically significant relationship along component axes was a ternary character of seeds being fused, intermediate, or distinct. Including *A. glauca*, seed fusion showed a positive relationship with component 3 ($F_{1,12} = 7.31, P = 0.02$); and excluding *A. glauca*, a positive relationship with component 1 ($F_{1,11} = 5.13, P = 0.05$).

One diaspore trait that has extensively been studied and is thought to correlate with other life history traits is seed mass. Regressing individual seed mass after \log_{10} transforming the data to fit normality assumptions of the linear model against the other life history traits revealed two statistically significant relationships (Table 6). Including *A. glauca*, height was marginally positively correlated with \log_{10} individual seed mass ($F_{1,12} = 4.06, P = 0.07$). Excluding *A. glauca*, the degree of seed fusion showed a positive relationship with individual seed mass ($F_{1,11} = 5.81, P = 0.04$).

Comparison with environmental variables and an ecological equivalent taxon

I compared the seed mass of 23 *Arctostaphylos* species across six environmental gradients: median latitude, median elevation, precipitation, temperature, NPP, and fire return interval. *Arctostaphylos* seed mass only showed a statistically significant relationship with median elevation ($F_{1,22} = 5.56, P = 0.03$; Table 7, Figure 5). Regressing 26 *Ceanothus* species with environmental gradients, I found that *Ceanothus* more strongly correlated with these gradients than *Arctostaphylos*. *Ceanothus* showed a strong or marginally statistically significant relationship with all gradients considered in the study, except for mean annual temperature ($F_{1,25} = 3.45, P = 0.08$) and median elevation ($F_{1,25} = 2.29, P = 0.12$).

DISCUSSION

The main goal of the study was to delimit seed dispersal syndromes in *Arctostaphylos* by using diaspore morphology as a proximate indicator. From the morphometric analysis, I found considerable variation in diaspore morphology along at

least two multivariate axes that corresponded to size and nut-related characteristics. I then compared these multivariate axes and seed size to life-history traits that are often found in coordination with dispersal syndromes and seed mass, and failed to find significant relationships with traits like height, sprouting or seeding in response to fire, and spatial extent. Next, I compared seed mass along environmental gradients and against an ecological equivalent group as a control, *Ceanothus*. There was no relationship found between *Arctostaphylos* seed mass and most environmental gradients, whereas *Ceanothus* covaried with most environmental gradients. This leads me to reject the idea that the large variation in diaspore morphology—interpreted in this study as a strong indicator of seed dispersal syndromes—in *Arctostaphylos* is a result of either covarying with life-history syndromes or environmental pressures; thus failing to reject the hypothesis that the variation in *Arctostaphylos* corresponds to seed dispersal syndromes.

I detected considerable variation in *Arctostaphylos* diaspores. Although this was largely driven by a single species (*A. glauca*; e.g., Figure 2), when removing it from our analyses (e.g., Figure 3) I found diaspore traits aligned in a very similar multivariate pattern. The first axis that explained most of the variation largely decomposed individual traits into a gradient of large fruits and seeds, with a positive correlation with fused seeds. The second axis was positively correlated to large fruits and small seeds. Along the first axis in Figure 3, *A. glauca* has an extremely high score of 10.3. *A. glauca* is straight forward to diagnose because its characteristics more clearly follow our understanding of what a nut syndrome is like, as a large, dry, single seed (i.e., fused nutlets), with a thick seed coat and leathery exocarp (Vander Wall 2001). With respective means of equatorial

and polar diameters of 12.8 and 11.8 mm, the dimensions of *A. glauca*'s seeds are within the range of some oaks species (e.g., diameters of *Quercus vaccinifolia* 12.5 mm and *Chrysolepis sempervirens* 10.5 mm (Jepson Flora Project (eds.) 2014)). The only major way in that *A. glauca* differs from other scatter-hoarded nut syndromes is that it has a relatively small endosperm reward, 0.027 g per seed (3% total seed mass). What was somewhat surprising was that after *A. glauca* was removed from the morphometric analysis, the multivariate patterns were qualitatively nearly identical. The species that were the drivers of the large, nut-like seeded species included *A. glandulosa*, *A. pringlei*, and *A. parryana*. A close examination of their morphology reveals a nut-like syndrome, with a single seed, dry-to-absent mesocarp, with a leathery exocarp. The main difference is that these species are much smaller than what has traditionally been interpreted as nuts, with the mean seed mass for the three aforementioned species ranging from 0.08–0.13 g. For a typical nut syndrome this would be small, but these species are still within the range of other scatter-cached seeds like antelope bitterbrush (Vander Wall 1994) and Indian ricegrass (Longland et al. 2001; respective means approximately 0.24 and 0.035 g).

Attempting to classify the diaspores into seed dispersal syndromes proved to be more difficult and would require investigation of seed dispersal studies on some of the species along the component axes. This is true because the species investigated in this study did not fall into discrete categories, but rather along more of a continuous gradient (with the exception of *A. glauca*). In chapter 1 of this dissertation, *A. patula* was studied in detail because it ostensibly had an ambiguous seed dispersal syndrome. It has a reddish fruit with some nutlets fused, and the seeds are relatively small compared to other

obvious and well-studied scatter-hoarded species, like oaks, hickories, and some pines. Nevertheless, several experiments demonstrated that scatter-hoarding rodents are likely the effective dispersers of that species. In figure 2, along the *x* and *y* coordinates, *A. patula* occurs around 0,-0.5, and in Figure 3, around 0,0. It is therefore not unfounded to posit that seeds that are larger and more nut-like likely have a scatter-hoarding seed dispersal syndrome. This means that *A. otayensis*, *A. pungens*, *A. parryana*, *A. pringlei*, *A. glandulosa*, and *A. glauca* are demonstrative of a scatter-hoarding syndrome. The lower values along the first component without *A. glauca* are generally very small seeded, which may be indicative of an uninvestigated seed dispersal syndrome, like abiotic dispersal. Considering the second component where the lower values were more nut-like, however, all of the species with values greater than *A. patula* have more mesocarp mass and a lower dry:wet mass. The species that have large fruits and seeds still may be indicative of a scatter-hoarding syndrome (i.e., *A. nevadensis*, *A. catalinae*), while others may be dispersed by frugivores (e.g., *A. viscida*, *A. tomentosa*, *A. columbiana*, *A. pumila*). Animal-mediated seed dispersal is often a two-phased process (Chambers and MacMahon 1994, Vander Wall and Longland 2004, 2005), and syndromes, as described by van der Pijl (1961), are often "classes with bad boundaries but a clear center."

Factors that have been attributed as shaping fruit- and seed-trait evolution are changes in climate and physiognomy on large temporal scales (Eriksson et al. 2000), dispersal (Tiffney 2004), predation and parasitism (Whitehead and Bowers 2013, Tohge et al. 2014), environment (Keeley and Fotheringham 2000, Moles et al. 2007), and coordination with the evolution of other life-history traits (Baker 1972, Moles and

Westoby 2003, Moles et al. 2005a). Not examined in this study, changes in climate and physiognomy in the middle Pliocene to a Mediterranean-type climate with cool wet winters and hot dry summers set the stage for the diversification of *Arctostaphylos* within the California Floristic Province's diversity of topography, edaphic communities, and fire regimes (Raven and Axelrod 1978). But without having a precise or functional phylogeny of the group (see Hileman et al. 2001, Wahlert et al. 2009), it is difficult to assess the role of diversification on diaspores or vice versa over evolutionary time. What I do know, with confidence, is that the extant sister taxa to *Arctostaphylos* within Arbutoideae (i.e., *Arctous*, *Ornithostaphylos*, *Comarostaphylos*, *Xylococcus*, *Arbutus*) all unambiguously have fruits dispersed by frugivorous animals, meaning that there was likely a transition from frugivory to scatter-hoarding that may be a synapomorphy of the group. Predation and parasitism were not investigated in this study, but could very well play a strong role in the evolution of *Arctostaphylos* diaspores. In this study, populations varied in seed parasitism (incidence per fruit) from approximately 5–40%.

Within this study, however, I was able to assess the relationships between diaspore traits and both environmental gradients and life-history correlates. *Arctostaphylos* did not appear to show strong relationships along any environmental gradients, except for elevation, and there was a weak, statistically insignificant relationship with latitude. Using a global dataset of > 11,000 species, Moles et al. (2007) found a negative relationship between seed mass and latitude, attributed to changes in growth form and vegetation type. I observed similar relationships, but only statistically significant in *Ceanothus*. *Arctostaphylos* not only showed a weak relationship with latitude, but it also showed a weak (including *A. glauca*) or insignificant (excluding *A.*

glauca) relationship with shrub height. I interpret this as the evolution in diaspore traits being more complex, perhaps suggesting that other selective pressures, such as seed dispersal, were also acting on diaspore traits. Several environmental factors in addition to latitude (i.e., NPP, mean annual precipitation, mean annual temperature) covary with characteristics of the fire regime. None of the factors, including mean fire return interval, showed significant relationships with seed mass (Figure 5, Table 7). Given that most of the seeds were relatively large compared to all seeds found in the fire-prone California Floristic Province, on the one hand, this is perplexing given that it has been shown that large seeds better survive fires than small seeds (Keeley and Fotheringham 2000, Keeley et al. 2005). On the other hand, abiotic burial of seeds takes longer (Chambers and MacMahon 1994), especially considering there are no obvious ancillary structures such as awns (Peart 1984, Garnier and Dajoz 2001, Humphreys et al. 2011), and the depressed-spherical shape of large seeds is the opposite of seeds that more easily incorporate into the seed bank, typical of small or lanceolate-shaped seeds (Chambers et al. 1991). Nevertheless, the lack of obvious ancillary traits or morphology that would facilitate burial in addition to most of the species in this study being nut-like, suggests that large-seeds are an adaptation for dispersal by scatter-hoarding animals, rather than to decrease mortality due to fire.

The morphological variation in *Arctostaphylos* is impressive given that it has undergone a relatively recent diversification, with the origin of the genus estimated around the end of the Miocene, about 5.3 MYA (Edwards 2004). This is in contrast to, for example, *Ceanothus*, whose evolutionary origins date to the Paleocene–Eocene, about 65–33 MYA (Hardig et al. 2000). Although, it is not entirely surprising given that seed

trait evolution has been shown to happen very rapidly, including as recently as the development of urban environments (Cheptou et al. 2008) or over-hunted areas that lose seed dispersers (Galetti et al. 2013), and on longer-term temporal scales, like when humans introduced fire into the Chilean matorral in the mid-16th century that otherwise did not experience a fire regime (Gómez-González et al. 2011). Nevertheless, for a recent clade to have that much variation is not common. Most of the dispersal syndrome investigations have been on older genera, like *Ficus* (Lomáscolo et al. 2008, Lomáscolo et al. 2010). *Ficus*, for instance, has many more species (~850) than *Arctostaphylos* and according to molecular data the genus is approximately 83 MYA (Datwyler and Weiblen 2004). *Acacia* is another older clade showing dispersal syndrome variation (Davidson and Morton 1984) and diverged 24–21 MYA (Miller et al. 2013).

In this study, I have performed a morphometric analysis of diaspores in the genus *Arctostaphylos*, and assessed putative evolutionary pressures on their morphology by comparing traits along environmental gradients that have been shown to affect diaspore morphology. The lack of relationships between *Arctostaphylos* diaspore traits and environmental gradients suggests that factors other than the abiotic environmental variables included in this study have influenced the evolution of their diaspore traits. Several species have characteristics that are strongly indicative of a scatter-hoarding nut dispersal syndrome, while others (e.g., *A. hookeri*) remain unresolved and should be investigated to fully understand how members of *Arctostaphylos* are dispersed.

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Chapter 2, Table 1. Comparisons of three different dispersal modalities. Seed dispersal syndromes are suites of correlated traits matched to the behavior, physiology, and morphology of each of these dispersal modalities.

Disperser	Home range	Gut-retention time	Risk of seed mortality	Delivery to suitable microsite	Concentration of dispersed seeds
Bird	Large	Short	Low	Medium to low	Low to high
Carnivore	Large	Long	Low	Medium to low	High
Rodent	Small	N/A	High	High	Low to high

Chapter 2, Table 2. Mean values for the 13 diaspore traits measured on 13 manzanita (*Arctostaphylos* sp.) species. *Arctostaphylos glauca* has a very different morphology than all other species and is highlighted in bold.

	Fruit width	Fruit height	Fruit mass	No. seeds	Seed mass	Ind. seed mass	Ind. seed height	Ind. seed width	Seed:length	Ind. seed mass	Seed:fruit mass	Dry:wet mass	Fruit volume	Fruit dry mass
<i>A. catalinae</i>	10.62	8.60	0.352	4.8	0.170	0.036	5.48	3.39	3.48	0.483	0.939	507.3	0.330	
<i>A. columbiana</i>	8.44	5.54	0.118	4.4	0.054	0.012	3.13	2.93	2.36	0.460	0.922	206.4	0.109	
<i>A. glandulosa</i>	8.52	5.78	0.147	1.0	0.133	0.133	6.70	6.36	0.997	0.926	0.926	219.4	0.137	
<i>A. glauca</i>	15.30	15.64	1.358	1.0	0.949	0.949	12.78	11.84	11.84	0.705	0.938	1914.8	1.274	
<i>A. hookeri</i>	5.08	4.02	0.033	4.2	0.018	0.004	2.38	1.83	1.65	0.541	0.913	54.3	0.030	
<i>A. otayensis</i>	8.46	5.54	0.133	2.8	0.090	0.043	4.21	3.59	3.99	0.674	0.929	207.4	0.124	
<i>A. pringlei</i>	6.98	7.10	0.124	1.0	0.082	0.082	6.52	5.56	5.56	0.655	0.922	180.9	0.115	
<i>A. tomentosa</i>	8.76	5.96	0.141	5.0	0.059	0.012	2.59	2.77	2.23	0.426	0.906	239.2	0.127	
<i>A. nevadensis</i>	9.18	7.74	0.170	4.2	0.105	0.038	5.40	3.46	3.82	0.219	0.966	341.5	0.101	
<i>A. parryana</i>	9.23	6.68	0.632	2.4	0.512	0.102	5.12	6.18	6.38	0.810	0.924	297.3	0.473	
<i>A. patula</i>	9.87	8.02	0.447	3.6	0.342	0.034	4.32	3.36	3.36	0.765	0.966	403.3	0.432	
<i>A. pumila</i>	6.88	6.40	0.081	4.0	0.013	0.008	2.61	2.43	2.01	0.388	0.919	158.6	0.012	
<i>A. pungens</i>	6.50	6.16	0.141	4.0	0.117	0.083	4.52	3.56	2.70	0.830	0.925	357.5	0.130	
<i>A. viscosa</i>	9.20	6.70	0.155	3.8	0.039	0.039	5.42	3.70	3.58	0.290	0.915	296.6	0.142	

Chapter 2, Table 3. Principal components analysis for 13 diaspore morphological traits of manzanitas (*Arctostaphylos*). Analysis were conducted with and without an outlying species, *A. glauca*, and the same qualitative patterns were observed. Namely, the first component was largely composed of traits related to diaspore size, the second component was composed of the two nut-related traits of seed:fruit mass and fusion of seeds, and the third component only detected one strong loading, which was the fruit dry:wet mass. In both analyses, only the first three components explained > 5% of the variation.

	with <i>A. glauca</i>			without <i>A. glauca</i>		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	9.94	1.75	0.66	6.34	4.28	0.88
Percent variation explained	76.46	13.47	5.04	48.73	32.88	6.80
Eigenvectors						
Fruit equatorial diameter	0.88	0.33	0.15	0.65	0.59	-0.18
Fruit polar diameter	0.96	0.24	0.03	0.78	0.47	-0.29
Fruit mass	0.96	0.23	-0.02	0.76	0.63	0.01
Number of seeds	-0.61	0.73	0.15	-0.43	0.83	-0.05
Total seed mass	0.97	0.14	-0.04	0.91	0.17	0.33
Ind. seed mass	0.97	0.07	-0.18	0.66	-0.67	-0.11
Ind. seed height	0.96	-0.13	-0.03	0.84	-0.35	-0.22
Ind. seed width	0.95	-0.20	-0.16	0.69	-0.63	-0.28
Ind. seed length	0.94	-0.24	-0.12	0.71	-0.61	-0.22
Seed:fruit mass	0.39	-0.85	0.13	0.42	-0.71	0.52
Fruit dry:wet mass	0.68	-0.11	0.71	0.79	0.17	0.45
Fruit volume	0.91	0.25	-0.08	0.45	0.59	0.05
Fruit dry mass	0.96	0.23	-0.01	0.76	0.62	0.02

Chapter 2, Table 4. Correlations between diaspore traits measured in this study. The upper panel is the Pearson product-moment correlation (r) and the lower panel is the Spearman's rank correlation coefficient (ρ). Many of the correlations were strong, except for seed:fruit mass and dry:wet mass.

	Fruit width	Fruit height	Fruit mass	No. seeds	Seed mass	Ind. seed mass	Ind. seed height	Ind. seed width	Ind. seed length	Seed:fruit	Dry:wet	Fruit mass	Fruit Volume	Fruit dry mass
Fruit width	0.93	0.92	-0.27	0.88	0.84	0.82	0.79	0.78	0.09	0.64	0.92	0.92		
Fruit height	0.74	0.98	-0.43	0.96	0.93	0.92	0.88	0.87	0.15	0.64	0.98	0.98		
Fruit mass	0.97	0.80	-0.42	0.99	0.97	0.89	0.88	0.87	0.20	0.60	1.00	1.00		
No. seeds	0.05	-0.21	-0.15	-0.49	-0.56	-0.73	-0.77	-0.80	-0.78	-0.41	-0.40	-0.42		
Seed mass	0.62	0.64	0.70	-0.37	0.99	0.90	0.91	0.90	0.30	0.60	0.99	0.99		
Ind. seed mass	0.38	0.54	0.55	-0.86	0.72	0.91	0.92	0.89	0.33	0.53	0.94	0.97		
Ind. seed height	0.52	0.73	0.68	-0.73	0.78	0.76	0.94	0.95	0.43	0.67	0.85	0.89		
Ind. seed width	0.43	0.60	0.60	-0.85	0.65	0.96	0.82	0.99	0.52	0.58	0.81	0.88		
Ind. seed length	0.38	0.54	0.55	-0.86	0.72	0.87	0.79	0.94	0.55	0.62	0.79	0.87		
Seed:fruit mass	-0.05	0.05	0.12	-0.76	0.63	0.70	0.60	0.70	0.70	0.42	0.17	0.20		
Dry:wet mass	0.47	0.51	0.57	-0.39	0.87	0.65	0.72	0.58	0.65	0.58	0.59	0.61		
Fruit Volume	1.00	0.74	0.97	0.05	0.62	0.10	0.38	0.22	0.17	-0.05	0.47	1.00		
Fruit dry mass	0.97	0.80	1.00	-0.15	0.70	0.55	0.68	0.60	0.55	0.12	0.57	0.97		

Chapter 2, Table 5. Relationships between principal components and life-history traits, including and excluding *Arctostaphylos glauca*. Height was found to have a statistically significant relationship with PC1 including *A. glauca*, and marginally significant excluding *A. glauca*. Ternary predictor, degree of seed fusion, was the only other trait to show a statistically significant relationship with components.

		β	St. Err.	t-value	P > t	R^2
Including <i>A. glauca</i>						
PC1	Height	1.91	0.70	2.75	0.02	0.35
	Seeds	0.80	1.08	0.74	0.47	-0.04
	Burl	-0.69	2.06	-0.34	0.74	-0.08
	Med. lat.	0.26	1.12	0.23	0.82	-0.09
	Area	0.77	0.88	0.88	0.40	-0.02
	Lat. range	0.26	1.12	0.23	0.82	-0.09
PC2	Height	0.10	0.38	0.25	0.80	-0.08
	Seeds	-0.30	0.45	-0.67	0.52	-0.05
	Burl	-0.67	0.84	-0.79	0.45	-0.03
	Med. lat.	-0.41	0.45	-0.90	0.39	-0.02
	Area	-0.21	0.38	-0.55	0.59	-0.06
	Lat. range	-0.41	0.45	-0.90	0.39	-0.02
PC3	Height	0.15	0.23	0.66	0.52	-0.05
	Seeds	0.59	0.22	2.70	0.02	0.34
	Burl	-0.38	0.51	-0.73	0.48	-0.04
	Med. lat.	-0.49	0.25	-1.98	0.07	0.20
	Area	-0.18	0.22	-0.81	0.43	-0.03
	Lat. range	-0.49	0.25	-1.98	0.07	0.20
Excluding <i>A. glauca</i>						
PC1	Height	1.48	0.82	1.79	0.10	0.17
	Seeds	1.68	0.74	2.27	0.05	0.27
	Burl	0.58	1.72	0.33	0.75	-0.09
	Med. lat.	-1.12	0.86	-1.31	0.22	0.06
	Area	-0.37	0.76	-0.48	0.64	-0.07
	Lat. range	-1.12	0.86	-1.31	0.22	0.06
PC2	Height	0.48	0.76	0.64	0.54	-0.06
	Seeds	-0.16	0.74	-0.21	0.84	-0.10
	Burl	-1.20	1.36	-0.88	0.40	-0.02
	Med. lat.	-1.16	0.66	-1.75	0.11	0.16
	Area	-0.66	0.59	-1.12	0.29	0.02
	Lat. range	-1.16	0.66	-1.75	0.11	0.16

Chapter 2, Table 6. The relationship between individual seed mass and other life history traits, both with and without *Arctostaphylos glauca*. Statistical significance is denoted in bold. Surprisingly, there were weak or marginally significant relationships detected.

	β	St. Err.	t-value	$P > t$	R^2
Including <i>A. glauca</i>					
Height	0.27	0.13	2.02	0.07	0.20
Seeds	0.26	0.18	1.46	0.17	0.09
Burl	0.03	0.36	0.08	0.93	-0.09
Med. lat.	0.12	0.19	0.61	0.56	-0.06
Area	0.19	0.15	1.26	0.23	0.05
Lat. range	0.12	0.19	0.61	0.56	-0.06
Excluding <i>A. glauca</i>					
Height	0.08	0.15	0.52	0.62	-0.07
Seeds	0.28	0.12	2.41	0.04	0.30
Burl	0.19	0.27	0.72	0.49	-0.05
Med. lat.	0.07	0.15	0.50	0.63	-0.07
Area	0.11	0.12	0.94	0.37	-0.01
Lat. range	0.07	0.15	0.50	0.63	-0.07

Chapter 2, Table 7. The relationship between seed mass and environmental gradients for *Arctostaphylos* ($N = 23$) and *Ceanothus* ($N = 26$). The only environmental gradient with which *Arctostaphylos* showed a statistically significant relationship was median elevation. *Ceanothus*, in contrast, showed statistically significant or marginally non-significant relationships with almost all of the variables. Statistical significance is denoted in bold.

	β	St. Err.	t-value	$P > t$	R^2
<i>Arctostaphylos</i> sp.					
Median latitude	-0.065	0.046	-1.411	0.172	0.041
Median elevation	0.380	0.162	2.349	0.028	0.164
Precipitation	-0.218	0.288	-0.757	0.457	-0.019
Temperature	-0.014	0.042	-0.347	0.732	-0.040
NPP	0.000	0.000	-0.096	0.924	-0.045
Fire return interval	0.005	0.004	1.261	0.221	0.025
<i>Ceanothus</i> sp.					
Median latitude	-0.056	0.018	-3.126	0.005	0.260
Median elevation	-0.147	0.097	-1.513	0.143	0.049
Precipitation	-0.340	0.115	-2.943	0.007	0.235
Temperature	0.032	0.017	1.858	0.075	0.089
NPP	0.000	0.000	-2.274	0.032	0.143
Fire return interval	0.003	0.002	2.094	0.047	0.119

Chapter 2, Figure 1. Seed size of five species of manzanita (*Arctostaphylos*): A. bigberry manzanita, (*A. glauca*), B. Eastwood's manzanita (*A. glandulosa*); and C. Hooker's manzanita (*A. hookeri*), whiteleaf manzanita (*A. viscida*), and Catalina island manzanita (*A. catalinae*). These species demonstrate some of the differences in diaspore traits that are examined in this study, including number of seeds per fruit and size. Seeds of manzanitas range three orders of magnitude in volume, shown between *A. glauca* and *A. hookeri*.

Chapter 2, Figure 2. Principal components biplot of manzanita diaspores (*Arctostaphylos*), including bigberry manzanita (*A. glacua*). The first component largely describes the size of the diaspore, the second component describes nut-like characteristics, and the third component describes fruit-like characteristics. The translucent grey circles are individual diaspore samples, the triangles are individual species, and the lines are the loadings (eigenvectors) for each component.

Chapter 2, Figure 3. Principal components biplot of manzanita diaspores (*Arctostaphylos*), excluding bigberry manzanita (*A. glacua*). The translucent grey circles are individual diaspore samples, the triangles are individual species, and the lines are the loadings (eigenvectors) for each component. *A. glauca* was an outlying point, but even after its exclusion from this analysis, the results were qualitatively similar to Figure 2, which included *A. glauca*

Chapter 2, Figure 4. Positive, statistically significant principal component 1 regressed against the median height of manzanita (*Arctostaphylos*). This was the only life-history trait to show a significant relationship with component 1, which was only for the analysis

including *A. glauca* (left). Ordinary least squares line of best fit is dashed, with the 95% confidence intervals as gray bands.

Chapter 2, Figure 5. The relationship between seed mass and three environmental gradients for *Arctostaphylos* (top row) and *Ceanothus* (bottom row). The seed mass of *Arctostaphylos* did not tend to statistically significantly vary along environmental gradients, whereas *Ceanothus* did. This includes the mean fire return interval (years), for which suggests that fire may not have been a significant pressure on seed mass. For this dataset, I used 23 species of *Arctostaphylos* and 26 *Ceanothus*.

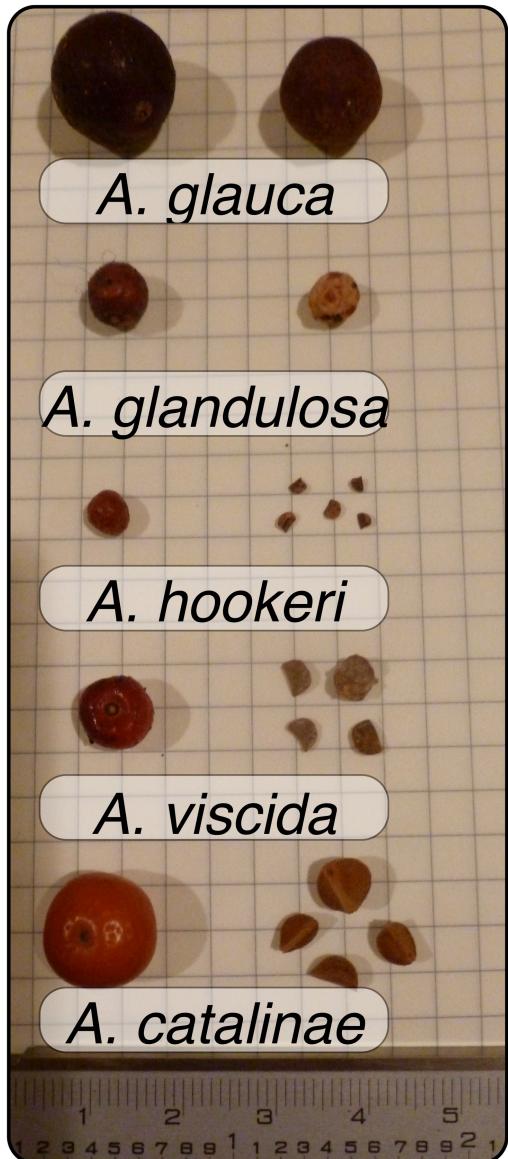


Figure 1.

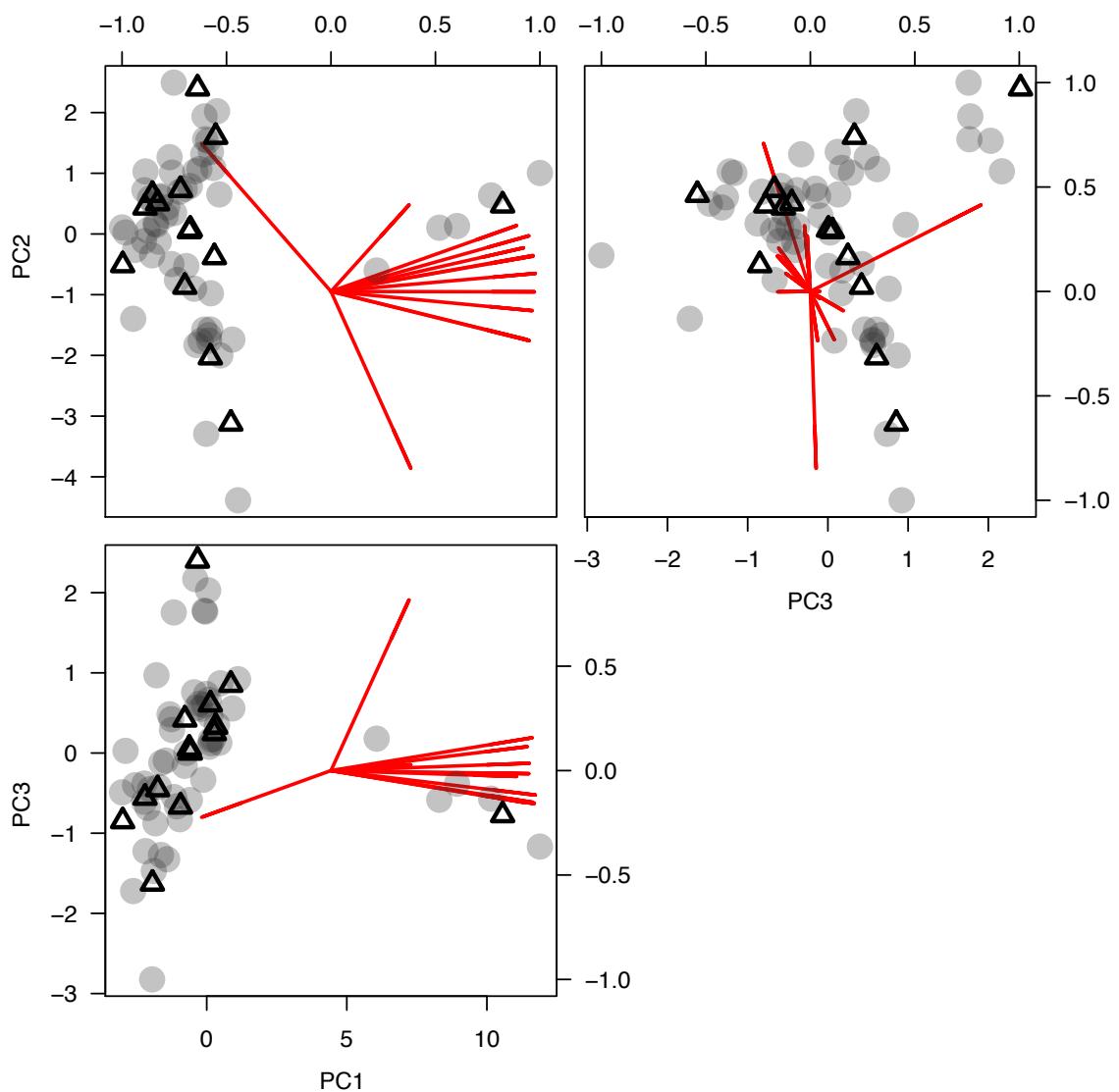


Figure 2.

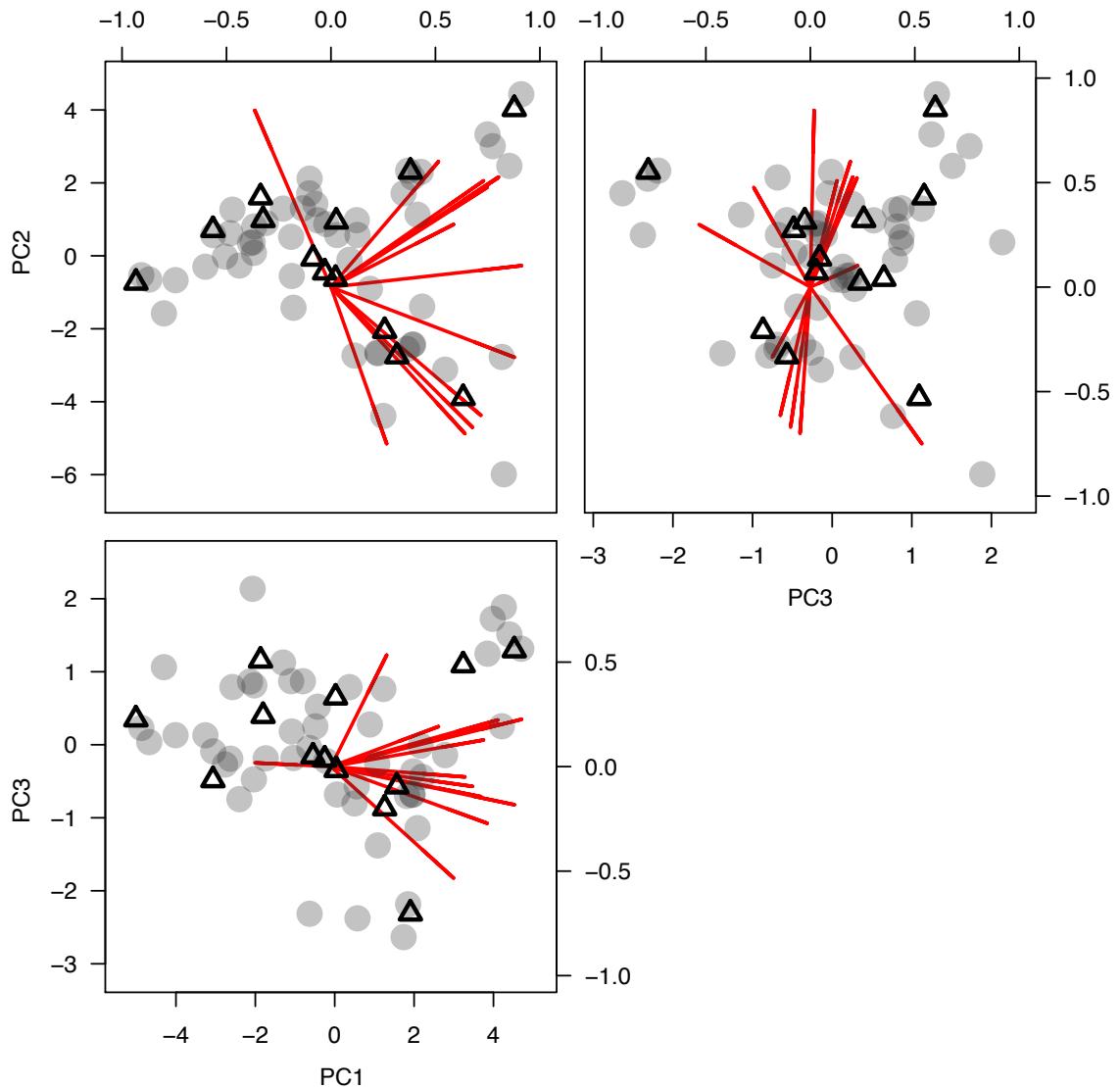


Figure 3.

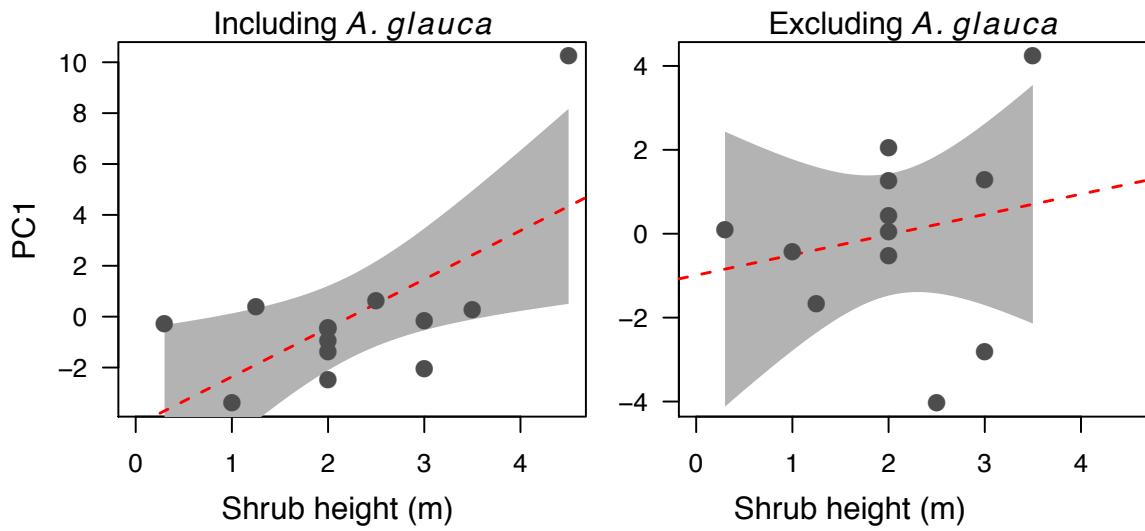


Figure 4.

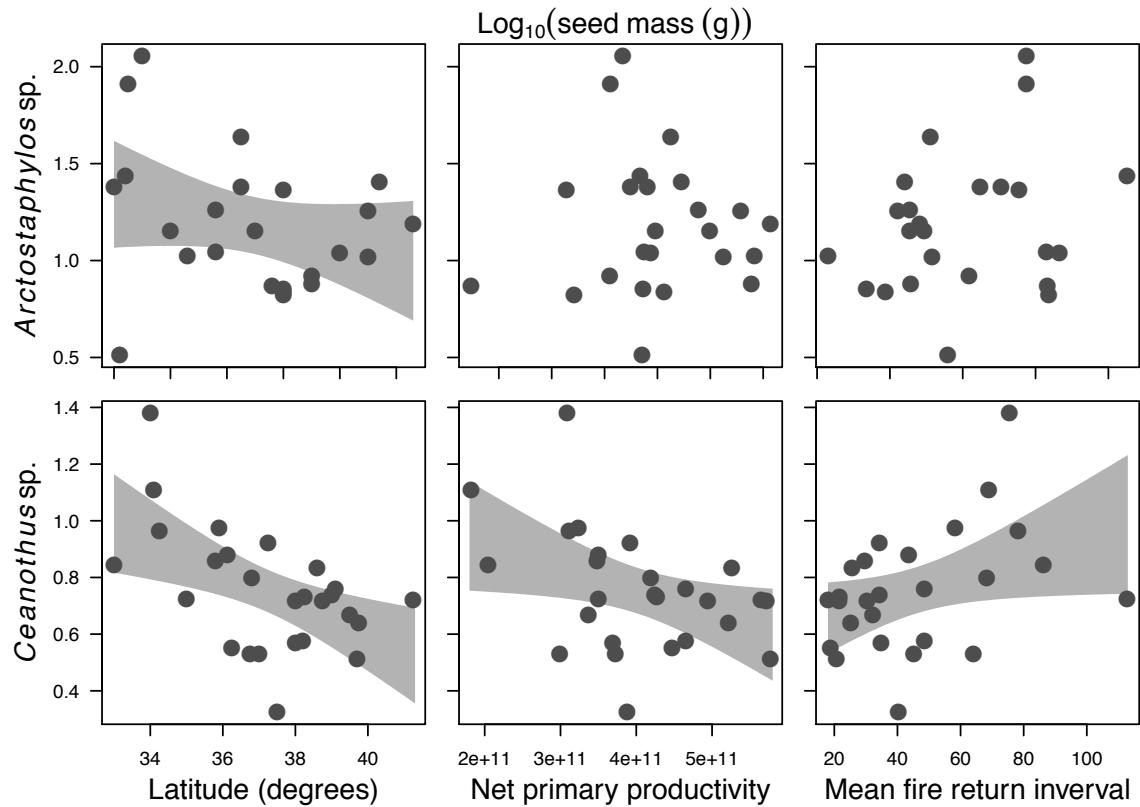


Figure 5.

Chapter 3: Patterns of seed-dispersal mutualisms across temperate North America

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Abstract. Interactions between individuals belonging to species and guilds ultimately mediate ecological dynamics. Mutualistic interactions are a subset of direct interactions where both participants incur an increase in fitness. These types of interactions are found in virtually all communities and differently contribute to ecological structure and dynamics compared to other interaction types. The goal of our study was to examine the spatial distribution of plants that putatively engage in mutualistic seed-dispersal interactions with animals, inferred from their fruit morphology, and correlate those patterns with various environmental gradients. Our main a priori hypothesis was that higher-order patterns of mutualistic interactions covary with patterns of species richness and distributions, and along environmental gradients. We tested this hypothesis by compiling previously published plant lists for 197 sites across the North American continent, then attributing dispersal and other life-history characteristics, such as growth form and higher-order taxonomic grouping, for each species. Our main analytical approach employed multiple regression and principal component analysis to detect relationships of mutualisms and mutualism types in space and across environmental gradients. Using incidence data from each site, plants with seed-dispersal mutualisms

accounted for roughly one-sixth of all records and one-eighth of all species. We found expected relationships of species richness at sites, including positive significant relationships with mean annual precipitation, elevational range, sampling area, and latitude. Non-mutualist richness accounted for five-sixths of the records and largely mirrored patterns of species richness. Plant species with mutualists showed stronger relationships with precipitation and latitude and no relationship with sampling area. Dividing the mutualisms into dispersal modes, frugivory was the most abundant and drove most of the patterns of mutualisms. The relative abundance of frugivory was highest in the eastern US, seed-hoarding being relatively abundant in the eastern US and arid southwest, and myrmecochory showed the highest relative abundance in Appalachia and around the Great Lakes. We further identified univariate diversity metrics and bivariate type-abundance distributions of mutualism types across sites. Our main finding was that similar type-abundance distributions were observed for interactions as are normally found with species. This is the first attempt to examine patterns of seed-dispersal mutualisms at this spatial scale and we hope this stimulates future research.

Keywords: *ecogeography; dispersal; food hoarding; frugivory; interaction diversity; mutualism; myrmecochory; seed dispersal; seed dispersal syndromes*

INTRODUCTION

Examining ecological patterns at large spatial scales allows us to make inferences about processes that are difficult to distinguish at the local scales on which most ecological research is conducted (e.g., Turner 1989, Levin 1992, Willig et al. 2003).

Local stochasticity can be ameliorated by scaling out, which increases the extent of the sample and averages out local heterogeneities (Chesson 1998); therefore more clearly revealing the strength, direction, and identity of the processes shaping the observed patterns. Although, an important caveat is that scale-dependent processes are unlikely to scale up linearly (Chesson 2012) and are affected by higher-scale processes (O'Neill et al. 1986, Wiens 1989). As examples of large-scale ecology, Alexander Von Humboldt sought to determine processes underlying *geographiae plantarum lineamenta* ("lines of the geography of plants") across continents and large topographic extents (Hawkins 2001), and modern geographic information systems have provided a trove of information against which ecologists can compare data on spatial distributions ranging from landscape to global spatial scales. The power of analysis at these spatial scales has pervaded ecology, leading to the genesis of entirely new disciplines (e.g., biogeography, landscape ecology, macroecology), multitudes of studies, and semi-autonomously derived bodies of theory.

The large-scale patterns that ecologists have elucidated have been multifarious. As examples, systematics have described patterns of species, higher order classification (e.g., generic, familial), or phylogenetic diversity (Wiens et al. 2006, 2010). Ecosystem patterns have described production (Potter et al. 1993) and nutrient dynamics (Vitousek 1984, Reich and Oleksyn 2004) across large spatial scales. Eponymous macroecology (Brown and Maurer 1989, Brown 1995) is primarily concerned with large-scale ecological patterns. As a last example, there has been a tremendous amount of work examining organismal traits at large spatial scales (Mayr 1956, Wright et al. 2004, Sack

et al. 2012). In this paper, we report on a lesser-considered type of large-scale pattern; namely, species interactions.

Interactions ultimately mediate ecological dynamics and can be quantified through their frequency, strength, and direction. Our conceptual basis of interactions largely comes from the discipline of trophic ecology, which has contributed to the elucidation of large-scale patterns of trophic interactions. For example, Martinez and Lawton (1995) demonstrated the relationship between different food web structure metrics and number of species, from local to the global scale. These studies of trophic interactions have been very valuable, but they only represent one type of many interaction types within a community (i.e., predation, where one benefits at the cost of another), the proportion of trophic interactions to total interactions within any given community is theoretically a trivial fraction, and contribute to one specialized type of community structure and dynamics.

Mutualistic interactions are one different, distinct interaction type that are a subset of direct interactions where both participants gain a fitness advantage (Bronstein 1994). These types of interactions are found in virtually all communities, and they contribute differently than other interaction types (e.g., trophic, neutral) to ecological community structure and dynamics (Waser and Ollerton 2006, Bascompte and Jordano 2014) and evolution (Thompson 1994, 2005) both theoretically (Holland et al. 2002, McGill 2005, Holland and DeAngelis 2010) and empirically (Dodd et al. 1999, Bascompte et al. 2003, Rezende et al. 2007). A recent synthesis further reported that experimental studies of mutualisms are not more or less conditional when compared to competition and predation (Chamberlain et al. 2014). Thébaud and Fontaine (2010), for example, demonstrated

with a model that was corroborated by a meta-analysis that network topologies for stable communities were different between mutualistic (nested and highly connected) and trophic (compartmentalized and weakly connected) interactions. As another example as to how mutualistic interactions uniquely affect community structure, Bastolla et al. (2009) showed that the size of the mutualistic networks (i.e., number of species) was positively dependent on observed nested network structure that reduced interspecific competition.

The structure of mutualistic interactions between communities at large-scales spanning environmental gradients has been examined in the past (Regal 1982, Jordano 2000, Ollerton and Cranmer 2002, Olesen and Jordano 2002, Ollerton et al. 2006, Moles et al. 2007, Almeida-Neto et al. 2008, Schleuning et al. 2012). Olesen and Jordano (2002), for instance, analyzed the topological structure of 29 bipartite plant-pollinator communities to find significant relationships between network size, latitude, and elevation with connectance, number of interactions, and number of interactions per plant species. As another example, Schleuning et al. (2012) found that for both pollination and seed dispersal mutualisms, that specialization was positively correlated with latitude, growing degree days, and annual precipitation. As a last and relevant example, Almeida-Neto et al. (2008) performed a study on the relationship between the proportion of vertebrate-dispersed woody plants and various environmental gradients at 135 sites along the Atlantic forest, Brazil. The study was unable to detect a latitudinal signal because the study only spanned 12.5° and the study area was within a "... relatively homogenous biogeographical and floristic assemblage." Nevertheless, Almeida-Neto et al. (2008) found that the relative number of fleshy fruit species is mainly driven by moisture rather

than geographical location. These studies have lent great insight into the patterns of mutualistic interactions that we would expect to see at large spatial scales. Although, many of the studies suffer from incomplete or low sampling sizes, were not conducted across a sufficient range to capture the relationship with the environmental gradient, only measured a subset of plant taxa or growth forms, or considered one mutualism modality (e.g., only frugivory).

This study investigates the distribution of plants with putatively coevolved traits representative of mutualistic interactions between plants and seed-dispersing animals. The spatial scale is across a continent to capture sufficient variation across several environmental gradients, and the taxonomic breadth includes all seed plants. One key advantage of using seed dispersal as a model for distributions of mutualistic interactions is that, unlike other mutualisms, it is highly likely that if a plant is present it once had interacted with its mutualist. The evidence for this claim is that in the absence of seed dispersers, recruitment (Vander Wall 2008) and establishment (Redford 1992, Wright et al. 2007) seldom occur. This is unlike plant-pollination mutualisms, for instance, where the inference is that the maternal plant interacted with a mutualist; thus rendering its presence an outcome of dispersal, which is ostensibly unrelated to the mutualistic interaction. "Effective mutualistic interaction," in this study, would be analogous to measuring seed set in obligate outcrossing plants to identify plant-pollination mutualisms. The main hypothesis of the study relates interaction diversity (*sensu* Dyer et al. 2010) of mutualisms to large-scale environmental gradients in an analogous fashion to the way that ecologists have related species diversity to environmental gradients. Specifically, we hypothesize that if biological hierarchy scales, then interaction diversity will covary with

species diversity. The processes underlying these patterns are not being rigorously investigated, as much more and better data of species diversity have not resolved why a given point on Earth has a specific species richness (Pianka 1966, Willig et al. 2003, Mittelbach et al. 2007).

METHODOLOGY

Data collection and categorization

Because data are not available for the occurrence of all North American temperate plants, we searched for well-defined sites with published lists of seed plants in peer-reviewed journals and on the Internet. Sites are not spatially random, which therefore made random sampling impossible. Instead, we spatially chose sites in a uniform manner that reduced the effects of spatial autocorrelation and maximized inclusion of different habitat and climate types. In the end, we digitized and compiled a total of 197 lists into a single database after eliminating numerous sites for being too small, incomplete, or inaccurate.

For each of the 14,211 plant species in our study, we assessed its seed dispersal mode and vector, including secondary dispersal. We first searched peer-reviewed literature for investigations of dispersal on each species. If there were no results, we searched other forms of primary (e.g., books, natural history accounts), secondary, and grey literature. In all instances, including species for which no published information on its dispersal was found, we respectively corroborated and described dispersal mode and vector with photographs from Internet searches by using criteria described below.

With respect to modes of dispersal, we categorized plants into three coevolved mutualistic groups: frugivory, scatter-hoarding, and myrmecochory. Frugivorous mutualisms are the outcome of plant species providing a nutrient reward for passive dispersal services by animals that inadvertently ingest seeds. The criteria for the frugivory group is a fleshy fruit with small seeds. Scatter hoarding by animals is a form of external energy storage whereby animals store food for later consumption. Many plants have evolved to produce seeds in numbers that satiate hoarding animals that inevitably fail to recover stored seeds, and hoarding is considered a mutualistic interaction because of the dispersal and burial service provided by the hoarding animals. Plants grouped under hoarding are usually large seeds (> 10 mm in diameter) and may be dehiscent. Lastly, plants that have coevolved with ants as seed dispersers have external reward structures known as elaiosomes that are relatively discrete characters that are provided in exchange for a dispersal service.

Dispersal modes are broad ways to characterize seed dispersal, but dispersal vectors are more precise, as they identify specific guilds of dispersers. Dispersal vectors, as opposed to modes, are relatively less discernable, with the exception of myrmecochorous plants that are relatively easy to distinguish with the incidence of an elaiosome as a binary character. Frugivorous plants can be grouped into three types of dispersal vectors: mammals, birds, or both birds and mammals. In North America, mammals refers to medium-to-large mammals that have generalist diets and incidentally are almost always carnivores. The fruits that are exclusively dispersed by mammals have dark coloration (e.g., brown, green) and are large (generally 5–10+ cm in diameter). Bird frugivory as a vector refers to birds that eat fruit that have evolved fruit smaller than bird

gapes (generally < 12 mm in diameter) that are scattered on the plant, usually in trees where it is difficult for mammals to access. Both bird and mammal vectors are the most common vector of frugivory. The fruits of the plants that coevolved with both birds and mammals usually are an amalgam of the previously described characteristics. Lastly, plants that are scatter-hoarded can have either rodent vectors alone (e.g., walnuts) or can be hoarded by both rodents and birds (e.g., certain *Pinus*). Because plants can be diplochorous (i.e., have two-phased dispersal), we included plants whose diaspores are primarily dispersed by abiotic vectors and secondarily dispersed by hoarders or ants. The diaspore characteristics still match our description above for myrmecochory and hoarding, but have a different presentation to the animals, such as a samara for primary wind dispersal or primary ballistically dispersed diaspores with elaiosomes. We chose to include these diplochorous plants and identify them as distinct because it is respectively a case of plant adaptation to animal dispersal (i.e., the objective of the study). The combination of vectors including both primary and secondary means of dispersal we call dispersal pathway, as it is the fullest and most precise description of the putatively coevolved mutualism.

Abiotic data were collected for each site. We gathered data from the source publication when possible, but supplemented missing data for site area, median latitude (hereafter latitude), median longitude (hereafter longitude), minimum elevation, and maximum elevation from GoogleEarth, and mean annual precipitation (hereafter precipitation) from the nearest RAWS USA Climate Archive (<http://www.raws.dri.edu/index.html>). For precipitation, we chose to use the longest-term average value we could obtain. Two derived abiotic data that we chose to use were

elevational range and median elevation (hereafter elevation). Elevational range is a relatively strong proximate measure of habitat diversity, which we can include as a within-site variable representing site heterogeneity, and median elevation relates to productivity at a site. Lastly, each site was assigned to a climate type of either arid, semi-arid, mesic, or hydric.

We collected taxonomic, growth habit, and longevity data on each species from the PLANTS database (USDA, NRCS 2014). The taxonomic groupings included division, category (dicotyledonous or monocotyledonous), class, order, and family. The growth habits (forb/herb, graminoid, shrub, subshrub, tree, vine) and longevity (annual, biennial, perennial) were reduced into five groups for this study: annual, graminoid, perennial herb, succulent, and woody for functional purposes.

Data manipulation and analysis

For this study we aimed to investigate the distribution of plants with seed-dispersal mutualisms, and therefore excluded non-native plants. We chose to exclude these taxa because they are not a result of historical ecological and evolutionary processes within the spatial extent of the study, and would potential obscure our findings because non-native taxa's establishment is often a result of other historical contingencies like length of Western settlement and propagule pressure. Conceding that analyzing non-native taxa would likely demonstrate the contemporary strength of seed-dispersal mutualisms, that is an investigation beyond the scope of the current study. Secondly, we chose to exclude aquatic plants because their dispersal mechanisms are less understood and plant lists often excluded aquatic plants.

We included area (ha), latitude (dd.dd), longitude (dd.dd), precipitation (cm × year⁻¹), median elevation (m), and elevational range (m) as predictor variables. Site area, precipitation, elevation, and elevational range were log₁₀-transformed to conform to the requirements of subsequent statistical analyses. Given the nature of our sampling scheme (site incidence data), we were unable to standardize taxon sampling curves and therefore had to make several assumptions: (i) sampling effort was the same across sites, (ii) sampling effort was high enough that we were sampling from the asymptote of the species sampling curves, and (iii) densities of individuals samples were the same across sites (sensu Gotelli and Colwell 2001, 2011). The former two are reasonable assumptions, but the latter is unknowable as to if and how it influenced our results. Because we are aware that there is a species-area relationship (Arrhenius 1921, Rosenzweig 1995), we chose to standardize for it by dividing the response variable by log₁₀(area) to standardize sampling effort, despite the pitfalls (Gotelli and Colwell 2001, 2011), because we were comparing between sites rather than generating a precise estimate of richness.

The main response variables included area-adjusted numbers of species, non-mutualists, mutualists, three dispersal modes (frugivory, hoarding, myrmecochory), and 14 dispersal pathways. We standardized response variables into z-scores and found no significant differences for all analyses when using proportion of mutualists per site or total number of mutualist taxa, and chose to report the latter because coevolution should be relatively independent of the total non-mutualist taxa in a community. None of the response variables, being counts of mutualists, modes, or pathways, needed to be log₁₀-transformed to fit assumptions of normality for subsequent statistical analyses after

adjusting for sample effort (area). Lastly, niche conservatism likely has an effect but we were unable to phylogenetically adjust for all 14,211 taxa in the study, so we chose to ignore it.

Another set of response variables was derived to compare the number and types of interactions across sites. We adapted the type-abundance framework commonly used for species abundance distributions for the 14 interaction types (i.e., dispersal pathways) as a bivariate (McGill et al. 2007), parametric (McGill 2011) method to capture interaction diversity within and between sites and minimizing the loss of information by the use of univariate, non-parametric metrics of diversity (e.g., variants of S , D , E , C , R). The abundance of interactions were \log_{10} transformed and ranked descending across the x axis to allow interpretation beyond the slope (the decrease in abundance-by-type). Namely, the y -intercept would be interpreted as the abundance of the most abundant interaction type (a measure of dominance) and the x -intercept interpreted as the number of interaction types (a measure of richness). Both of these were highly correlated with the actual measured value (see results). The empirical cumulative distribution function has been proposed to use for rank abundance-type analyses because of its statistical properties (McGill 2011). But because our hypothesis concerns the aforementioned parameters of the linear model (namely, the x -intercept) that would be lost if we used any cumulative distribution function and the shape of the distribution is ancillary, we chose to use the rank abundance-type. The rank abundance-type framework has been used for species abundance distributions, and the extension to interactions we call interaction abundance distributions (IAD).

We assessed non-independence of samples in two ways: (i) spatial autocorrelation and (ii) community similarity. Spatial non-independence was largely avoided by both choosing sites that were distant and sites that did not have species overlap. With our main response variables (species, non-mutualists, mutualists), we confirmed spatial independence by finding only one statistically significant lag using Moran's I (fifth order, $I_{obs} = 0.0706$, $I_{exp} = 0.00512$, $P(I) < 0.05$; Figure 1), which we interpret as spurious. Because of this, we chose to not include a spatial autocorrelation covariate in our statistical models. We did, however, analyze spatial similarity separately as a way to determine if there were differences between the spatial distribution of different kinds of mutualism. We secondly assessed non-independence by calculating the Sørensen-Dice coefficient (β_{sor} , for incidence-type data) for all sites. No sites had an intersection of both a high β_{sor} and close distance (Figure 2), so we chose to keep all sites in the remaining analyses.

Principal component analysis (PCA) was used as an indirect gradient analysis to orthogonally decompose data into axes that maximally explain variation in the data for our response variables across sites. Additionally, factor analysis using variance maximization (varimax) and optimal coordinates, as a non-graphical solution to determine the number of factors to retain (Ruscio and Roche 2012), were used to determine the number of factors to retain. The PCA dimensions that explained more than 10% of the variance were regressed using linear multiple regression to determine what predictor variables correlated with the various response variables. General linear models were used to assess the relationship between latitude and predictor variables, which included linear regression and analysis of covariance (ANCOVA). Multiple linear

regression was conducted to contrast the univariate response variables to the predictors. Minimum adequate model selection was performed by reverse stepwise regression by eliminating variables that did not statistically correlate with the response variables, for both standardized and unstandardized data.

RESULTS

The dataset contained 123,359 seed plant records from 197 sites. Taxonomically, this spanned 3 divisions, 5 classes, 74 orders, 202 families, 2,003 genera, and 14,211 species. The growth habit distribution of records included 12,133 annuals, 24,206 graminoids, 62,470 perennial herbs, 909 succulents, and 20,641 woody plants. Table 1 shows the distribution of records by both growth form and dispersal pathway. Overall, there were 20,384 records with seed dispersal mutualisms and 102,975 records of plants without a seed dispersal mutualism, meaning that approximately that 16.5% of the plants across temperate North America have seed dispersal mutualisms. Of those records with mutualisms, including some overlap because of diplochory, there were 12,302 incidences of plants with a frugivory mutualism, 4,583 incidences of plants with a scatter-hoarding mutualism, and 4,862 incidences of plants with a myrmecochory mutualism. Figure 3 shows the records for each of the 14 dispersal pathways. Frugivory by birds/mammals is more than twice as common ($\bar{x} = 7.6, s = 3.8\%$) as the next most abundant dispersal pathway, myrmecochory ($\bar{x} = 2.8, s = 1.6\%$). The least abundant dispersal pathway was two-phased, of primary dispersal by frugivorous birds and then secondary dispersal by myrmecochory ($\bar{x} = 0.02, s = 0.08\%$). Seeds dispersed by frugivores are often secondarily dispersed by scatter-hoarding animals, and diplochory accounted for 14.5%

of all mutualisms. Figures 4 and 5 show the geographic distributions of our site locations and main response variables. Figure 4 shows that the patterns of total species very closely resembling the non-mutualists, whereas mutualists are distributed largely in the eastern United States, around the Great Lakes, and on the Mexico-United States border. The upper row in Figure 5 shows frugivory and scatter-hoarding as being rich in the eastern United States, with scatter-hoarding more diverse in the southwest. Myrmecochory is largely most diverse in Appalachia and the Great Lakes region. The bottom row in Figure 5 shows the geographic distribution of the interaction abundance distributions (IADs). There was less variation in the y - and x -intercepts, and the most prominent visual pattern is along the latitudinal gradient. Similarly, the Coefficient showed a strong latitudinal decline.

We used rank type-abundance distributions as a bivariate, parametric mean to assess interaction abundance distributions of the 14 dispersal pathways. The log-linear abundances fit linear models well, with $\bar{x} = 0.910$ and $s = 0.053$ of the adjusted coefficient of determination, R^2 . Table 2 shows parametric (Pearson's product-moment correlation coefficient, r) and non-parametric (Spearman's rank correlation coefficient, ρ) correlations between the interpreted parameters of the IAD (y -intercept, Coefficient, and x -intercept) and univariate measures of biodiversity, including the Shannon index (H'), the Simpson Index (D), Hill's numbers (N_{0-2}), and Pielou's evenness (J'). Within the IAD parameters, the x - and y -intercepts strongly correlated ($r = 0.821$, $\rho = 0.801$). Between the IAD parameters and other univariate measures, the x -intercept was highly correlated with richness ($S-1$, N_0 ; $r = 0.861$, $\rho = 0.849$), the Coefficient was correlated with the

Shannon index ($r = 0.757$, $\rho = 0.744$) but not Pielou's evenness ($r = 0.235$, $\rho = 0.367$), and the y -intercept was only slightly correlated with richness ($r = 0.681$, $\rho = 0.698$).

Bivariate linear relationships between latitude and the major groups of response variables are found in Table 3 and Figure 6. There were statistically significant relationships ($P < 0.05$) between latitude and species ($F_{1,193} = 35.04$), non-mutualist plant species ($F_{1,193} = 32.04$), mutualist plant species ($F_{1,193} = 21.31$), plants with frugivory ($F_{1,193} = 20.59$), plants with scatter-hoarding ($F_{1,193} = 85.42$), the y -intercept of the IAD ($F_{1,193} = 14.41$), the coefficient of the IAD ($F_{1,193} = 145.8$), and the x -intercept of the IAD ($F_{1,193} = 97.83$). The only major response variable to not show a statistically significant relationship ($P > 0.05$) with latitude was myrmecochory ($F_{1,193} = 0.47$). Two ANCOVAs were performed to assess the relationship of latitude and between non-mutualist and mutualist plant species (Figure 7B), and between species and interaction richness (Figure 8) on standardized score values to meet the assumptions of homoscedasticity. There were no differences between the slopes of non-mutualist and mutualist plants ($F_{1,386} = 0.4215$, $P > 0.517$), but significant difference between the slopes of species richness and interaction richness ($F_{1,386} = 0.4215$, $P = 0.034$).

PCA for the three dispersal modes as variables revealed PC1 explaining 82.9% (eigenvalue, $\lambda = 2.462$), PC2 explaining 13.4% ($\lambda = 0.403$), and PC3 explaining 4.5% ($\lambda = 0.135$) of the variance (Figure 9). The loadings were highly correlated with PC1, where each variable loading was $w_{\text{frugivory}} = 0.96$, $w_{\text{scatter-hoarding}} = 0.89$, and $w_{\text{myrmecochory}} = 0.87$. PCA and factor analysis results for the 14 dispersal pathways can be found in Table 4 and Figure 10. There were three optimal components for the factor analysis, which explained 64% of the variation of the data. All dispersal pathway variables had at least one factor

loading > 0.50, except for the pathway of primary dispersal by frugivorous birds and secondarily by ants. The first factor was characterized by ballistic dispersal, general bird/mammal frugivory, and myrmecochory. The second factor was characterized by primary dispersal by scatter-hoarding and specific frugivory of birds and mammals. Similarly, PCA revealed that the first three components each explained > 10% of the variance, and 71% overall. Many of the variables were correlated, with somewhat of a dichotomy in PC2. These groups were the same ones identified by the factors analysis.

Multiple linear regression with the multivariate dispersal mode components as response variables and three predictor variables (latitude, precipitation, and elevation range), found that PC2 ($F_{3,191} = 40.3$, $R^2 = 0.38$, $P < 0.05$) had a better overall fit than PC1 ($F_{3,191} = 28.3$, $R^2 = 0.30$, $P < 0.05$). PC1 found latitude ($\beta_{\text{latitude}} = -0.056$, $t = -4.642$) and precipitation ($\beta_{\text{precipitation}} = 2.341$, $t = 7.139$) to have slopes significantly different than zero, whereas PC2 found all to be different ($\beta_{\text{latitude}} = 0.042$, $t = 9.203$; $\beta_{\text{precipitation}} = 0.593$, $t = 4.759$; $\beta_{\text{elevation range}} = 0.168$, $t = 3.503$). Similarly, dispersal pathways showed the strongest relationship with the second component ($F_{3,191} = 43.7$, $R^2 = 0.40$, $P < 0.05$) compared to the first ($F_{3,191} = 28.8$, $R^2 = 0.30$, $P < 0.05$) and the second ($F_{3,191} = 29.8$, $R^2 = 0.31$, $P < 0.05$). The second component also found all slopes of the predictor variables to be different than zero ($\beta_{\text{latitude}} = -0.114$, $t = -9.430$; $\beta_{\text{precipitation}} = -1.601$, $t = -4.835$; $\beta_{\text{elevation range}} = -0.508$, $t = -3.987$), the first found latitude ($\beta_{\text{latitude}} = -0.084$, $t = -4.677$) and precipitation ($\beta_{\text{precipitation}} = 3.282$, $t = 6.651$) to be different than zero, and the third found latitude ($\beta_{\text{latitude}} = 0.060$, $t = -6.043$) and elevation range ($\beta_{\text{elevation range}} = 0.784$, $t = 8.054$) to be different than zero.

Results of the multiple linear regression on the main nine univariate response variables can be found in Table 5. We chose to report the minimum adequate model (MAM) using step-wise removal of predictor variables with the lowest *t*-value with $P > 0.05$. The MAMs with the lowest coefficient of multiple determination (R^2) were species ($R^2 = 0.218$) and non-mutualists ($R^2 = 0.202$), both of which included latitude, precipitation, and elevation range. Mutualist species fit a MAM with all variables with $R^2 = 0.461$. The highest amount of variation explained by all of the response variables was the *x*-intercept of the IAD (interpreted as the number of interactions) with $R^2 = 0.525$ with all predictor variables included in the model. Of the predictor variables, latitude was the only one to appear in all MAMs. Elevation showed a significant response in eight of the models, precipitation in seven, and both median elevation and longitude in five of the nine models.

DISCUSSION

Seed dispersal mutualisms showed different responses to environmental gradients. Frugivory showed the strongest relationship with precipitation and scatter-hoarding responded most strongly to latitude. We expected the observed positive relationship between fleshy-fruited plants that are dispersed by frugivorous animals and precipitation (Jordano 2000, Almeida-Neto et al. 2008), but we were less sure what to expect given the distribution and diversity of succulents in the arid southwestern United States (but see Bronstein et al. 2007). Of the 909 records of succulents, 53% were dispersed by frugivorous animals, and did not seem to disproportionately increase the amount of frugivory in arid environments. Scatter-hoarded plants were most abundant in the eastern

and the southwestern United States. They showed a strong negative relationship with latitude because above 50° there are very few plants dispersed by scatter-hoarding animals in our dataset. For both frugivorous and scatter-hoarded plants, it would be interesting to extend the geographic scope of this study into subtropical Mexico because both abundances began to increase on the border. Myrmecochorous plants were the most abundant in the Great Lakes region and Appalachia. Myrmecochorous plants made of 56% of perennial herb dispersal by animals, which correlated with the presence of perennial herb diversity ($F_{2,192} = 39.36$, $R^2 = 0.28$, $P < 0.05$).

We quantified interaction diversity along several environmental gradients known to covary with species diversity (Pianka 1966, Willig et al. 2003, and references therein). Our goal was not to determine the actual mechanisms, but rather, identify patterns of interaction diversity along environmental gradients. In recent years, there have been calls to the attention of these patterns, as they have largely been missing from empirical research (e.g., see Schemske et al. 2009, Dyer et al. 2010). We believe that these data provide reliable estimates of one type (seed dispersal) of interaction (mutualism). The observed patterns may have been predicted *a priori*, but here we quantify them. For instance, median elevation was found to be a significant predictor of the number of mutualist plant species, the number of the most abundant interaction type (IAD y -intercept), and the total number of interaction types (IAD x -intercept) at a given site. The relationship was negative, which would support the idea that at higher elevations environmental stochasticity may play a role in shaping communities by filtering out species that depend upon the presence of another species, like in a mutualistic interaction. Latitude was another gradient where we expected a relationship with mutualisms

(Willson et al. 1990, Ollerton et al. 2006, Moles et al. 2007), and it was the only variable to be found as statistically significant in each multiple regression model for all species, mutualists, non-mutualists, and all IAD metrics. Because the sites in our study spanned ~ 50° latitude and it was a significant predictor variable for all mutualist response variables, we are confident in our result that there is a strong relationship between seed-dispersal mutualisms and latitude. Precipitation was a variable that we expected to be statistically significant in all of the models, but was only found in seven of the nine (Table 5). The two response variables that were not found to be significant were scatter-hoarding and the IAD coefficient (evenness). Not finding a relationship with scatter-hoarding is intuitive because it occurs not only in areas where primary productivity and precipitation are high, but it also occurs in areas where precipitation is low and plants allocate energy to seeds for embryos to survive harsh climates (Westoby et al. 2002), like the arid southwestern United States, and burial of large seeds is important in seedling establishment (e.g., Beck and Vander Wall 2010). The other response variable that did not show a relationship with precipitation is the IAD coefficient. We attribute this largely to the large variation in interaction richness (x -intercept) affecting the shape of the slope.

This study sheds light on some ecological differences between animal- and abiotically-dispersed plants. Historically there has been incongruity between observed dispersal dynamics from an individual or population perspective and patterns at larger spatiotemporal scales, which has been largely been alleviated mathematically (Skellam 1951, Clark 1998). It is important, however, to acknowledge that not all dispersal mechanisms provide the same quality of dispersal (e.g., distance, site deposition). For instance, Montoya et al. (2008), showed that data from 90,000 plots of 34 species across

Spain, that animal-dispersed species were less sensitive to habitat loss. In Montoya et al. (2008), animal-dispersed plants were better able to recolonize areas from where they were once extirpated, compared to otherwise ecologically equivalent species. In our study, we found a surprising result that animal-dispersed plants did not follow the seemingly invariant species-area relationship (SAR; $\beta = 0.019$, $t = 0.837$, $P = 0.404$; Figure 11). Similar to Montoya et al.'s study, this suggests that animal-dispersed plants may be more robust to spatial limitations because dispersal is less a stochastic process than for those plants with abiotic vectors. Additionally, plants that are dispersed by animals show a stronger relationship with latitude and precipitation. Brown (2014) posited from a kinetic perspective that we would expect more diversity at lower latitudes due to higher and faster rates of species interactions and thus coevolution. This is not a new perspective for those who study mutualisms, as guild coevolution has often been evoked for explanations of angiosperm diversity (Tiffney 2004, Lorts et al. 2008 , but see Herrera 1989) and the largest network analysis to-date found that generalist mutualistic interactions are more common at lower latitudes (Schleuning et al. 2012).

Species diversity has predominantly been of interest in studying global biodiversity. In this study, we aimed to contrast species diversity with interaction diversity by looking at a subset of mutualistic interactions, seed dispersal, to test the hypothesis that they are the same. Although species and interaction diversity tended to covary, the response of interaction diversity tended to be more pronounced across all environmental gradients (e.g., latitude in Figure 8; Table 5). This leads us to conclude that although species and interaction diversity covary, they do so synergistically. This supports the idea that diversity begets diversity because "the Red Queen runs faster when

she is hot" (Brown 2014). Of secondary interest was the number of mutualists and non-mutualists, and their relationship across environmental gradients. Similar to species and interaction diversity, these two responses tended to covary (Figure 7), but we were able to explain less of the non-mutualist group with abiotic variables (Table 5). Lastly, our approach using interaction abundance distributions (IADs) to describe interaction type-abundance relationships seemed to be an adequate way to compare interaction diversity between communities. The results interpreted from IAD (i.e., y -intercept, coefficient, x -intercept) seemed not to be entirely concordant with the analogous traditional univariate measures of diversity (C , J , S ; Table 2), but there was less loss of information in decomposing the two-dimensional distribution into a univariate index.

Our measure of interaction diversity is a new approach to examining the abundance and distributions of ecological interactions. Decomposing the abundant-type distributions into a single metric of biodiversity seemed theoretically insufficient because of the loss of information, and because it is empirically less intuitive and malleable than simple linear modeling. In this study, we chose to ignore fitting the precise, non-linear shape of the curves. The precise shapes of species abundance distributions can be predicted from primary physical (Sharma and Annila 2007, Würtz and Annila 2008) and statistical (Frank 2009, 2011, Harte 2011) principles, but there is a lack of theory on the number and abundances of ecological interactions (Brown 2014).

Mutualistic interactions are fundamentally different types of interactions than those most commonly examined and are the bases for ecological theory (e.g., Thébaud and Fontaine 2010); namely, competition and parasitism. The recent incorporation of mutualistic and other positive interactions into ecological theory has perturbed our

understandings of some of the most fundamental ecological concepts (e.g., Bruno et al. 2003, Bastolla et al. 2009, Chamberlain et al. 2014). Schemske et al. (2009) highlight that all interactions (e.g., predation, mutualism) increase with frequency at lower latitudes. It would be interesting to compare the distributions of trophic interactions compared to mutualistic interactions across latitudinal and other environmental gradients.

Coevolution and ecological interactions are respectively ultimately and proximately responsible for the patterns observed in this study. Over evolutionary history, guilds of dispersers with correlated behaviors have been shown to influence diasporae (the dispersing unit) morphology (Lomáscolo et al. 2008, Lomascolo et al. 2010, Valido et al. 2011). Although coevolution has putatively shaped diasporae traits, ecological interactions must have taken place to recently disperse the plants to their current locations. The Quaternary may be the most relevant timescale in which to consider a long-term ecological view of processes shaping contemporary communities through extinction, colonization, and demographic cycles. This period is defined by a dynamic climate with repeated interglacial cycles, including eight in the last 750,000 years (Augustin et al. 2004). The most recent glacial advance, the Last Glacial Maximum (LGM), was 26–20K years ago (Clark et al. 2009). At that time, all of the eastern United States was either taiga or some open boreal woodlands, and the western United States was largely forest steppe and semi-arid temperate woodland or scrub (Ray and Adams 2001). Most of the species distributions that we observe today, therefore, are likely a result of colonization of these areas since the LGM, given the drastically different climatic conditions. If plants had to disperse during interglacial cycles and animal-dispersal a more robust dispersal mechanism, then that might explain why there are more

animal-dispersed plants in the eastern United States. Namely, because during these interglacial cycles the eastern United State cycles does not have continuous southern habitat to which plants can migrate and could therefore possibly go extinct (e.g., Jackson and Weng 1999), unlike the western United States.

Our comparison of plants with seed-dispersal mutualisms has been enlightening. We have demonstrated the relationships between various types of seed-dispersal mutualisms across several environmental gradients. Most notably, we found that interaction and species diversity decrease with latitude, but the former at a faster rate. We also found that different dispersal modes (frugivory, scatter-hoarding, myrmecochory) and patterns of plants with and without seed dispersal mutualisms corvaried differently with different abiotic variables. Lastly, we were also able to describe the proportion of seed dispersal mutualism modes and specific 14 dispersal pathways for all seed plants in a large sample (200 sites; 14,000 native, terrestrial species) across the North American continent.

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Chapter 3, Table 1. Comparison of records of dispersal pathways by growth habit across North America.

Primary mode		Abiotic		Ballistic		Frugivory				Hoarders				Myrmecochory		Wind							
Primary vector		N/A		Rodents		Ants		Bird/mammal		Birds		Mammals		Birds/rodents		Rodents		Ants		Birds/rodents		Rodents	
Secondary vector		N/A		Rodents		Ants		N/A		Rodents		Ants		N/A		Rodents		N/A		Birds/rodents		Rodents	
Primary mode	Annual	14044	25	93	137	0	1	0	0	93	0	0	140	600	0	0	0	0	15133				
Primary vector	Graminoid	23669	0	0	0	0	0	0	0	0	0	0	0	482	0	0	0	0	24206				
Secondary vector	Perennial herb	55111	0	1247	2839	0	68	0	30	445	0	0	424	2306	0	0	0	0	62470				
	Succulent	368	0	0	130	0	9	0	0	340	0	0	62	0	0	0	0	0	909				
	Woody plant	9783	58	7	6445	846	324	119	0	108	368	1165	1143	97	130	48	130	48	20641				
Totals		102975	83	1347	9551	846	402	119	30	986	368	1165	1824	3485	130	48	130	48	123359				
Primary mode	Primary vector	102975	1430																	123359			
Secondary vector																				18776			
																				2971			

Chapter 3, Table 2. Correlations within interaction abundance diversity (IAD) regressions and between univariate measures of diversity. In this study, the y -intercept is interpreted as the abundance of the most abundant interaction; the coefficient as the rate of abundance-interaction decay (or evenness); and the x -intercept as the number of interactions. The upper panel is the Pearson product-moment correlation (r) and the lower panel is the Spearman's rank correlation coefficient (ρ).

	y -intercept	Coefficient	x -intercept	H'	D	N_0	N_1	N_2	J
y -intercept		0.070	0.821	0.210	0.032	0.681	0.143	-0.102	-0.610
Coefficient	-0.169		0.531	0.757	0.668	0.579	0.719	-0.707	0.235
x -intercept	0.801	0.384		0.592	0.379	0.861	0.546	-0.431	-0.335
H'	0.016	0.744	0.429		0.935	0.633	0.984	-0.932	0.296
D	-0.137	0.592	0.197	0.914		0.381	0.934	-0.982	0.556
N_0	0.698	0.338	0.849	0.358	0.114		0.571	-0.440	-0.479
N_1	0.016	0.744	0.429	1.000	0.914	0.358		-0.903	0.380
N_2	0.137	-0.592	-0.197	-0.914	-1.000	-0.114	-0.914		-0.471
J	-0.601	0.367	-0.331	0.494	0.685	-0.513	0.494	-0.685	

Chapter 3, Table 3. Ordinary least square estimates of major response variables and latitude. All slopes were found to be statistically different than zero, except myrmecochory. Myrmecochorous plant species were relatively abundant in Appalachia and south of the Great Lakes. The strongest pattern, and only one that positively covaried with latitude, was the rank interaction abundance distribution coefficient. This demonstrates that there was a strong decrease in the number of interaction abundance across types at higher latitudes.

	Coefficient	Standard Error	t-value	P > t	Adjusted R ²
Species	-2.51	0.42	-5.92	0.00	0.15
Non-mutualists	-1.99	0.35	-5.66	0.00	0.14
Mutualists	-0.52	0.11	-4.62	0.00	0.09
Modes					
Frugivory	-0.31	0.07	-4.54	0.00	0.09
Hording	-0.22	0.02	-9.24	0.00	0.30
Myrmecochory	-0.02	0.04	-0.69	0.49	0.00
Interaction abundance distribution					
y-intercept	-0.01	0.00	-3.80	0.00	0.06
Coefficient	0.01	0.00	12.07	0.00	0.43
x-intercept	-0.12	0.01	-9.89	0.00	0.33

Chapter 3, Table 4. Principal component and factor analysis results for 14 dispersal pathways. There were three optimal components for the factor analysis, which explained 64% of the variation of the data. All dispersal pathway variables had at least one factor loading > 0.50, except for the pathway of primary dispersal by frugivorous birds and secondarily by ants. Similarly, the first three PCs explained greater than 10% of the data. The PCs were used in regression to determine what environmental variables correlate with the groups of response variables described in this analysis (see the results).

Dispersal pathway	Factor analysis			PCA		
	Factor 1	Factor 2	Factor 3	Dim 1	Dim 2	Dim 3
Percent of variance explained	29.9	25.1	9.5	40.1	21.0	10.6
Cumulative percent of variance	29.9	55.0	64.5	40.1	61.0	71.7
Ballistic, hoarding-rodents	0.71			0.77	-0.27	-0.21
Ballistic, myrmecochory	0.83			0.59	-0.60	0.24
Frugivory-birds/mammals	0.82	0.45		0.93	-0.18	-0.03
Frugivory-birds/mammal, hoarding-rodents	0.68			0.52	-0.52	0.29
Frugivory-birds		0.57		0.22	0.63	0.40
Frugivory-birds, hoarding-rodents	0.69	-0.32		0.72	0.35	-0.20
Frugivory-birds, myrmecochory			0.09	-0.39	0.51	
Frugivory-mammals	0.75			0.43	0.71	0.22
Frugivory-mammals, hoarding-rodents	0.79			0.68	0.53	-0.08
Hoarding-birds/rodents	0.31	0.80		0.76	0.40	0.08
Hoarding-rodents	0.31	0.73		0.73	0.37	0.26
Myrmecochory	0.88			0.86	-0.34	-0.01
Wind, hoarding-birds/rodents		0.89		-0.30	-0.13	0.82
Wind, hoarding-rodents	0.80			0.62	-0.54	-0.22

Chapter 3, Table 5. Minimum adequate multiple regression models of the nine response variables and five predictor variables. Unstandardized and standardized coefficients are reported. All models and predictor variables included had a $P < 0.05$, and the degrees of freedom ranged between 2–5 and 189–192.

Response variable	Predictor variables	Coefficient	Standardized coefficient	t-value	F-value	Adjusted R ²
Species	Latitude	-0.003	-0.418	-6.375	19.07	0.218
	Precipitation	41.229	0.245	3.587		
	Elevation range	15.772	0.248	3.565		
Mutualist	Latitude	-0.327	-0.197	-3.307	34.13	0.461
	Longitude	-0.285	-0.406	-5.969		
	Precipitation	12.433	0.286	4.554		
	Elevation range	4.638	0.283	3.877		
	Median elevation	-0.003	-0.228	-2.904		
Non-mutualist	Latitude	-2.257	-0.427	-6.450	17.37	0.202
	Precipitation	20.335	0.147	2.127		
	Elevation range	15.130	0.289	4.112		
Frugivory	Latitude	-0.167	-0.165	-2.858	38.72	0.493
	Longitude	-0.182	-0.424	-6.435		
	Precipitation	7.553	0.284	4.666		
	Elevation range	1.982	0.198	2.793		
	Median elevation	-0.002	-0.217	-2.846		
Scatter-hoarding	Latitude	-0.214	-0.534	-8.697	37.15	0.427
	Longitude	-0.037	-0.217	-3.192		
	Elevation range	0.982	0.248	3.297		
	Median elevation	-0.001	-0.330	-4.239		
Myrmecochory	Latitude	-0.089	-0.431	-6.263	36.34	0.353
	Longitude	4.811	0.376	5.701		
	Precipitation	1.651	0.342	5.190		
y -intercept	Latitude	-0.005	-0.168	-2.735	30.01	0.428
	Longitude	-0.004	-0.295	-4.218		
	Precipitation	0.348	0.430	6.654		
	Elevation range	0.090	0.295	3.929		
	Median elevation	0.000	-0.165	-2.039		
Coefficient	Latitude	-0.006	-0.686	-12.349	76.64	0.438
	Elevation range	0.010	0.121	2.172		
x -intercept	Latitude	-0.109	-0.168	-9.621	43.80	0.525
	Longitude	-0.016	-0.295	-2.994		
	Precipitation	1.558	0.430	4.976		
	Elevation range	0.576	0.295	4.197		
	Median elevation	0.000	-0.165	-2.662		

Chapter 3, Figure 1. Spatial non-independence within plant species, non-mutualist plant species, and mutualist plant species. The correlograms (top row) and nearest-neighbor (bottom row) analyses failed to detect significant spatial autocorrelation in these variables. Although, the mutualist plant species' correlogram and first-order neighbor does show a non-significant positive relationship. The asterisk indicates a statistically significant fifth order neighbor of non-mutualist plants that we interpret at spurious.

Chapter 3, Figure 2. Sørensen-Dice coefficient for 197×197 sites. No sites were to be too close and similar to be eliminated from our analysis.

Chapter 3, Figure 3. We identified 14 dispersal pathways for 20,384 records of plants with a seed dispersal mutualism with animals. The width of the arrows is proportional to the number of records of all seed plants. The most common seed dispersal pathway is frugivory by birds and mammals, and the least is primary dispersal by frugivorous birds with secondary dispersal by ants. Modes are in similar colored boxes and vectors are italicized under the mode type. Myrmecochorous plants are only dispersed by ants, so the vector is not indicated in that box.

Chapter 3, Figure 4. Geographic distributions of the sites used in the study, and scaled relative densities of all species, species without a seed dispersal mutualism, and species with seed dispersal mutualisms. Species and non-mutualist richness declines with latitude, and mutualist plants have highest richness at southern latitudes and eastern longitudes.

Chapter 3, Figure 5. Geographic distributions of the scaled relative densities of dispersal modes (top) and interaction-abundance parameters (bottom) across North America. Frugivory is the most abundant type of seed dispersal mutualism. Patterns of frugivory

and scatter-hoarding are similar by being relatively abundant in the eastern United States, but scatter-hoarding is slightly more abundant in the southwestern United States-Mexico border. The interaction-abundance parameters can be interpreted as follows: the y -intercept is the most abundant type of interaction, the coefficient is the rank abundance decay, and the x -intercept is the number of interaction types. The most abundant type of interaction types negatively covaries with latitude and the highest values are along the eastern United States. The coefficient positively covaries with latitude. The number of interactions also negatively covaries with latitude.

Chapter 3, Figure 6. Bivariate relationships between the major response variables and latitude. Points are sites and the shaded areas are 95% confidence intervals of the least squares estimate of the slopes (Table 2). All were statistically significant except for myrmecochory, and all significant response variables negatively covaried with latitude except for the coefficient (interaction type-abundance decay).

Chapter 3, Figure 7. The relationship of latitude and richness of non-mutualist (diamonds) and mutualist plants (triangles). There are fewer species with mutualists ($\bar{x} = 23.6, s = 182.4$) than non-mutualists ($\bar{x} = 115.8, s = 1,853.7$; left). Because of heteroscedasticity between these groups, richness values were score standardized (right) and there was no statistical differences between the slopes of plants with and without seed dispersal mutualists across latitude (right). The shaded areas are 95% confidence intervals of the least squares estimate of the slopes for 195 sites.

Chapter 3, Figure 8. The relationship between species richness (diamonds) and interaction richness (triangles) at each site. Standardized scores were used because of heteroscedasticity between these groups ($\bar{x}_{\text{species}} = 139.4, s_{\text{species}} = 2,736.1; \bar{x}_{\text{interactions}} =$

$5.5, s_{\text{interactions}} = 2.7$). An analysis of covariance detected a significant difference between the slopes ($F_{1,386} = 0.4215, P = 0.034$). The shaded areas are 95% confidence intervals of the least squares estimate of the slopes for 195 sites.

Chapter 3, Figure 9. Principal component analysis for the three dispersal modes, frugivory, scatter-hoarding, and myrmecochory. The three components respectively explained 82.8, 13.4, and 4.5% of the variance, with the majority explained by not differentiating the three modes. The bottom and left axes of the PCA biplot correspond to the PCA scores, and the top and right axes correspond to the PCA loadings.

Chapter 3, Figure 10. Principal component analysis for the 14 dispersal pathways. The first three components each explained $> 10\%$ of the variance, and 71% overall. Many of the variables were correlated, with somewhat of a dichotomy in PC2. The bottom and left axes of the PCA biplot correspond to the PCA scores, and the top and right axes correspond to the PCA loadings.

Chapter 3, Figure 11. The relationship between plants without (red diamonds) and with a seed-dispersal mutualism (blue triangles). We found a surprising result that animal-dispersed plants did not follow the seemingly invariant species-area relationship ($\beta = 0.019, t = 0.837, P = 0.404$; Figure 11). The shaded areas are 95% confidence intervals of the least squares estimate of the slopes.

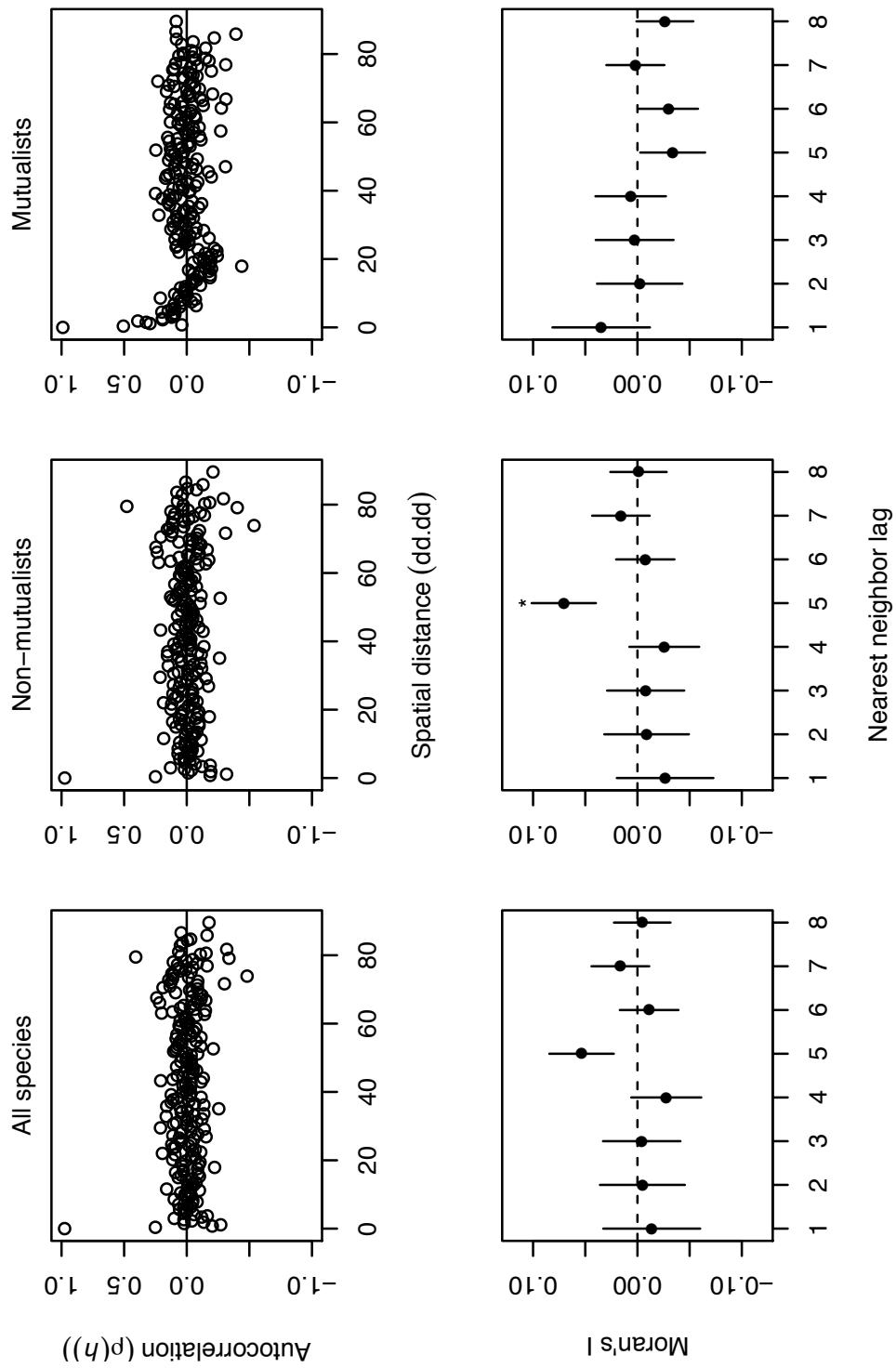


Figure 1.

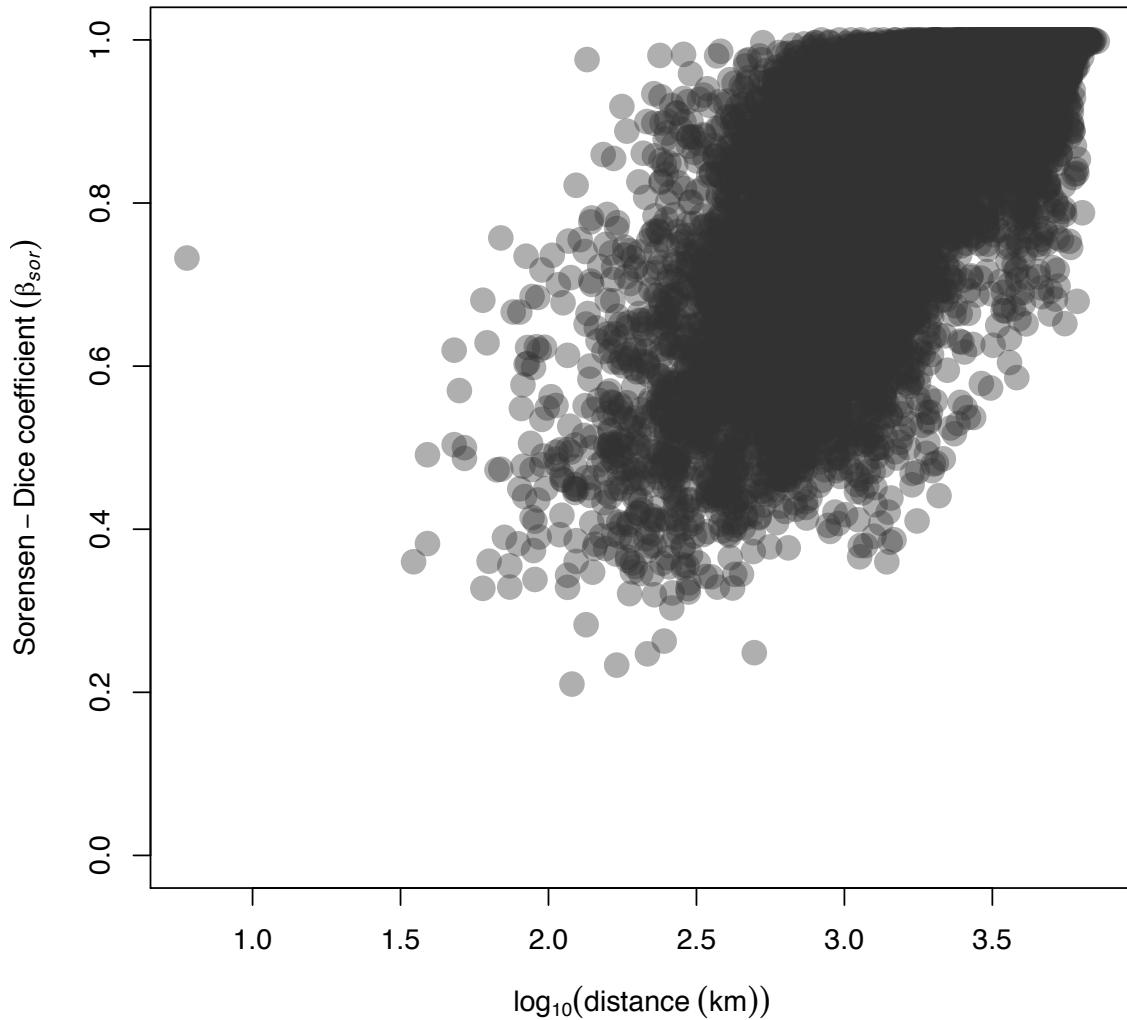


Figure 2.

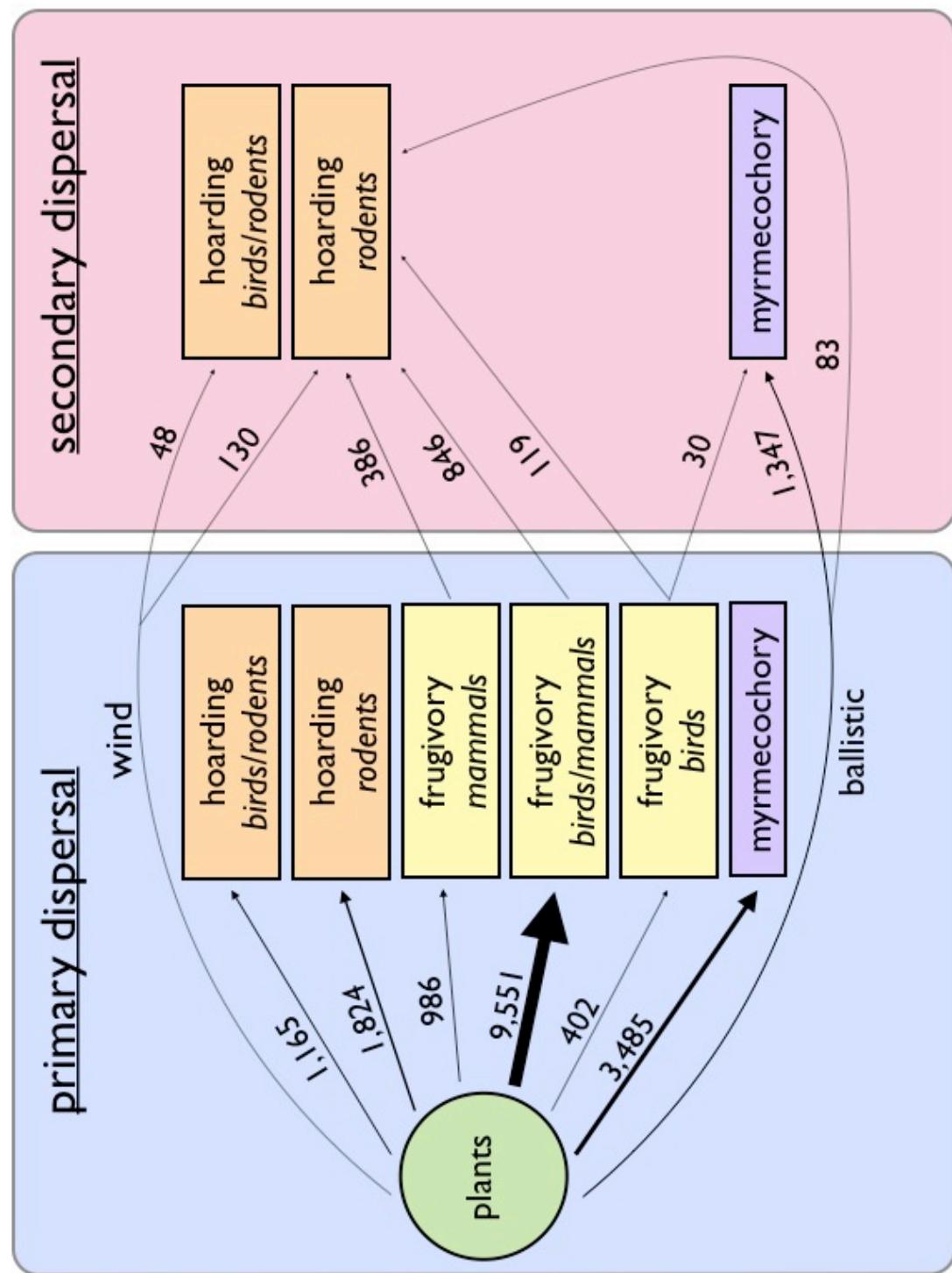


Figure 3.

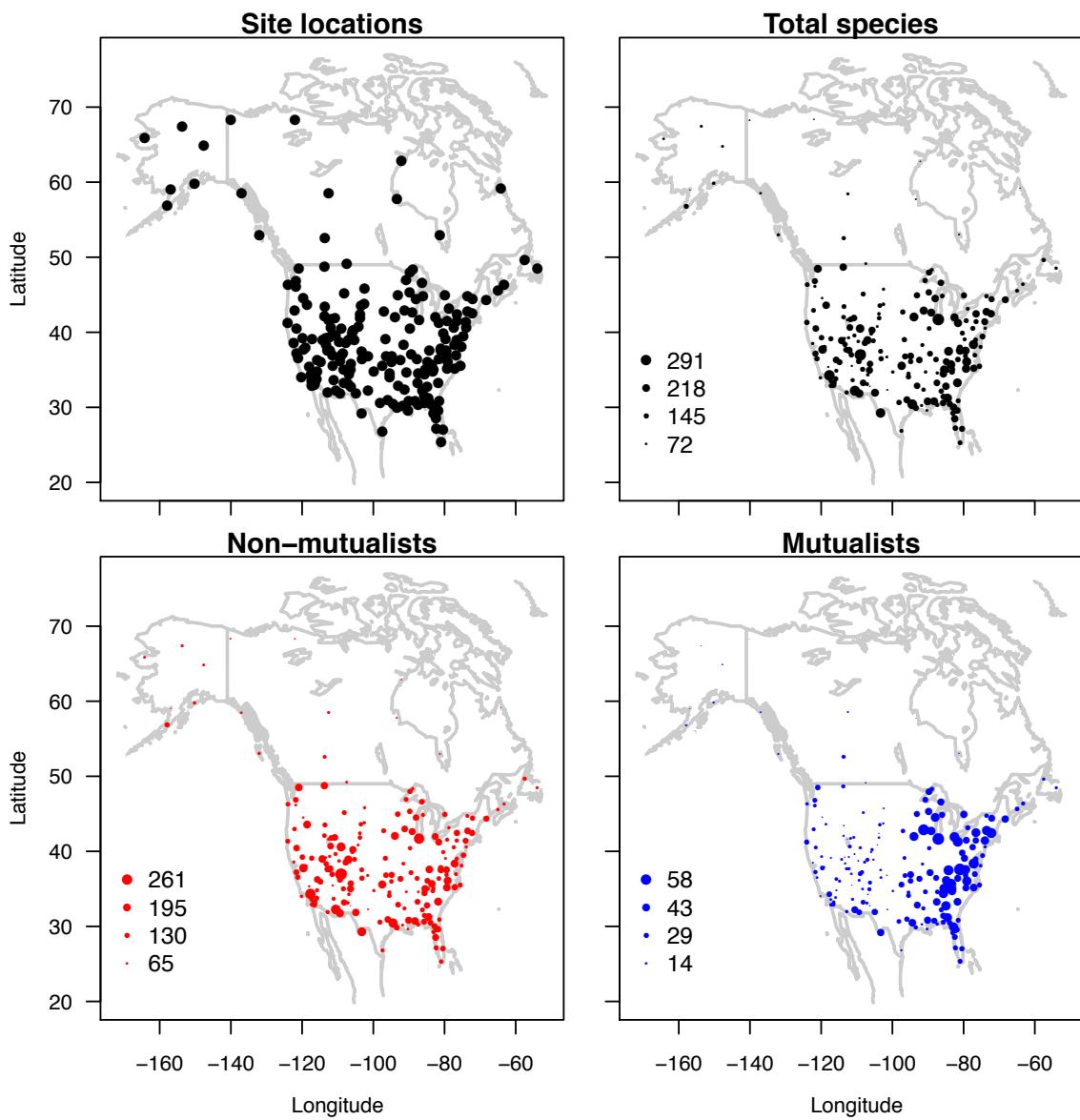


Figure 4.

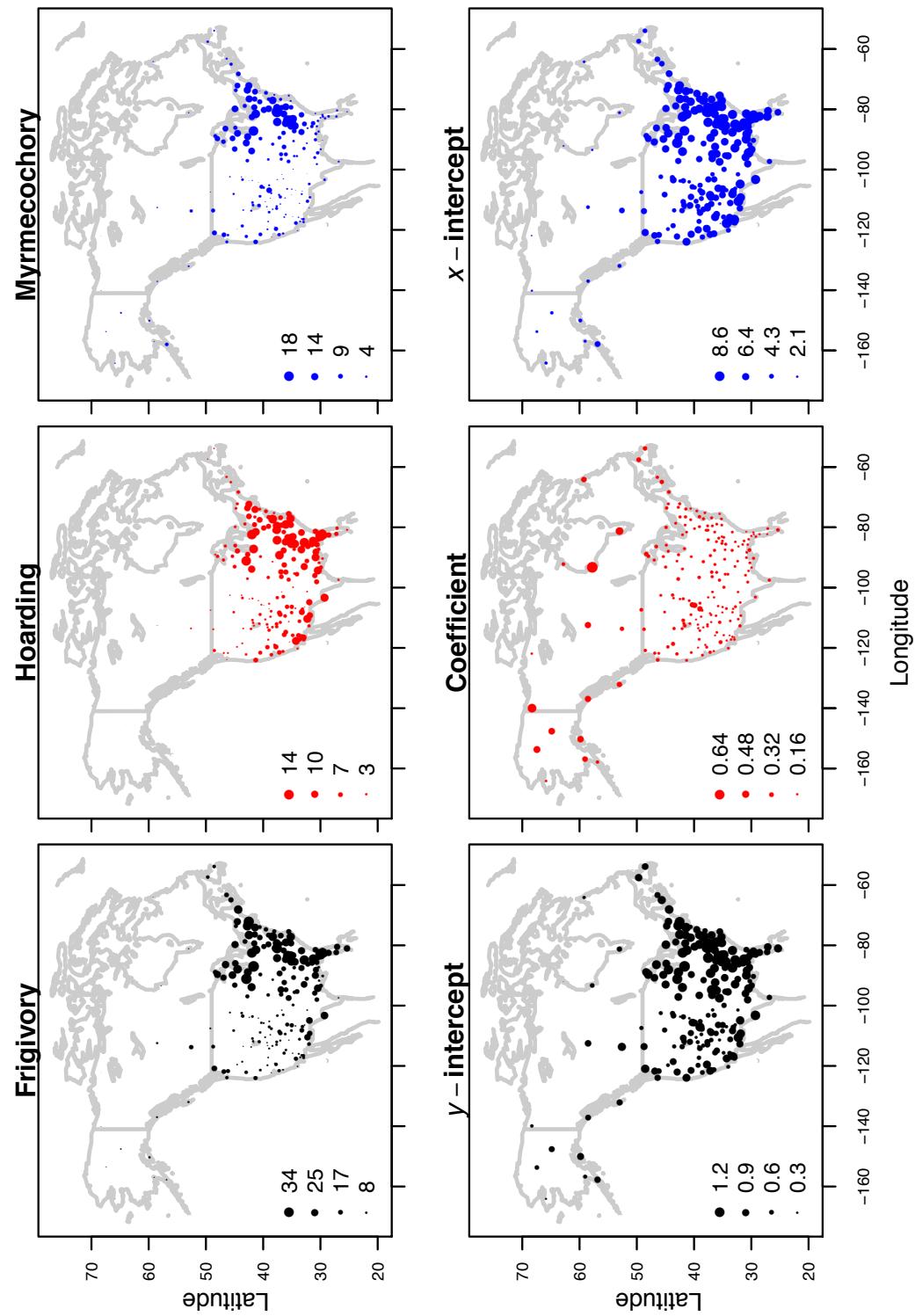


Figure 5.

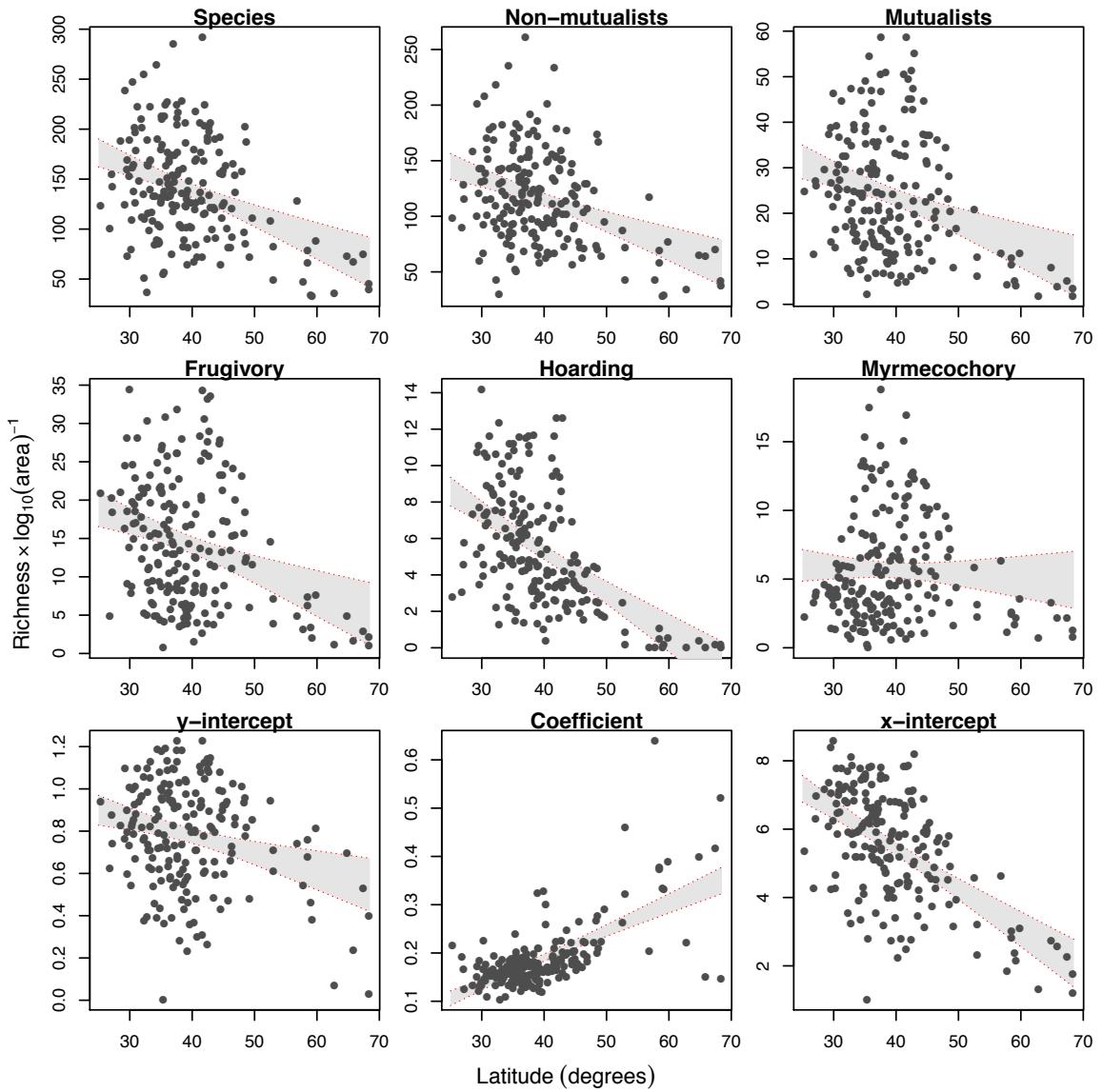


Figure 6.

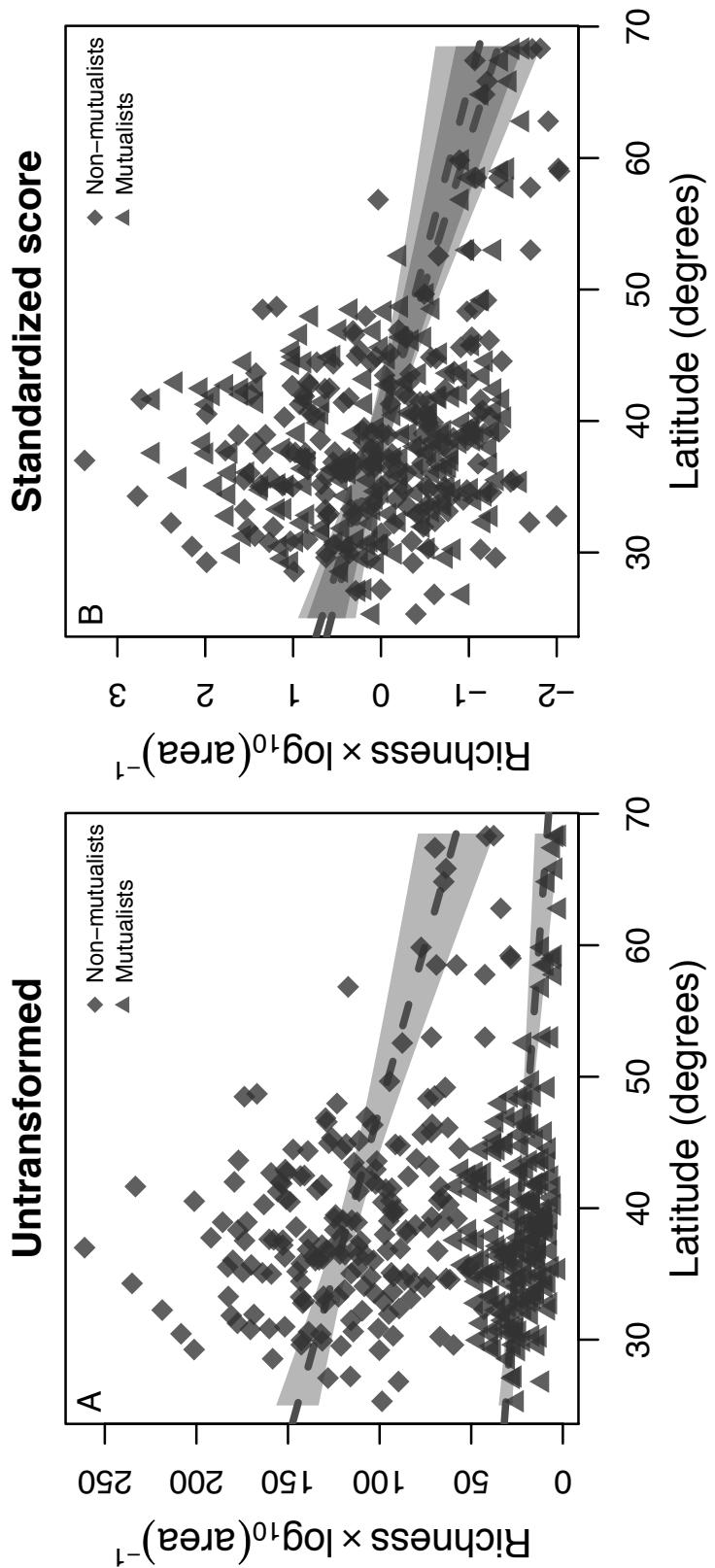


Figure 7.

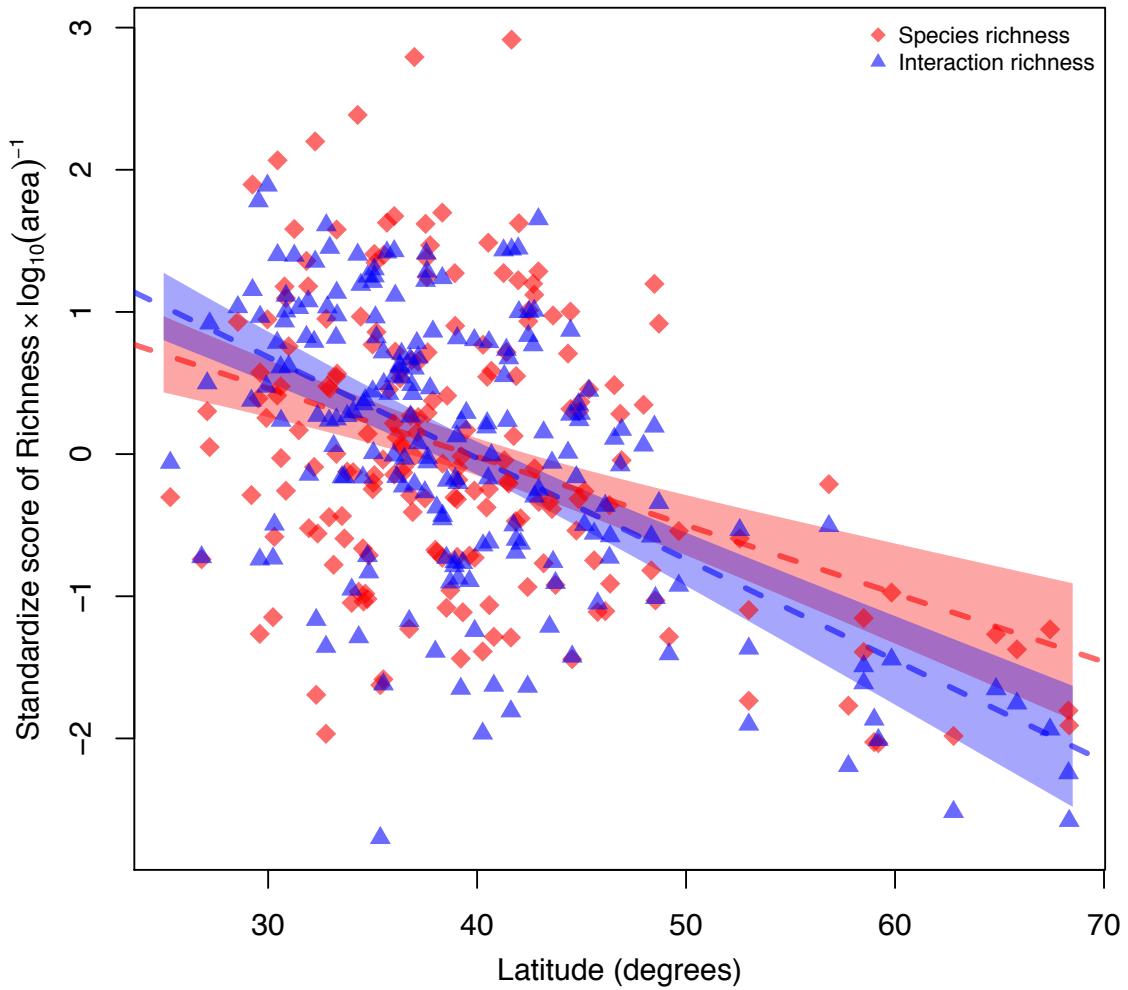


Figure 8.

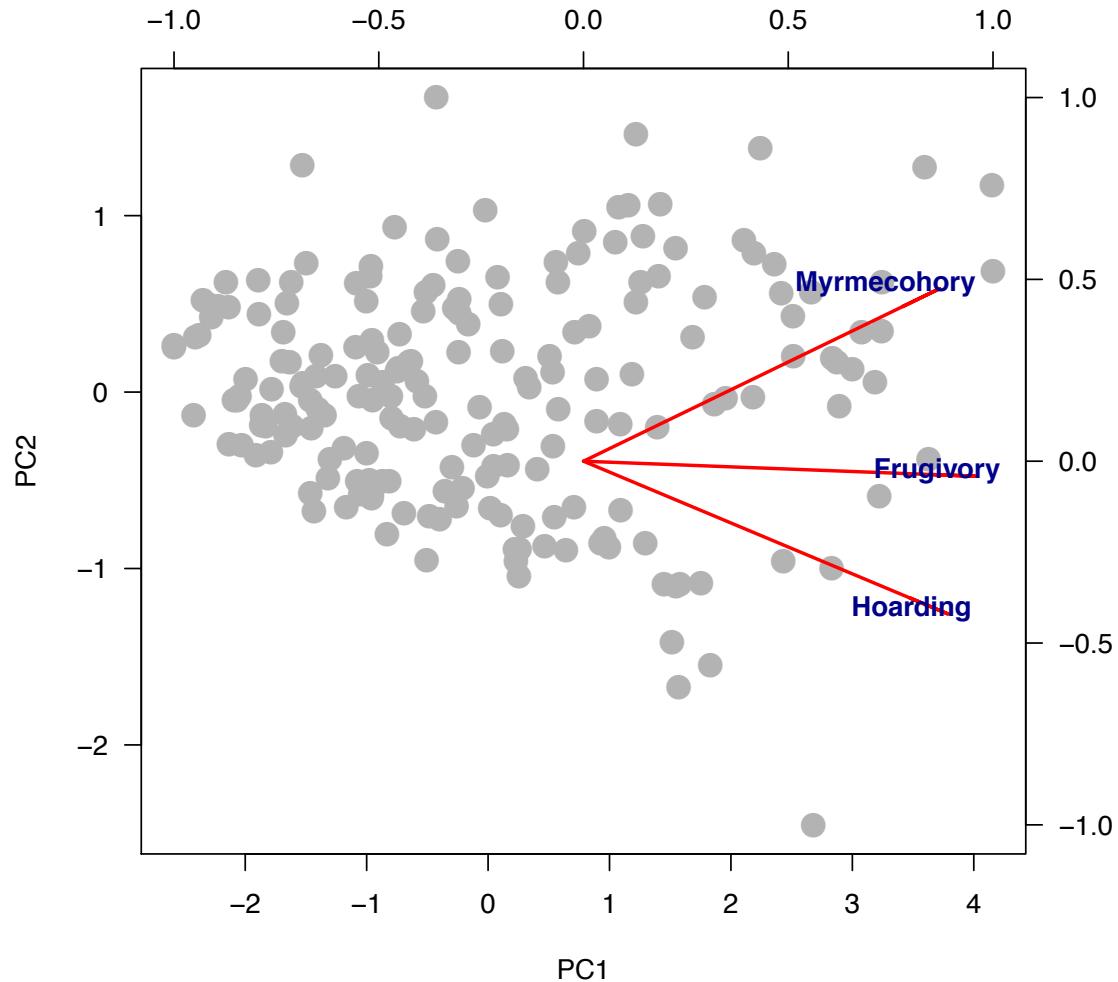


Figure 9.

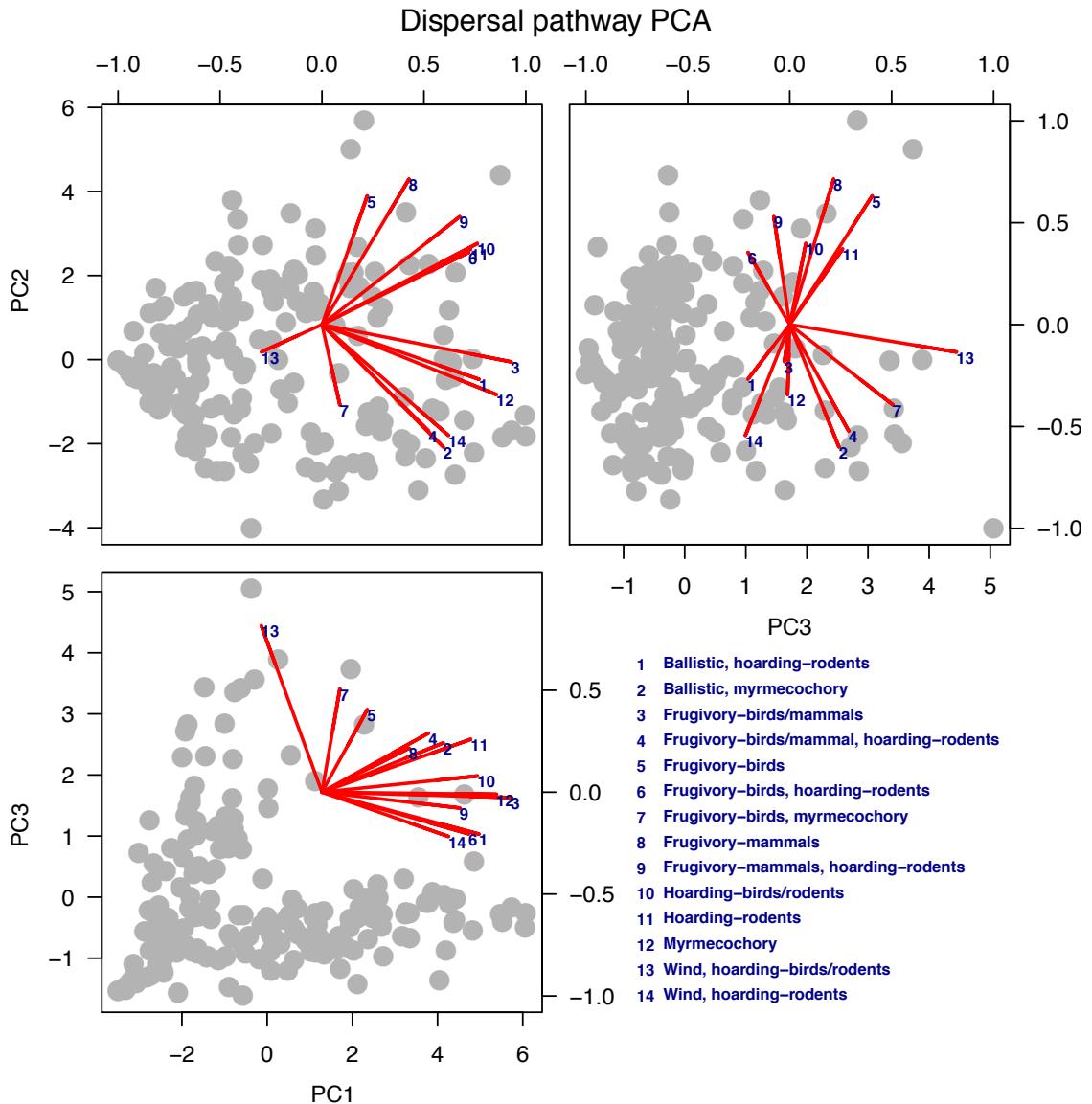


Figure 10.

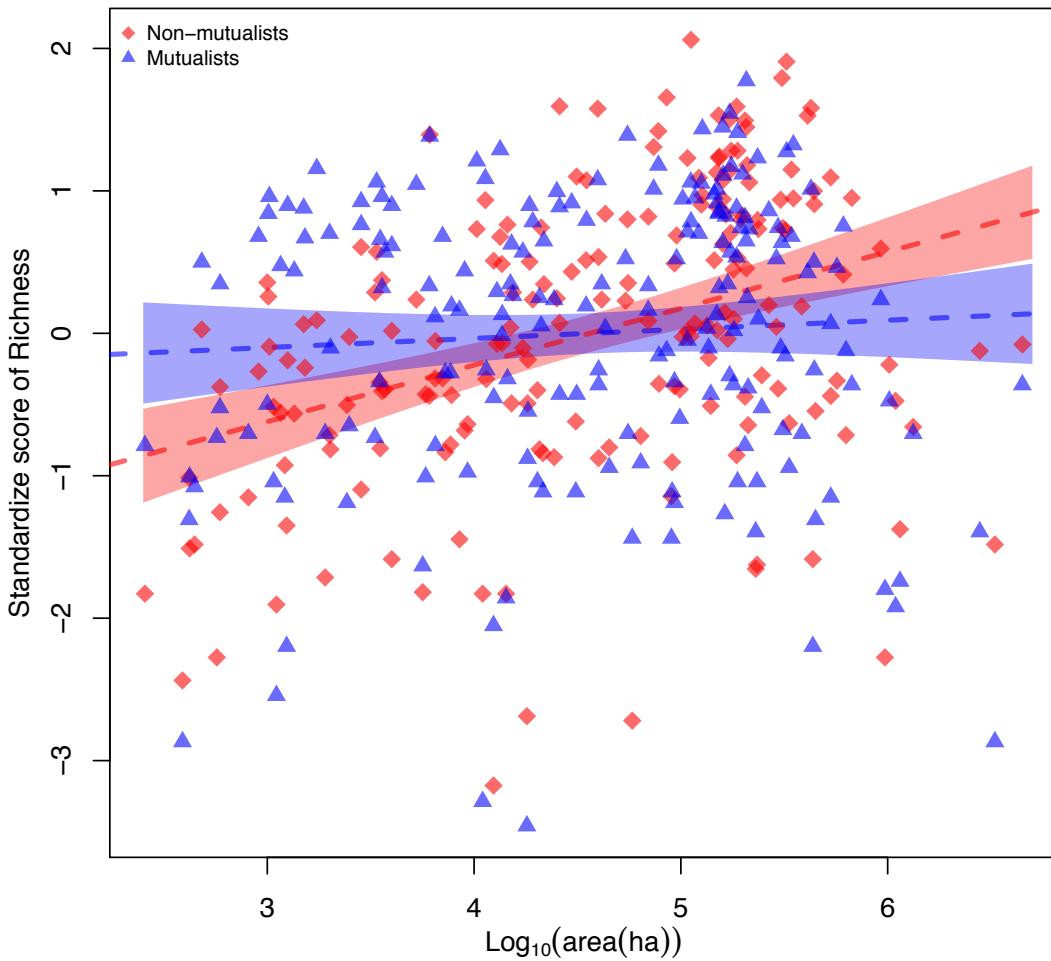


Figure 11.

SUMMARY

This core of this dissertation examines dispersal syndromes across different scales of biological organization. The first chapter attempted to determine how a single species of plant (greenleaf manzanita, *Arctostaphylos patula*) with an ambiguous dispersal syndrome is dispersed. I conducted a series of experiments to determine how the species' seeds are dispersed and what are the consequences of that particular mode of dispersal. The main conclusion redrew the boundary of how a scatter-hoarding syndrome is understood. Specifically, seeds need not be fused and can still be smaller than what has traditionally been understood as a nut syndrome dispersed by scatter-hoarding animals. Curiously, there is a relatively small endosperm reward, which should warrant further investigation by those attempting to study scatter-hoarding syndromes. A secondary main conclusion is that this syndrome appears to benefit seeds in fire-prone ecosystems because scatter-hoarding immediately deposits the seeds under the soil, and area that buffers the heat of fire. This is opposed to passive or abiotic dispersal, where seeds are thought to self-incorporate; the rates of which are highly variable and need to be studied in greater depth.

The second chapter expands beyond the single-species perspective and used a morphometric analysis to compare the focal species of chapter one (greenleaf manzanita, *Arctostaphylos patula*) to other species in the same genus (manzanitas, *Arctostaphylos*). Because I had studied one species in depth, I conclude with high certainty that a number of species in the same genus are very likely to have the same mode of dispersal; namely, a scatter-hoarding syndrome. I additionally examined seed and fruit characteristics (diaspores) to find patterns across environmental gradients that are known to affect

diaspore morphology, and only one was found (elevation). I compared manzanita seed mass to another, similar clade of sympatric plants (*Ceanothus*) and found that *Ceanothus* followed the predicted patterns and manzanita did not. This leads me to conclude that other factors are responsible for the diaspore morphology in manzanitas, and the hypothesis remains that it is animal-mediated seed dispersal.

Lastly, in chapter 3, I scaled-out further and examined patterns of seed dispersal syndromes across a continent, with specific foci on patterns of distribution of all plant species, plant species without mutualist seed dispersers, plant species with mutualist seed dispersers, plant species distributions of the three major modes of animal dispersal (frugivory, scatter-hoarding, myrmecochory), and the differences between species and interactions across several environmental gradients at a large spatial scale. This was the largest investigation into seed dispersal syndromes of its kind. I not only found spatial patterns of different kinds of seed dispersal syndromes, but I found provocative patterns along environmental gradients, such as relatively fewer seed-dispersal mutualisms at higher elevations. One of the findings that I believe will resonate the most with the scientific community was our use of interaction abundance and diversity. I used what I believe to be a novel method that retains a maximal amount of information to describe patterns of interaction diversity. The most interesting finding of which is that there is a stronger relationship between interactions and latitude than species and latitude.