

Scatter-hoarding rodents disperse seeds to safe sites in a fire-prone ecosystem

Christopher M. Moore · Stephen B. Vander Wall

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Abstract Fire can potentially decimate soil seed banks, even for species that are abundant in fire-prone areas. Many plants, like the widespread and dominant members of the genus *Arctostaphylos* in the fire-prone California Floristic Province, have seeds that (i) have no clear adaptations for dispersal and (ii) experience lethal fire temperatures if present on or near the soil surface. In this study, we aim to resolve these juxtaposed observations by mechanistically determining how one species, *Arctostaphylos patula*, is dispersed. To distinguish among dispersal modalities and determine the seed shadow, deposition patterns, and the conditions under which seeds germinate, we employed full-shrub exclosure treatments to monitor fruit removal, used a mark-relocation technique by radioactively labeling seeds, identified dispersers using motion-sensor cameras, and surveyed seedlings following fire to relate natural germination patterns to

measured patterns from our experiment. Seed removal from exclosure treatments that allowed rodents access to shrubs was higher than those that prevented rodent access to shrubs, and cameras at radioactively labeled-seed stations failed to detect the presence of any other disperser; thus implicating rodents as the primary disperser of *A. patula* seeds. This evidence is corroborated by our finding from tracking radioactively labeled seeds that the depth at which rodents bury seeds completely overlaps with the depth from which we observed seedlings germinate following two fire events. Our study extends the boundary of what is understood as a scatter-hoarding seed dispersal syndrome and identifies a mechanism that allows populations of *Arctostaphylos* to exist in spite of recurrent fires that can be lethal to seeds and hazardous to plant populations.

Keywords *Arctostaphylos* · Dispersal · Immaturity risk · Mutualism · Scatter-hoarding · Seed dispersal syndrome

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C. M. Moore (✉) · S. B. Vander Wall
Program in Ecology, Evolution, and Conservation
Biology, Department of Biology, University of Nevada,
Reno, Max Fleischmann Agriculture Building, 1664
North Virginia Street, Reno, NV 89557, USA
e-mail: life.dispersing@gmail.com

Present Address:

C. M. Moore
Department of Biology, Case Western Reserve
University, DeGrace Hall, 2080 Adelbert Road,
Cleveland, OH 44106, USA

Introduction

Scatter-hoarding as a seed dispersal mutualism

Many plants have evolved seeds that are dispersed by scatter-hoarding animals through mutualism, where seed embryos and other nutrient-rich tissues are produced by the plant so that scatter-hoarding animals

store excess seeds in high-quality microsites and imperfectly re-harvest seeds. Scatter-hoarding as a seed dispersal mutualism has been found to occur across all continents except Antarctica [including convergent evolution between plants and marsupials in Australia, (Dennis 2003)], all biomes except tundra, and across dozens of plant families. In some communities in North America, for instance, up to 7.8 % of all vascular plants are dispersed by scatter-hoarding rodents (Vander Wall et al., *submitted*). Once thought of as simply seed predation, careful study and experimentation on seed fates have illuminated the various ways that scatter-hoarding rodents can be beneficial as seed dispersers, including enhanced dispersal quality and increased consistency of microsite deposition (Hirsch et al. 2012), escape from seed predators (Janzen 1977; Smith and Reichman 1984), and escape from negative density-dependent effects (Jansen et al. 2014).

Although we have only begun to fully appreciate the ecological implications of this dispersal mode, most research has focused on the most conspicuous plants with conspicuous dispersal-related structures—trees with large nuts, like oaks (Barnett 1977), pines (Vander Wall 2008), and palms (Jansen et al. 2004). Nevertheless, recent studies have discovered this mutualism to be present in plants with different growth forms and habits. For example, studies of shrubs (Roth and Vander Wall 2005), herbs (Barga and Vander Wall 2013), and grasses (Longland et al. 2001) have expanded our understanding of what growth forms can take on a scatter-hoarding syndrome. Similarly, plants with differing ecological habits have further been investigated. In fire-prone ecosystems, for instance, several studies have implicated scatter-hoarding rodents as dispersers of some serotinous pines, like *Pinus coulteri* (Coulter pine) and *P. sabiniana* (Gray pine) (Borchert et al. 2002, 2003).

Seed dispersal in fire-prone ecosystems

A characteristic way that plant species respond to fire in most fire-prone ecosystems is a combination of persisting by resprouting (Bond and Midgley 2001) and regenerating from dormant seed banks (Keeley and Fotheringham 2000). To regenerate from seed is indeed a precarious life history—plants must produce and disperse seeds to microsites that allow them to both escape fire intensity and be in a position to

receive the physical or chemical cue given off by the fire (Keeley 1991). The inability for plants to grow, produce seeds, and disperse seeds to safe microsites before the next fire is known as immaturity risk (*sensu* Zedler 1995). If, following a fire, plants with fire-stimulated seeds (also known as refractory seeds) cannot produce seeds and disperse them to safe microsites before the next fire event, then the population is at a high risk of local extinction. This has been demonstrated to have disastrous consequences for plant populations (Zedler et al. 1983). Fig. 1 illustrates immaturity risk by superimposing the cumulative probability of a subsequent fire event in the California chaparral (Moritz 2003) over various rates of seed burial, and the time it would take for populations to avoid immaturity risk. Namely, Fig. 1 highlights that even when using an exponential model of seed burial, after plants mature, it may take more time to replenish their seed banks relative to the probability of a recurrent fire. Understanding seed bank dynamics is therefore important

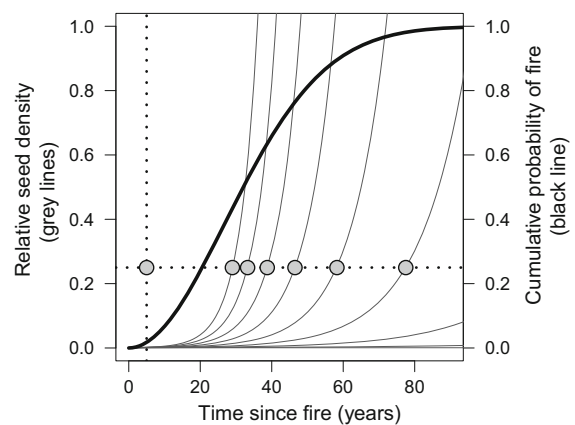


Fig. 1 Conceptual representation of immaturity risk in fire-prone ecosystems. If the seed delivery rates (*thin gray lines*; representing various rates of exponential burial) of a plant population cannot reach a minimum reproductive threshold (arbitrary *horizontal dotted line*; seed production + arrival at microsites that meet germination requirements) following a fire, then the population growth rate, r , is <1 , and potentially $\ll 1$. Seed dispersal by scatter-caching animals can reduce this risk by caching seeds at depths that are safe from fire once an individual reaches maturity (*vertical dotted line*; 5 years in this example). The cumulative probability of fire (*thick black line*) is observed from the center of the California Floristic Province (Moritz 2003), where the highest diversity of *Arctostaphylos* (manzanitas) is found. The *dots* on the threshold represent the years it would take, given a rate of seed burial, for a population to overcome immaturity risk, $r \geq 1$

for understanding population and community processes and dynamics in fire-prone ecosystems.

For many plant species, an examination of the diaspore—the seed and ancillary structures that assist in dispersal—allows for reasonable inferences to be made about how they are dispersed (Pijl 1982; Jordano 1995; Janson 1983). Otherwise known as seed dispersal syndromes, certain suites of diaspore traits are often found to be highly correlated, and are interpreted as adaptations for a particular mode of dispersal. Small, brightly colored, fleshy fruits, for instance, are characteristics of diaspores that are dispersed by frugivorous birds, which independently evolved dozens of times across spermatophyta (e.g., Lomáscolo et al. 2008; Valido et al. 2011). In fire-prone ecosystems—especially those with such a hazard, like immaturity risk—we would therefore expect that seeds in those communities would have traits that would allow them to disperse to safe microsites efficiently, unlike what we observe in some plants (e.g., *Arctostaphylos*).

Seed dispersal in *Arctostaphylos*

In the California Floristic Province, there are three dominant fire-adapted woody genera in the fire-prone chaparral: *Adenostoma* (Chamise), *Arctostaphylos* (manzanita), and *Ceanothus*. The first and last have clear dispersal syndromes: *Adenostoma* has long, linear (approximately 1×2.5 mm) achenes, and *Ceanothus* has small seeds (usually 1-mm d, sphere to slightly prolate spheroid shaped) with a very smooth seed coat [see Thompson (1993) for a discussion on seed dimensions and soil seed banks]. These traits, coupled with both species producing enormous seed sets (e.g., Warzecha and Parker 2014, measured the average seed rain of *C. papillosus* at 17,206 seeds m^{-2} in 2012 and 3219 seeds m^{-2} in 2013, a severe drought year), are characteristic of plants that are abiotically dispersed. *Arctostaphylos*, in contrast, produces a berry with a leather-like (coriaceous) exocarp, mealy mesocarp, and woody nutlets (see Wells (2000) or Parker et al. (2012) for full descriptions of each species). During development, the fruits are fleshy and change color from bright green, to a red, then dry out and become russet (with relatively high interspecific variation in color when ripe). The nutlets are sometimes fused, individual nutlets can be somewhat

smooth-to-granular, and the total seed volume spans three orders of magnitude across species.

It is curious that a plant without an obvious mode of dispersal could exist in the fire-prone California chaparral, especially given that germination studies have found increased seed mortality with temperatures experienced during fires on or near to the soil surface compared to what the seeds would experience at greater depths (lower temperature and light availability, Keeley 1987a; Parker 1987), suggesting that seeds without obvious means of burial are lethally sensitive to being on the soil surface. The aim of this study was therefore to investigate seed dispersal processes and patterns in *Arctostaphylos*, a plant that forms persistent seedbanks in fire-prone areas yet has no clear dispersal mechanism. We used *Arctostaphylos patula* (greenleaf manzanita), a widespread, locally abundant, and often ecologically dominant member in the eastern California Floristic Province, which has diaspore characteristics (e.g., size, nutlet fusion) that are intermediate compared to other members of *Arctostaphylos* (Moore 2014). Diaspores of *Arctostaphylos patula*, and *Arctostaphylos* in general, do not conform well to known dispersal syndromes, and our understanding of seed bank dynamics is based on studies that have been equivocal on the role of dispersal in their findings (Keeley and Hays 1976; Keeley 1987b; Kelly and Parker 1990; Parker and Kelly 1989).

To date, no study has focused exclusively on examining seed dispersal of any *Arctostaphylos*. Some studies have suggested that *Arctostaphylos* is not specialized for dispersal and that most seeds remain underneath or nearby the canopy radius (e.g., Parker and Kelly 1989; Keeley 1991). Other studies have implicated three modes of animal-mediated dispersal: (i) frugivorous birds, (ii) scatter-hoarding rodents, and (iii) omnivorous carnivorous mammals. One study reported that *Turdus migratorius* (American Robins) consumed *A. uva-ursi* fruit when given a choice between *A. uva-ursi* and *Vaccinium macrocarpon* (Cipollini and Stiles 1993). Several studies cite evidence that rodents eat and possibly disperse *Arctostaphylos* seeds, but considered most rodents to be seed predators (Keeley and Hays 1976; Keeley 1977, 1987b; Kelly and Parker 1990). Tevis (1953) found evidence of *A. patula* seeds in the cheek pouches, and endosperm in the stomachs of long-eared chipmunks (*Tamias quadrimaculatus*). He also noted that *A. patula* seedlings emerged in clumps after a fire

from what appeared to be rodent caches. The last and most cited candidates as dispersers of *Arctostaphylos* seeds belong to omnivorous mammals in the order Carnivora (Bowyer et al. 1983; Delibes et al. 1989; Wilson and Thomas 1999; Nielsen et al. 2004; Silverstein 2005). Carnivorans, such as *Urocyon cinereoargenteus* (gray foxes), *Nasua narica* (coatis), *Canis latrans* (coyotes), *Ursus americanus* (American black bears), and *Ursus arctos* (grizzly bears), have been reported to consume *Arctostaphylos* fruits. Silverstein (2005) examined germination from coyote scat, and found 0.2–1.6 % emergence, suggesting that consumption by carnivoran mammals does little to increase germination.

The main question of this study is therefore: How are *Arctostaphylos patula* seeds dispersed? Based on the morphology of *A. patula* and the few anecdotal descriptions of dispersal of *A. patula* described in the previous paragraph, we hypothesize that *A. patula* is primarily, if not exclusively dispersed by scatter-hoarding animals. To test this hypothesis, we employed three main methods: (i) whole-shrub exclosures to measure the effects of different guilds of animals on fruit removal, (ii) motion-sensored cameras and radiolabeled seeds to determine which animals remove the seeds and patterns of dispersal and deposition, and (iii) quantified patterns of seedling emergence following fire and compared them to patterns of rodent caching. Our main finding fails to reject our hypothesis, and strongly implicates scatter-hoarding rodents as responsible for the removal and dispersion of *A. patula* seeds.

Materials and methods

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°14'–17'N, 119°52'–53'W), with an average elevation of 1975 m. Little Valley is characterized by a Mediterranean climate, with hot, dry summers, and cool, wet winters in the eastern 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 to 200 % of the mean. Mean monthly temperatures range from 11 to 16 °C in the summer, and –4–0 °C in the winter. Historically, large-scale disturbances that occurred in Little Valley were 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 1990s (Vander Wall 2005).

Soils of Little Valley are primarily granitic in origin with little organic matter. Major vegetation types consist of *Pinus jeffreyi* (Jeffrey pine)-*Abies concolor* (white fir) forest, *P. contorta* (lodgepole pine) forest, *Ab. magnifica* (red fir)-mixed subalpine forest, *Populus tremuloides* (aspen), riparian, montane shrub, and meadows. *Arctostaphylos patula* is common throughout Little Valley in associations with *Ceanothus velutinus* (tobaccobrush) on dry slopes. At higher elevations (>2500 m, in the red fir-mixed subalpine forests, *A. patula* becomes rare, and a prostrate *Arctostaphylos*, *A. nevadensis* (pinemat manzanita), becomes common.

Fruit removal

To examine removal of *A. patula* fruits, three types of wire-mesh exclosures were constructed around individual shrubs designed to exclude select groups of vertebrates (Fig. 2a). Each exclosure was a 2 × 2 × 1.3-m galvanized, wire mesh (12 × 12 mm) cuboid on a 5 × 5-cm wooden frame. Each exclosure was placed around an individual shrub and the base was buried ~15 cm deep in soil to discourage digging animals. Shrubs were haphazardly selected throughout the study site, with the criteria that shrubs were producing fruit, were small enough to be comfortably enclosed, and grew separate from other shrubs, trees, and boulders. There were four treatments, each replicated five times and repeated for 2 years. One treatment was a full exclosure designed to keep out all vertebrates (hereafter, full exclosure). We did not observe evidence that vertebrates had entered the exclosures in the duration of the study. A second treatment was identical to the full exclosure, except we cut eight 8 × 8-cm holes along the ground to allow access to small rodents, but exclude birds and large mammals

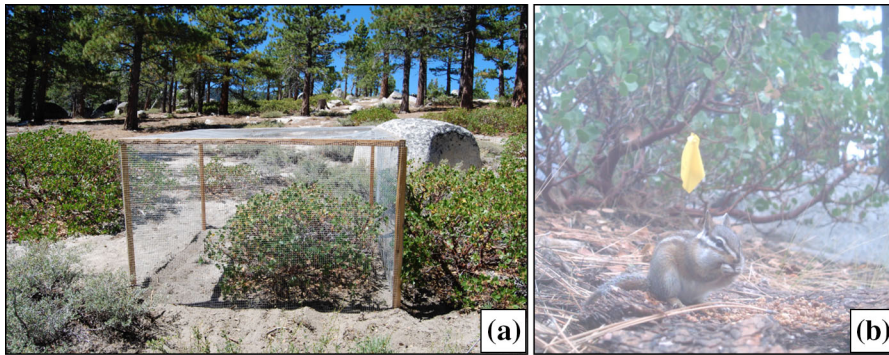


Fig. 2 Photographs of a full-shrub enclosure (a) and a chipmunk at a seed station with *Acrostaphylos patula* seeds (b). This enclosure is one (full enclosure that prevented access of all vertebrates) of the four treatments used to determine what animals remove fruit. Further, motion-sensor cameras were set

up at seeds stations with radioactively labeled seeds. In this photograph taken from a video, a *Tamias quadrimaculatus* (long-eared chipmunk) is both pouching seeds to cache and consuming some seeds

(hereafter, rodent access). A third treatment had walls 0.5 m high covered with aluminum flashing to prevent rodents from climbing in but had no wire-mesh top. This enclosure was designed to allow birds and large mammals access to the shrubs, but to exclude rodents (hereafter, rodent enclosure). The final treatment acted as a control and consisted of unfenced plots around shrubs, the same size as the enclosures that allowed access to all foragers. Enclosures were erected during late summer (late August and September), while fruits were immature in the summers of 2010 and 2011.

At the time enclosures were established, five branch tips per shrub that each had 10–40 fruits as subsamples were haphazardly selected to be monitored. These fruiting branches were labeled with numbered, plastic poultry bandettes (National Band and Tag Co.; KY, U.S.). Fruits were counted on weekly visits until either all fruits were removed from the shrubs or snow prevented access to the field site.

Seed dispersal

To examine seed dispersal patterns, we tracked seeds from a point source to determine seed dispersion. We labeled *A. patula* seeds with radioactive scandium-46 (2009, 2010) and iron-59 (2011), and placed the seeds beneath *A. patula* shrubs (our supplier discontinued manufacture of Sc-46 in 2011). Sc-46 is a γ -emitting radioisotope with an 84.5-day half life and Fe-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 h at 30 °C for better nuclide absorption. The nuclide was mixed with water and the seeds were wetted in the solution for 1 h until the isotope was absorbed, and then air-dried for 48 h. In the field, we deployed seeds once fruits were mature (September). Approximately, 300 seeds were placed under shrubs that had numerous ripe fruits (Fig. 2b). After substantial numbers of seeds were removed (generally >75 % within a few days), seeds were relocated with a Geiger counter by walking in concentric circles around the seed source until we had searched a radius of 50 m. When a cache was discovered, we exposed the seeds, determined the depth at the top and bottom of the cache, counted the number of seeds, measured the distance to the source shrub, and recorded microsite conditions [placement relative to woody shrub canopy: under, edge ± 10 cm from the edge, or open; leaf litter: light (<10 mm thick), medium (10–30 mm), heavy (>30 mm thick, bare soil)]. This procedure was repeated at 13 different shrubs over the three-year period. Additionally, at several of the seed sources in 2009 and 2010, infrared cameras (HCO ScoutGuard SG550 Camo, 5 megapixel IR game camera; GA, U.S.) were set out to determine the identity and behavior of the species of animals that removed seeds.

To analyze the point patterns of caches and seeds, we derived probability density functions (pdf) using a Gaussian kernel density estimator (Silverman 1986) in two dimensions using the kde2d function in the MASS package (Venables and Ripley 2002) in R (R Core Team 2014). To estimate parameter values, we randomly

sampled our data by converting our Cartesian locations to polar coordinates, randomizing the angular coordinate (θ) while keeping the distances (r) constant, and sampling from the pole ($r = 0$) to the end of kernel 1×10^4 times. This process yields a one-dimensional estimate of seed arrival at a point from a source; known as a density pdf, $\omega_\theta(r)$ (hereafter omitting the θ subscript because there were no detectable symmetrical biases in our data). Alternatively, estimates of dispersal distance away from a source (i.e., parent) are also of interest for those model dispersal from a parent (e.g., individual-based models), so we additionally report the estimates of how far seeds will be dispersed relative to the parent, the distance pdf, $f(r)$. Density and distance pdfs can, respectively, be interpreted as the probability of dispersal to a point and dispersal to an annulus. Density and distance pdfs can be converted by accounting for the relationship between the estimated number of seeds at a point with an annular area and radius as

$$\omega(r) = \frac{f(r)}{2\pi r}, \quad (1)$$

which completely changes the shape of the function (see results and Cousens et al. (2008) for a lucid explanation). As a pdf, the area under each kernel estimate was converted to unity. Lastly, we analyzed the point patterns as both caches and seeds to infer how animals disperse seeds and the ultimate distribution of seeds, respectively. Annotated code for the procedure described above can be found in a repository at <https://github.com/dispersing/2DKernSim/blob/master/2DKernSim.R>.

For the sake of balancing model overfitting (*sensu* Mayer et al. 2010) and biological meaningfulness, deterministic model selection was limited to two exponential functions that have been shown to have biologically meaningful parameters (see Wichmann et al. 2009; Bullock et al. 2011). For both pdfs ($\omega(r)$, $f(r)$) we chose the following models:

$$p(r) = ae^{-br} \quad (2)$$

and

$$p(r) = ae^{-r^b}. \quad (3)$$

Equations (2) and (3) are first both described by parameter a , which is the estimated density or number of seeds at the source ($r = 0$) after animals have

dispersed all seeds. Secondly, these equations both include a rate at which seeds are dispersed, the b parameter. In Eq. (2), $p(r)$ changes at a rate of $-r$ multiplied by a constant, b , interpreted as a constant dispersal rate as a function of distance. In Eq. (3), $p(r)$ changes at a rate of $-r$ to the b th power, and therefore changes at a second order rate as either increasing or decreasing as a function of distance, respectively as $+b$ or $-b$. Equations (2) and (3) were applied both to the density ($\omega(r)$) and distance ($f(r)$) pdfs, accounting for annular area in the distance distribution such that $f(r) = 2\pi r \exp(-br)$ and $f(r) = 2\pi r \exp(-r^b)$. Equations (2) and (3) were qualitatively compared as they relate to underlying biological processes based on the residual sum of squares of each model using the nonlinear least-squares method in the `nls` function in the R stats package (R Core Team 2014).

Seedling emergence

Seed germination in *Arctostaphylos* only occurs after fire, stimulated by charred wood [otherwise known as ‘charate;’ e.g., Rogers (1950), Parker (1987), Keeley (1991)] leached into the soil. We investigated two burned sites in the spring of 1995 following the Crystal Peak Fire, in May 1994, which burned 2500 hectares of mixed coniferous forest with *A. patula* understory in eastern California, about 30 km NNW of our Little Valley site. Two 10×10 -m plots ~ 1 km apart were established in the interior of the burn. All *A. patula* seedlings were mapped and the number of seedlings per germination site were counted.

The second site was in Little Valley, where trees had been thinned by the Nevada Division of Forestry (NDF) to reduce fuels and arranged in piles. In November 2010, NDF burned those piles, including 18 piles in an *A. patula*–*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 in the interior of the pile (Korb et al. 2004). Nevertheless, the periphery of the piles does resemble naturally occurring fires based on the number of refractory seedlings 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.

Unless otherwise noted, because much of data deviate from a Gaussian distribution, summary statistics of central tendency is the median and dispersion are quantiles: the 1st and 3rd quartiles, denoted as $Q1$ and $Q3$.

Results

Fruit removal

We monitored 1891 fruits on 40 shrubs (10 replicates of each treatment) from ripening until snowfall prevented access to the fieldsite. Fruit removal was found to be different across the four treatments of animal exclosures (Kruskal–Wallis rank sum test, $N = 40$, $\chi^2 = 9.46$, $P = 0.023$, $df = 3$). Median fruits removed per shrub for each treatment were control = 42.0, rodent access = 37.5, rodent exclosure = 16.0, and full exclosure = 19.5 (Fig. 3). 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 the study was only over 2 years, there was no power to detect differences.

Seed dispersal

Radiolabeled seeds that were relocated in the field appeared to be removed, cached, and eaten exclusively by rodents. Of the approximately 3900 seeds (13 trials \times 300 seeds per trial), we accounted for 1856 (52.4 % of all seeds placed at stations). Approximately 360 seeds were not removed from seed stations; most appeared to lack edible contents. For five of the trials, we detected larders (many seeds deep in burrows), but excavation was not attempted because the seeds are not in suitable microsites for germination. Because animals were moving many seeds, consuming them, and leaving fragments behind, we conservatively determined (>1 seed, <100 seeds, and cache depth >1 mm) that 1242 seeds were dispersed in 100 caches.

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: *Tamias amoenus* (yellow-pine chipmunks), *T. quadrimaculatus* (long-eared chipmunks), and *Callospermophilus lateralis* (golden-mantled ground squirrels). The latter species is primarily a larder-hoarder and probably not an effective disperser of *A. patula* seeds. *Tamias amoenus* appeared to be responsible for most of the observed caching, as cache characteristics were similar to those previously reported for this species (e.g., Vander Wall 1993a, b). 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 *Peromyscus maniculatus* (deer mice), the known common nocturnal granivore in the area, did not appear to be involved in seed removal.

We recorded cache characteristics, including number of seeds, depth, soil type, and relation to shrub canopy. The median cache size was 8.5 seeds, $Q1 = 4.0$, and $Q3 = 14.0$, with a range of 1–76. Cache depth appeared to be slightly bimodal (Fig. 4a), with most caches at 10.0 and 20.1 mm deep, and ranged between 1 and 40 mm. There was no relationship between the number of

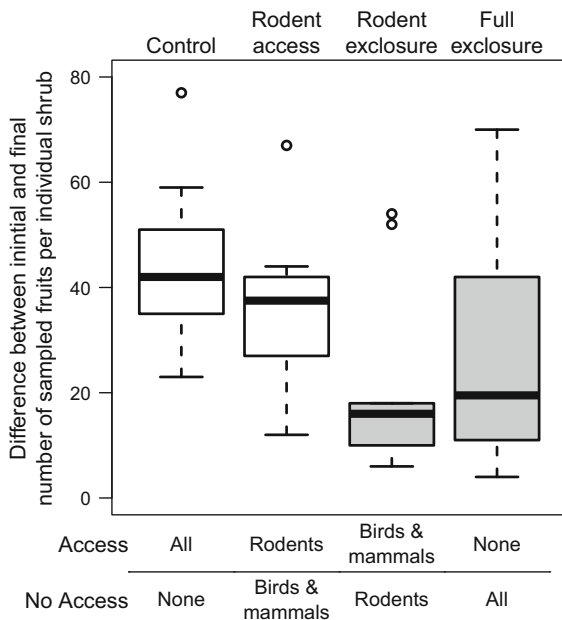


Fig. 3 The difference between initial and final counts of *Arctostaphylos patula* fruits from whole-shrub exclosure treatments in 2010 and 2011. Treatments that allowed (clear) and excluded rodents (shaded) had different means and medians, but they were similar within those groups. Each treatment was replicated 10 times, 5 per year

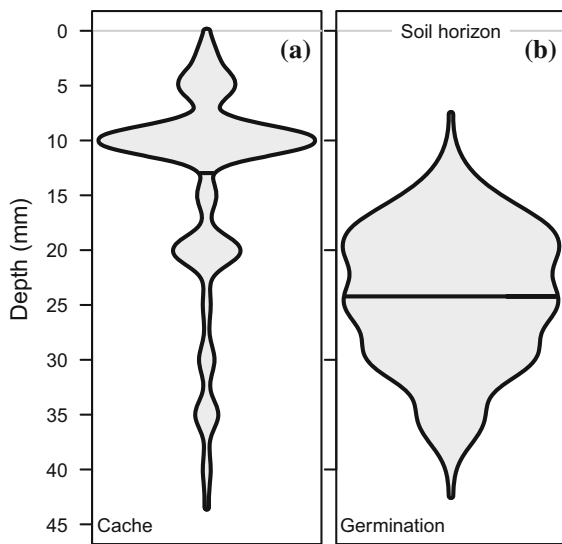


Fig. 4 A comparison of the minimum depth at which *Arctostaphylos patula* seeds are cached by scatter-hoarding rodents (a) and from which they germinated in a natural fire (b). Seed density is on the abscissa and burial depth is on the ordinate axis

seeds cached and the distance they were dispersed ($R^2 = -0.01$, $F_{1,98} = 0.11$, $P = 0.851$; Fig. 5). We found 61 caches in bare soil, 24 caches in light litter, 9 caches in medium litter, and 6 caches were found in heavy litter. With respect to the canopy of woody shrubs, we found 68 caches in the open, 20 caches on the edge of shrubs (± 10 cm), and 12 caches in the interior of the canopy.

Dispersal away from the seed stations showed a typical dispersal pattern, with most seeds dispersed near the seed source (Fig. 6). The density distributions of caches and seeds, $\omega(r)$, were qualitatively similar (Fig. 6a, c) by decreasing monotonically as a function of distance away from the seed stations, with respective medians of 6.2 and 3.9 m, and a steeper slope in the seed density distribution. The distance distributions of caches and seeds, $f(r)$, were qualitatively different than the density distributions by not being monotonic, but respectively showing patterns of uni- and bi-modality (Fig. 6b, d). The medians of cache and seed distance distributions were, respectively, 12.9 and 10.7 m.

We fit two deterministic models with biological meaningful parameters to our density and distance pdfs (Table 1; Fig. 7). The simple exponential model, Eq. (2), fit three of the four probability density

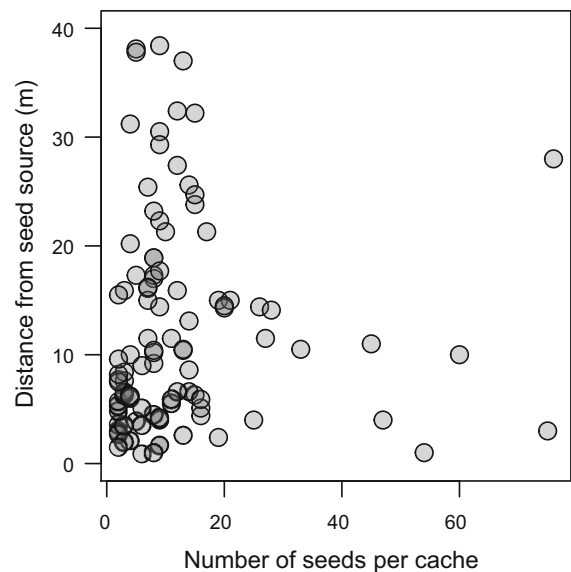


Fig. 5 The distances that rodents dispersed seeds (m) as a function of the number of seeds cached. There is no relationship, showing that despite the increased gain of collecting more seeds, rodents did not travel farther distances to cache them

functions better than the power exponential model, Eq. (3), based on the residual sum of squares (reported in Table 1) in all pairwise comparison of data \times pdf.

Seedling emergence

In spring following the Crystal Peak Fire, 2590 *A. patula* seedlings emerged in the two 10×10 -m plots. This included a total of 262 clumps of seedlings (≥ 2 seedlings per emergence site), containing a total of 1958 seedlings and accounted for 75.6 % of the seedlings (Table 2). The frequency of clumping is a useful measure of animal caching, because animals often put numerous small seeds in each cache. In this case, however, it could be misleading because the five or so seeds in *A. patula* fruits are often fused, so small clusters of seedling could potentially represent fused seeds that were buried abiotically or perhaps an entire fruit that was abiotically buried. To avoid this possibility, we also report the number of clumps of seedlings > 5 (Table 2). There were 89 such clumps, accounting for 52.9 and 65.2 % of all seedlings on the two plots. The maximum clump size was 56 and 43 seedlings on the two plots. Similarly, in spring following the artificial burn in Little Valley, we recorded 82.7 % of seeds emerging in clumps ≥ 2 and

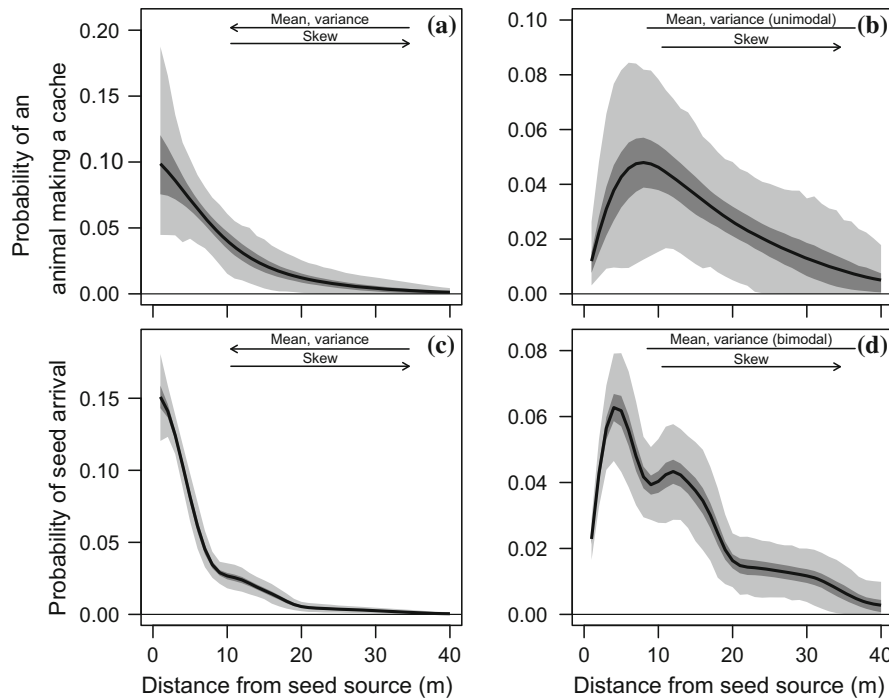


Fig. 6 The distribution of animal caches of *Arctostaphylos patula* seeds as density (left column, $\omega(r)$) and distance (right column, $f(r)$) probability density functions. The top and bottom rows are respectively simulated estimates of the probability of scatter-hoarding rodents making a cache or seed arrival as functions of distance. The shape and properties of the distance functions change across columns, depending if area is taken into

account (a, c; density pdf) or not (b, d; distance pdf). Each panel estimates probability density function parameter values at each meter. The mean is the black line, the Q1 and Q3 are the dark gray areas, and $1.5 \times \text{IQR}$ is the light gray area. The arrows at the top of each panel relate to the direction of the statistic with respect to distance

Table 1 Parameter estimates and model comparisons of probability density functions (pdfs) for the distribution of *Arctostaphylos patula* caches and seeds

Data	Probability density function	Model	a	b	Sum of squares
Caches*	Density pdf, $\omega(r)$	Simple exponential, Eq. 2*	0.117	0.108	1.13×10^{-4}
		Power exponential, Eq. 3	0.342	0.368	2.76×10^{-3}
	Distance pdf, $f(r)$ *	Simple exponential, Eq. 2*	0.002	0.121	3.01×10^{-5}
		Power exponential, Eq. 3	0.012	0.467	1.23×10^{-3}
Seeds	Density pdf, $\omega(r)$ *	Simple exponential, Eq. 2*	0.195	0.182	8.20×10^{-4}
		Power exponential, Eq. 3	0.497	0.440	3.31×10^{-3}
	Distance pdf, $f(r)$	Simple exponential, Eq. 2	0.004	0.161	1.12×10^{-3}
		Power exponential, Eq. 3*	0.017	0.507	9.45×10^{-4}

The distance and density pdfs were fit to simple and power exponential models, with b being the rate at which rodents disperse caches or seeds as a function of distance from a source of seeds. Across all comparisons but one, the simple exponential model better fits the data. The distance over the density pdf fits the cache data, and vice versa for the seed data. The cache data overall fit better than the seed data. Parameters a and b are nonlinear least-squares estimates of a two-dimensional kernel density estimate, with the asterisks marking the the best fit model for each set of response variables. The graphical result can be seen in Fig. 7

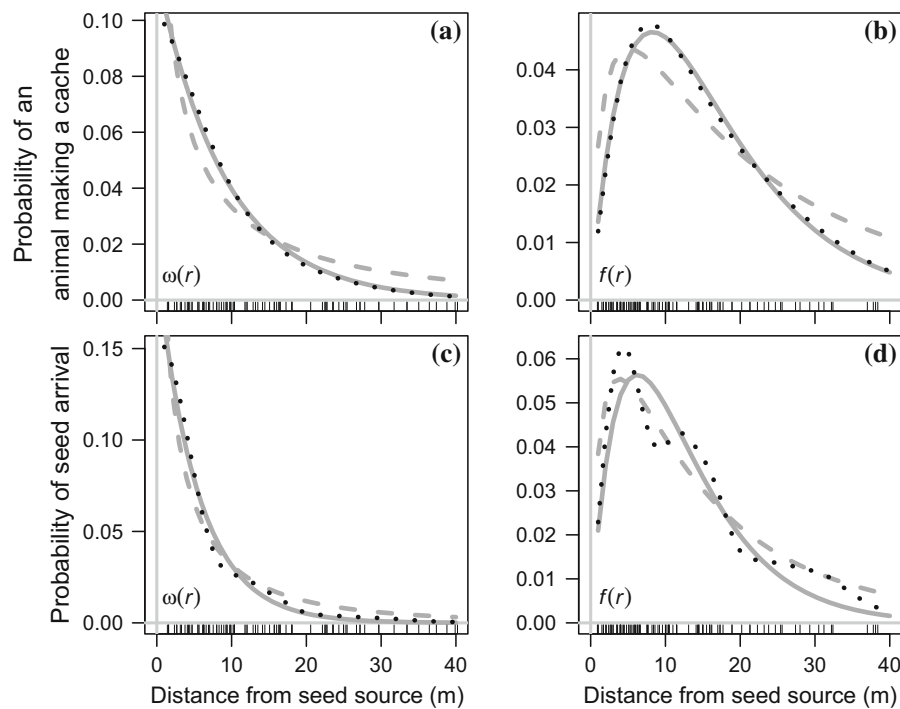


Fig. 7 Mean density (left column, $\omega(r)$) and distance (right column, $f(r)$) probability density functions fit to two deterministic models of seed dispersal with underlying biological parameters. The collected data (black, dotted) in three of the

four cases better fit the exponential (gray, solid line) than the power exponential model (gray, dashed line). Specific parameter values and model-fit statistics can be seen in Table 1

Table 2 The number of *Arctostaphylos patula* seedlings that emerged singly or in clumps of ≤ 2 or > 5 on 10 \times 10-m plots at 2 sites during spring following a wildfire near Crystal

Peak, California, United States, and at 1 site along an artificial burn in Little Valley, Nevada, United States

	Crystal peak		Little Valley
	Site 1	Site 2	Site 3
Number of emergence sites	468	403	64
Total number of seedlings	1236	1354	238
Seedling per emergence site (range)	1–56	1–43	1–68
Number of single seedlings	348	284	41
Clumps ≥ 2			
Number of clumps	120	119	23
Median ($Q1$, $Q3$)	3 (2,7)	4 (2,13)	4 (2,9)
Percentage of seedlings	71.3	79.0	82.7
Clumps > 5			
Number of clumps	36	53	8
Median ($Q1$, $Q3$)	12.5 (8.75,25)	15 (9,22)	11 (9.5,17.5)
Percentage of seedlings	52.9	65.2	64.7

Clumps of seedlings greater than one represent potential rodent caches, but because *A. patula* fruits typically contain five seeds, a more conservative measure of rodent caching is clumps greater than five seedlings

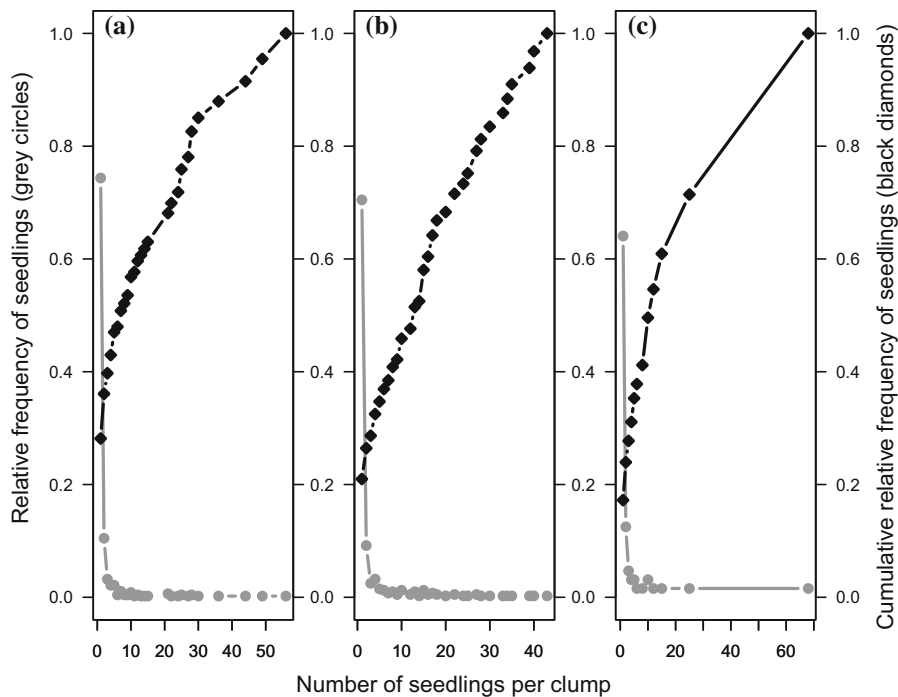


Fig. 8 The distribution of post-fire seedling clumps of *Arctostaphylos patula* from two plots following a wildfire (**a**, **b**) and one from an artificial burn (**c**). Although most emergence events are from seedlings emerging singly, they only accounted for 28.7, 21.0, and 17.3 of the total seedlings per plot. The horizontal axis corresponds to the ranked seedling clump size

(note they are different based on the maximum clump size). The left vertical axis is the relative frequency of the number of seedlings in a clump (gray circles), and the right vertical axis is the cumulative relative frequency of seedlings (black diamonds). Over half of the total seedlings from each emerged from clumps of >5 seedlings

64.7% in clumps >5. Fig. 8 shows the relationship between the number of seedlings per clump and both the absolute and cumulative relative frequency of seedlings.

We determined burial depth of 30 seedlings that germinated after natural fire by carefully excavating the area around the seedling to locate the seed coat that fractures at the depth from which it germinates (Fig. 4b). The mean germination depth (at top of seeds) was 24.2, with $Q1 = 20.0$ and $Q3 = 29.5$ mm. This is significantly lower than the depths of caches in the radiolabeled seed study, where the median burial depth was 12.9, with $Q1 = 10.0$ and $Q3 = 18.8$ mm.

Discussion

Fire can cause high mortality in persistent soil seedbanks, which, coupled with the ability to destroy seed-producing individuals above ground, can be extremely hazardous for plant population persistence

in fire-prone ecosystems. We studied dispersal dynamics—fruit removal, seed movement, microsite deposition, and seedling germination patterns—of an abundant and widespread species in a fire-prone ecosystem to understand how it may persist in such conditions. Our experimental results support the conclusion that scatter-hoarding rodents are the effective dispersers of *A. patula* (greenleaf manzanita), which, coupled with the theoretical arguments, sufficiently (i) negates the role of unassisted dispersal in this group of plants and (ii) reveals an important role that animal-mediated dispersal can play in fire-prone ecosystems.

Modes of dispersal of *Arctostaphylos patula*

Our full-shrub enclosure experiments monitored fruit removal that systematically allowed and excluded various guilds of potential dispersers, where rodent access determined not just the magnitude, but whether or not *any* fruits were removed (Fig. 3) compared to

the full-shrub exclosure treatment. Because erecting an artificial cage (Fig. 2a) around a shrub may have deterred apprehensive avian and mammalian foragers, this minimally demonstrates that rodents have the ability to remove the same number of fruits as an unexclosed shrub (Fig. 3, Control was not different than Rodent-access treatments). Our seed stations (Fig. 2b), however, only showed rodents removing seeds. Among the scatter-hoarding rodents at the site, *Tamias amoenus* appeared to be the main disperser of *A. patula*, in terms of number of seeds and visits to seed stations captured by the motion-sensor cameras. At sites where most *A. patula* seeds were scatter hoarded, cameras recorded only *T. amoenus* removing seeds. Further, before and during this study, we observed *T. amoenus* foraging in the canopy of *A. patula* shrubs, removing seeds from the fruit pulp, filling their cheek pouches, and making seed caches. Dispersal of seeds by *T. amoenus* has been studied in other plants in this area using a variety of methods (e.g., *Pinus* and *Prunus* in Vander Wall 2008, 1994, respectively). Additionally, we found that 53–83% of seedlings emerge in clumped patterns, interpreted as an indicator of scatter-caches made by seed-hoarding rodents.

Based upon this series of experiments, we further conclude that the two other guilds of potential dispersers, birds, and omnivorous carnivorous mammals, respectively, have no role or a limited role in dispersal of *A. patula* based on the lack of seed removal and germination patterns. Not only were the exclosure treatments that allowed birds access no different than the treatments that excluded all animals, but *Turdus migratorius* (American Robin)—one of the most frugivorous birds in North America—refused to eat ripe *A. patula* fruits in laboratory experiments (C.M.M. and S.B.V.W., unpublished data). With respect to mammals, it is well established that black bears and other carnivores consume ripe *Arctostaphylos* fruits (e.g., Bowyer et al. 1983; Delibes et al. 1989; Wilson and Thomas 1999; Nielsen et al. 2004; Silverstein 2005), but we found little evidence for this mode of dispersal in this study. The exclosure treatments that prevented rodent but allowed carnivorous access had fruit removal most similar to the treatment that prevented all animal access, but we regularly observed bear scat laden with *Arctostaphylos* seeds. It is likely that we failed to detect the effect of carnivores because they are comparatively rare. When carnivores do consume fruits, passage through

the gut has not been shown to significantly change germination rates of *Arctostaphylos* seeds (Kauffman and Martin 1991; Silverstein 2005), a common phenomenon observed in plants dispersed by carnivores. Germination in *A. glandulosa* increased with charate under dark conditions (Keeley 1991), suggesting that the quality of dispersal provided by carnivorous mammals is relatively poor if seeds in feces are exposed to light on the soil surface (e.g., exposure to ultra-violet light, temperature extremes). Lastly, the patterns of seedling emergence that we observed (Table 2; Fig. 8) were not consistent with the densities of seeds generally found in scat (e.g., hundreds-to-thousands of seeds per scat). It seems possible, however, that rodents could remove seeds from carnivorous feces and cache them in soil as secondary dispersers, as this has been found to occur in other species of plants (Enders and Vander Wall 2012), meaning that bears could act as primary dispersers of *Arctostaphylos* seeds when coupled with seed-caching rodents. If this two-phased dispersal does occur, then it is a possibility that carnivorous mammals may act as long-distance dispersers because they disperse seeds much farther than the relatively short distances we observed in this study by rodents.

From this study, we cannot estimate the proportion of seeds dispersed abiotically. The seeds of *A. patula* do not have ancillary structures (e.g., awns, *sensu* “burial syndrome” in Humphreys et al. 2011), but they do have a larger seed size than abiotically dispersed seeds and can have a similar seed shape (Chambers et al. 1991; Thompson 1993) to plants with seeds that are abiotically dispersed, depending on the degree of nutlet fusion (five free—one fused). We attempted to set out several hundred marked seeds to assess abiotic burial rates experimentally without excluding animal foragers, but animals appeared to have removed most seeds before they could move down into the soil. Foraging animals present an experimental problem because an exclosure would alter the abiotic conditions that cause seed burial (e.g., wind, precipitation, run-off, temperature affecting cryoturbation). However, about 20 % of the seedlings that we found after wildfire (Table 2) had emerged as individuals. This may be attributed to abiotic processes, or remnants of recovered or pilfered caches. The *experimentum crucis* would be in seedless soil, excluding animals, and burn plots at different time intervals after one-to-several decades. We regard that

this current study, as a set of proximate experiments, yields qualitatively similar information about dispersal dynamics of *Arctostaphylos* that we would see in such an experiment.

Extending the dispersal syndrome boundary

One aim of the study was to take a plant species with an ambiguous seed dispersal syndrome and study it to further our understanding of how plants are dispersed; thereby more clearly delimiting dispersal syndromes. This task is, by no means, trivial, as any examination of the seed dispersal literature will reveal that further studies are needed to delimit dispersal syndromes. Large global datasets, for instance, have labeled 61 % of plant species as having an “unknown” dispersal syndrome (Moles et al. 2005a, b, 2007). As another example, one 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). Truly unassisted dispersal would suggest that any reasonable level of gene flow, migration, or coevolution would happen over time scales inconsistent with observation, so it is likely that most of these plants have an effective, albeit unappreciated, means of dispersal. 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, as examples, then a thorough understanding of dispersal modes is needed—labeling 2/3 of species in a community as “unknown” is insufficient.

This study extends the breadth of what we understand to be the scatter-hoarding seed dispersal syndrome to include fire-adapted species that maintain a persistent seed bank. Before this study, nearly all seeds and nuts known to be dispersed this way germinated within a year. One study that has expanded our understanding of this seed dispersal syndrome demonstrated that a perennial grass with relatively small seeds, much smaller than the large rewards (e.g., acorns, hickory nuts, chestnuts, walnuts) thought necessary to entice animals to disperse seeds, can be dispersed by seed caching (Longland et al. 2001). Another example that has expanded our understanding of scatter-hoarding seed dispersal syndromes showed that perennial herbs with relatively unattractive seeds

can be dispersed by scatter-hoarding rodents (Barga and Vander Wall 2013).

Seed bank dynamics in fire-prone ecosystems

A species' ability to disperse seeds to suitable and safe microsites is an important life-history trait (Harper 1977; Grime 1977) that allows for a species to exploit spatiotemporally heterogeneous resources (Hastings 1980; Levins and Culver 1971), endure disturbance (Levin et al. 1984; Cohen and Levin 1991), and interact with con- and heterospecifics (Tilman 1994; Bolker and Pacala 1999). In fire-prone ecosystems, it has been observed that post-fire community composition is largely determined by the local, pre-fire residents, especially for the woody taxa (Keeley et al. 2006; Hanes 1971). A mechanistic understanding of seed bank deposition will therefore allow us to better model and predict single-species population dynamics, outcomes of interactions between species, and possibly community composition.

In the case of *A. patula*, revealing that scatter-hoarding rodents disperse seeds to safe microsites is tantamount to distinguishing between what limits population growth: seed production or safe sites. Individual *Arctostaphylos patula* shrubs in the two-year period of this study produced a range of ~375–7600 seeds. The median fire-return interval in the northern eastern Sierra Nevada is 9 years (Taylor 2004), meaning that an individual *A. patula* may produce within the range of $0.2\text{--}4.5 \times 10^4$ seeds. Under the central California probability of fire (i.e., Moritz 2003, Fig. 1), an individual *A. patula* could produce $0.1\text{--}2.3 \times 10^5$ seeds before the area reaches a 50 % probability of a recurrent fire. Both of these estimates for plants with refractory seeds would be akin to reproduction in discrete generations because recruitment occurs after a fire event, and they are extremely large, suggesting that recruitment in *Arctostaphylos patula*, like many other plants in fire-prone ecosystems, is not likely limited by seed production, but rather limited by arrival to safe sites (Harper 1977). This is similar to observations in other long-lived woody plants (e.g., Clark et al. 2007; Eriksson and Ehrlén 1992), where seed loss to predators—including mortality due to seed dispersal—is negligible to the populations (Andersen 1989).

The scatter-hoarding of seeds in *Arctostaphylos* likely varies in importance across this ecologically and evolutionarily diverse group. One main way the importance of scatter-hoarding likely varies is that *Arctostaphylos* has two main regenerative habits, with some species only regenerating by seed (obligate seeding) following a fire event and others regenerating by a combination of both regenerating by seed and resprouting following a fire event (facultative sprouting) (Wells 2000). Because obligate seeders only regenerate from seed and the adults are killed by fire, we hypothesize that seed burial is more critical to those species' persistence, of which burial by scatter-hoarding animals can be a very efficient mean. In fact, the one of the most widespread and dominant obligate-seeding members of *Arctostaphylos*, *A. glauca*, is morphologically unequivocally a scatter-hoarded species. *Arctostaphylos glauca* has a large, single nut that falls within the size range of local oaks, with seeds the size of *Quercus vaccinifolia* and larger than *Chrysolepis sempervirens* (a species that has been shown to be dispersed by scatter-hoarding rodents in Roth and Vander Wall (2005)). Scatter-hoarding may also vary in importance across the diverse group in other ways, like it may be less important for species that exist in areas with long-fire-return intervals or it may be more important for species that exist in patchy habitats (e.g., edaphic specialists that are common in California and in *Arctostaphylos*) where short, local seed dispersal allows for a higher competitive ability over limited space.

The role of animals dispersing seeds in fire-prone ecosystems can be an important burial syndrome (Peart 1984; Humphreys et al. 2011). To our knowledge, only one other set of studies demonstrated this phenomenon, in an ant-dispersed plant in Australia (Auld 1986a, b). These studies examined the population dynamics of *Acacia suaveolens*, a long-lived woody shrub with seeds that are stimulated by fire and are dispersed by animals, but by ants. Auld (1986b) conducted a series of burn treatments on seeds to determine under what conditions they germinate, while Auld (1986a) actually tracked seeds to determine where ants dispersed them. Like in many other studies (e.g., Odion and Davis 2000, this one), it was found that seeds near the soil surface experienced complete-to-extremely-high mortality. What was remarkable, however, is that depths from which *Acacia suaveolens* germinated were concordant with

the depths where the ants buried the seeds. We attempted to germinate seeds at different depths using controlled burns in two years at our field site, but we were unable to simulate the conditions needed for seed germination. As a proximate indicator, however, rodents dispersed seeds to microsites that spanned the range from which they germinate (Fig. 4); albeit, not as deep as the depth from which they germinate.

Spatial patterns of seeds dispersed by animals

The differences between spatial distributions of seed patterns are striking (Figs. 5, 6 and 7, Table 1). We emphasize the difference between the two distributions because they are functionally very different yet rarely distinguished in the literature despite attempts to encourage researchers to do so (Peart 1985; Nathan and Muller-Landau 2000; Cousens et al. 2008; Nathan et al. 2012). Concisely, the density distribution $\omega(r)$ gives the probability or frequency that a propagule will arrive at a *point*; whereas the distance distribution $f(r)$ gives the probability or frequency that a propagule will arrive at an *annulus*. The distance distribution is to be understood as the distribution of displacement of individuals from a source (i.e., the maternal plant) and should be used for individual-based models. But because space does not shrink or animals do not grow as a function of distance, when area is taken into account, we reveal the pattern of seeds on a 2-dimensional, Cartesian landscape; the density distribution. Although mathematically equivalent, the density distribution is mathematically more simple (e.g., probability density functions and integration over polar coordinates) and the Cartesian coordinate system upon which it is based (orthogonal pair of longitudinal and lateral axes) is more intuitive. It is for the latter two reasons that we suggest researchers to minimally report the density distribution of dispersal data.

We adopted a mechanistic modeling approach based on Wichmann et al. (2009) and Bullock et al. (2011) that fits models with biologically meaningful parameters; specifically b in Eqs. 2 and 3, respectively, as a constant or non-constant caching rate. Both models fit the data very well, capturing the relatively high density of caches at a seed source and the strong decline of seeds as the distance from the source is increased. Unfortunately, however, neither model fit convincingly better than the other (Table 1), so we were unable to detect a difference between caching

rate and distance from the seed source. There was large variation in our dataset (Fig. 6), but with more replication and under more controlled settings (e.g., a homogenous environment), we believe fitting mechanistic models to animal scatter-hoarding behavior could more exactly allow researchers to understand their behavior. To our knowledge, this has not yet been performed.

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