An ecological ménage à trois: a three-way interplay of plants, animals, and fire

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introduction

conceptual background

It has long been thought that plant-animal mutualistic interactions have played a key role in the success of seed-producing plants. Three inclusive hypotheses have been suggested as to why animal-mediated seed dispersal benefits plants (*sensu* Howe and Smallwood, *ARES*, 1982); the most understudied and poorly understood being the directed dispersal hypothesis. This hypothesis confers that a benefit of animal-mediated seed dispersal is the disproportionate dispersal of seeds to microsites that facilitate seed germination and survival. In our study, we examined this hypothesis in a novel way by studying the interaction between plants, animals, and disturbance (fire).

questions

1. Do seed-caching animals benefit plants in fire-prone ecosystems by protecting seeds from fire?
2. Do seed-caching animals benefit plants in fire-prone ecosystems by facilitating germination of seeds needing charate scarification?
3. Why am I here (all spatiotemporal scales)?

hypothesis

By burying and protecting seeds from fire, scatterhoarding animals are direct dispersers of seeds in fire-prone ecosystems by:

a. disproportionally dispersing seeds to favourable microsites, and
b. increasing post-dispersal survival

methods

study system

Arctostaphylos (Ericaceae) is a diverse group of woody shrubs mostly confined to the California Floristic Province with multiple dispersal modalities and different adaptations to fire.

experiment

Observation: 1. Label, set out, and relocate seeds with radioactive scandium-46 and determine dispersal distance, microsite characteristics, and dispersing animal. 2. Recording patterns of seedling recruitment. Manipulation: 1. Exclosure treatments with three levels (no seed-caching animals, allowing seed-caching animals, control). 2. Factorial greenhouse and field study placing seeds at different depths and prescribing fire.

figure 1: Seeds labeled with scandium-46 as they are presented to potential seed-caching animals. Once animals harvest and cache seeds, Geiger counters are used to relocate seeds and determine cache characteristics.

results

seed fate pathways

Pathways to establishment in *Arctostaphylos* are complex. **Figure 2** is a conceptual diagram of the possible pathways to establishment, and relative probabilities associated with each path are currently being determined.

Two paths are important to note:

(i) *Arctostaphylos* seeds obligately germinate and establish after a fire event, and
(ii) diplochory is ubiquitous and, presumably, important for dispersal, but not seed deposition

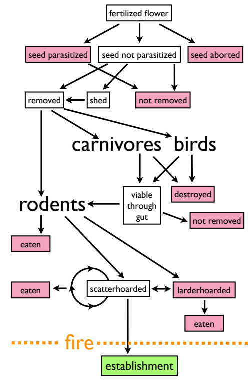

figure 2: Conceptual seed fate pathway diagram for *Arctostaphylos*. All *Arctostaphylos* taxa need charate scarification to germinate, and most are diplochorous.

cache characteristics and fire

Animals that cache food items place them in a microsite that may protect them from fire.

Fires severity is highly variable, and **figure 3A** shows that higher intensity fires promote germination from seed caches.

Figure 3B shows that animals can cache seeds at depths that may protect seeds from fire. Experiments are currently in progress to examine germination at different depths and fire treatments in the greenhouse and field.

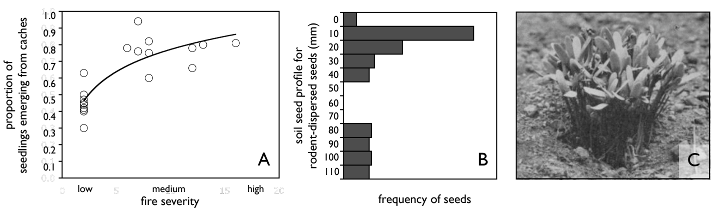

figure 3: Scattercaching animals deposit seeds in microsites that facilitate germination in fire-prone ecosystems. A higher proportion of *Arctostaphylos silvicola* seeds germinate from more severe fires **(A)**. Here, fire severity is measured by minimum stem diameter in 2009 after a 2008 fire in Santa Cruz, California ($r^2 = 0.705$, $n = 19$; data courtesy of Tom Parker, SFSU). Panel **(B)** depicts a soil seed profile for scattercachers of *A. patula* seeds by chipmunks in the northern Sierra Nevada in 2009. Sixty-five caches were found after deploying seven sets of seeds in the late summer and fall. The modal depth that seeds were buried is 10 mm, but many other seeds were cached at depths that may protect them from the heat of fires. Panel **(C)** shows a clump of *Arctostaphylos* seedlings after a fire. It has been known for a long time that *Arctostaphylos* seeds germinate in clusters, which further suggests that rodents cache seeds in microsites that protect them from fire (photo. from Tevis, *J. Mamm.* 1953).

rodents as seed dispersers

Rodents may act as primary **(figure 5C)** and secondary **(figure 4)** dispersers of manzanita seeds.

As primary dispersers, not only do rodents place seeds in suitable microsites, but they have the ability to move seeds substantial distances from the parent plant **(figures 5A & 5B)**. This may occur to a greater degree than we previously recognized with reciprocal cache pilferage.

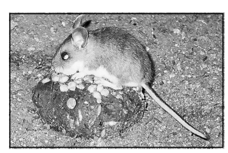

figure 4: *Peromyscus maniculatus* removing seeds from scat. Photo. courtesy of Mark Enders.

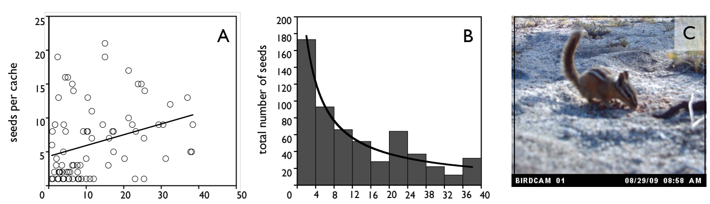

figure 5: Rodents not only place seeds in suitable microsites for germination, but they also disperse *Arctostaphylos* seeds throughout the landscape. Panel **(A)** shows the number seeds per cache as a function of distance. When consolidated, panel **(B)** shows a histogram of the distribution of seeds as rodents move them away from the parent plant. Motion-sensor cameras are able to capture rodents dispersing *A. patula* seeds, and can be identified to the species level **(C)**. All data in figure five was collected in the northern Sierra Nevada from seven trials of deploying and relocating radiolabeled seeds.

discussion

scatterhoarding in fire-prone ecosystems

Preliminary evidence suggests that scatter-hoarding rodents provide an additional benefit to plants in fire-prone ecosystems by protecting them from fire, which is showing to be accurate in *Arctostphylos*.

This interpretation presents an additional instance of directed dispersal, unique in the light of disturbance.

Given that scatter-hoarding is widespread in the fire-prone California Floristic Province, we propose that this benefit may be ubiquitous, not only in *Arctostaphylos*, but in many other animal-dispersed plants.

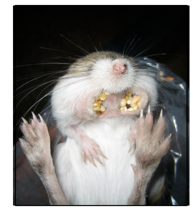

figure 6: Kangaroo rats (*Dipodomys* sp.) are common scattercachers in the arid southwestern US.

directed dispersal

Howe and Smallwood (*ARES*, 1982) first articulated the directed dispersal hypothesis, which confers that animal-dispersed plants benefit from being non-randomly and disproportionally dispersed to microsites that facilitate germination.

Although we see the utility in acknowledging this advantage, this hypothesis can be interpreted as one end on a continuum of seed specializations to microsites.

We recommend reconsideration of the continuum of specialist and generalist microsites that in which seeds germinate and ask:

What came first: the disperser or the microsite?

figure 7: Sclerophyllous leaves of *Arctostaphylos patula*. *Arctostaphylos* shares convergent habits with many other mediterranean-climate shrubs.

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