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Birds, lagomorphs, rodents, and patterns of *Juniperus osteosperma* recruitment

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Key words: diplochory; juniper seed dispersal; woodland expansion; woodland infilling

Abstract

Juniper woodland infilling and expansion, considered threats by rangeland managers, is driven by seed dispersal. We studied the roles of birds, lagomorphs, and rodents in *Juniperus osteosperma* recruitment in the Great Basin of western Utah, USA. Recruits were disproportionately in shrub microhabitats. Birds disperse no seeds, lagomorphs almost exclusively disperse seeds to open interspaces, and only rodents disproportionately cache in shrub microhabitats. Results suggest the primary driver of recruitment is seed-caching rodents.

Introduction

Conifer expansion into sagebrush shrublands in the western USA is of concern to rangeland managers, contributing to a reduction in shrub and grass cover, increased erosion, decreased soil water, and more (Chambers et al. 2014, McIver et al. 2014). In the Eastern Great Basin this process is driven primarily by *Juniperus ostesperma*, a monoecious conifer producing modified "fleshy" cones containing a single seed; cones dry within weeks, slowly dropping to the ground over an extended period (Schupp et al. 1995, Zlatnik 1999).

Key to juniper expansion is seed dispersal, especially where seeds are deposited, which determines the biotic (e.g. seed predators, mycorrhiza) and abiotic (e.g. microclimate, soil water) environments recruits encounter and thus recruitment probability (Schupp and Fuentes 1995, Schupp et al. 2010). *J. osteosperma* seed dispersal is not well understood, but lagomorphs (Schupp et al. 1995) and rodents (Dimitri et al. 2017) reportedly disperse their seeds. Further, Juniperus spp. are extensively dispersed by birds (Chambers et al. 1999). As a first step in assessing the role of seed dispersal in *J. osteosperma* recruitment, we quantified (1) the microhabitat pattern of recruitment and (2) the microhabitat pattern of seed deposition by birds, lagomorphs, and rodents. We compare patterns of recruitment and dispersal to determine the disperser group(s) most likely driving *J. osteosperma* recruitment.

Methods

We conducted this study in a 2-ha (100 x 200 m) juniper woodland plot in west-central Utah, USA, (39° 53' 19" N, 112° 08' 58" W, 1774 masl), a region with hot, dry summers and cold, wet winters. We distinguish four microhabitats: 1) "Juniper," beneath the canopy of a live *J. osteosperma*; 2) "Dead Juniper," beneath the canopy of a dead *J. osteosperma*; 3) "Shrub," beneath the canopy of a shrub; and 4) "Open," interspace without woody cover. We quantified proportional microhabitat cover with the Line Intercept Method (Fiala et al. 2006) along 40, 100 m transects across the plot. We located, marked, and measured all *J. osteosperma* recruits (≤1 m height) and recorded their microhabitat. We noted "seedling caches," where two or more recruits grew adjacent, assuming adjacent recruits likely came from a cache. We investigated seed dispersal by birds with timed watches of tree clusters during winter when cones are fresher and frugivorous bird density and diversity are highest. We assessed dispersal by lagomorphs by collecting pellets by microhabitat type along a 2-m wide 440 m long transect connecting 15 random points across the plot. Pellets were dissected to quantify seeds/microhabitat. Dispersal by rodents was sampled by coating cleaned, filled seeds with fluorescent powder and placing a set of 30 seeds in a petri dish in the middle of a powder-filled plate. Seeds were set at sunset. Before sunrise we returned and searched using an ultraviolet light, following powder trails and marking disturbed sites. We returned later to search flagged locations for caches. Analyses were based on comparing actual microhabitat distributions with expected distributions based on proportional cover of microhabitats using simple Chi-square tests conducted by hand.

Results

Recruits were not randomly distributed (n=263, Table 1). The dominant microhabitat was Open, while Shrub was substantially lower. However, recruits were much more frequent than expected beneath Shrubs and much less frequent than expected in Open.

Table 1. The proportion of each variable represented by each of the four identified microhabitat types. Significance refers to the significance of a Chi-square comparing the actual microhabitat distribution of variables (e.g. recruits) with the expected distribution based on proportional cover of the microhabitats; that is, the expected distribution if the variable (e.g. recruits) is distributed independently of microhabitat type.

	Proportion				
Variable	Juniper	Dead Juniper	Shrub	Open	Significance
Microhabitat Cover	0.16	0.02	0.25	0.58	N/A
Recruits	0.16	0.00	0.67	0.18	P<0.05
Seedling Caches	0.19	0.00	0.75	0.06	P<0.05
Bird-dispersed Seeds	--	--	--	--	--
Lagomorph-dispersed Seeds	0.04	0.00	0.00	0.96	P<0.05

Rodent-dispersed Caches	0.07	0.00	0.80	0.13	P<0.05

In over 100 person-tree-hours of observations the only bird species feeding on *J. osteosperma* cones was the Juniper Titmouse (*Baeolophus ridgwayi*), a seed predator (Fuentes and Schupp 1998).

In contrast, lagomorphs dispersed seeds (Table 1). We collected 692 pellets; 9% contained 1-4 intact seeds each for a total of 76 seeds. Many more of these seeds were dispersed to Open and fewer to Shrub than expected.

We addressed the role of rodents in *J. osteosperma* recruitment using the microhabitat distribution of “seedling caches” and of seed caches. We estimated 16% of recruits were in “seedling caches,” which were disproportionately beneath Shrub (Table 1). We located 30 seed caches; congruent with the distribution of “seedling caches,” many more were located beneath Shrub than expected, while very few were in Open (Table 1).

Discussion

Frugivorous birds are considered the most important dispersers of juniper, dispersing many seeds and depositing them beneath woody vegetation which is thought to facilitate establishment (e.g. Dimitri and Longland 2017, Isla et al 2024). Our evidence suggests that rodents fulfill this role in *J. osteosperma* – only dispersal and caching by rodents explains the microhabitat pattern of recruitment.

Both “seedling caches” and seed caches support the role of rodents. In both cases, caches were disproportionately frequent in Shrub and disproportionately infrequent in Open. The seed caches we located represent the first of potentially many sequential caching events. Rodents pilfer juniper seed caches, and although they consume some and larder hoard others, many are recached (Dimitri and Longland 2022). If caches in our system are pilfered, rodents apparently disproportionately recache beneath shrubs, reducing the number of seeds available for germination without altering the microhabitat distributions.

As noted, many believe that microhabitats beneath woody vegetation are favorable for juniper recruitment. Experimental seed sowings in our plot showed inconsistent, slight germination and survival benefits in Shrub relative to Open, with a small significant benefit in some cohorts during some sampling periods but not in others (Schupp et al., unpublished data). This benefit is insufficient to drive the pattern of recruitment. Facilitation appears to enhance rather than cause the distribution of recruits.

Although our work occurred within a woodland and does not directly address expansion into shrublands we can make informed speculation. First, although some rodents are restricted to woodlands, others use both woodlands and shrublands (Dimitri and Longland 2017) and likely contribute to local expansion at the ecotone through short-distance dispersal. Further, more rapid expansion might be due to diplochory, or two-stage dispersal, as has been suggested for bird-rodent diplochory of *J. occidentalis* (Longland and Dimitri 2016), with lagomorphs initially dispersing seeds out of the woodland and rodents subsequently harvesting seeds from faeces and caching some beneath shrubs. Although the density of seeds in lagomorph faeces drops off rapidly with distance from woodland edge, lagomorphs can disperse some seeds long distances into shrublands (Schupp et al. 1997). This could produce scattered reproductives far in front of the woodland that can create expanding nuclei of woodlands through local dispersal, a process known to accelerate tree movement (Clark et al. 1998).

Acknowledgements

Research was supported by the Utah Agricultural Experiment Station, projects UTA 1020, UTA 1523. Permission to use field sites was given by the Bureau of Land Management.

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