Received: 5 August 2025 | Accepted: 27 October 2025

DOI: 10.1002/ajb2.70151

RESEARCH ARTICLE

Wind-driven seed dispersal differentially promotes seed trapping and retention across alpine plants

Courtenay A. Ray[1,2,3,4] | **Savannah R. Troy**[4,5] | **Emily V. Xie**[2,4,6] | **Thomas M. Jenkins**[4,7,8] | **Gavin Belfry**[4,9] | **Aidan Wells**[4,10] | **Perry de Valpine**[2] | **Benjamin W. Blonder**[2,3,4]

[1]Department of Botany, University of Wyoming, 1000 E. University Ave., Laramie, WY 82017, USA

[2]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Mulford Hall, 120 Mulford Hall, Berkeley, CA 94720, USA

[3]School of Life Sciences, Arizona State University, P.O. Box 874501, Tempe, AZ 85287, USA

[4]Rocky Mountain Biological Laboratory, PO Box 519, Crested Butte, CO 81224, USA

[5]School of Natural Resources and the Environment, University of Florida, McCarty Hall, 1604 McCarty Dr #1008, Gainesville, FL 32603, USA

[6]Department of Plant & Microbial Biology, University of California, Berkeley, 111 Koshland Hall, Berkeley, CA 94720, USA

[7]Department of Zoology, University of Oxford, 11a Mansfield Rd, Oxford OX1 3SZ, UK

[8]School of Geosciences, University of Edinburgh, Drummond St, Edinburgh EH8 9XP, UK

[9]Department of Ecology and Evolutionary Biology, University of Tennessee, University of Tennessee, Knoxville, TN 37996, USA

[10]Department of Molecular Biology, Colorado College, 14 E. Cache La Poudre, Colorado Springs, CO 80903, USA

Correspondence

Courtenay A. Ray, Department of Botany, University of Wyoming, 1000 E. University Ave., Laramie, WY 82017 USA.
Email: cray10@uwyo.edu

Funding information

C.A.R. was supported through Arizona State University's RTI Graduate Student Support, the Colorado Mountain Club Kurt Gerstle Fellowship, the Rocky Mountain Biological Laboratory Snyder Endowment Graduate Fellowship, the Rocky Mountain Biological Laboratory Jean Langenheim Fellowship, the UC Berkeley chapter of Sigma Xi's Grants-in-Aid of Research Award, and the U.S. National Science Foundation (grant PRFB-2410511). E.X. was supported by the Sponsored Projects for Undergraduate Research (SPUR) grant from the Rausser College of Natural Resources at UC Berkeley. G.B. was supported by the Ryan Brown Scholarship. B.W.B. was supported by the Rocky Mountain Biological Laboratory (Navjot Sodhi fellowship and core fellowship programs), a grant from the Peder Sather Center for Advanced Study, and the U.S. National Science Foundation (grant DEB-2425575).

Abstract

Premise: Seed dispersal can mediate species interactions between plants across life stages. Plants can physically stop seed movement (seed trapping) and prevent further dispersal following entrapment (seed retention). We therefore hypothesized seed trapping and retention rates depend on the physical attributes of interacting seeds and plants, including seed traits and plant length.

Methods: For combinations of co-occurring plant species in an alpine community, we experimentally measured seed trapping and retention potential. To measure seed trapping, we determined the rate at which seeds were unable to physically pass through vegetation without stopping after being launched at plants. To assess seed retention, we compared the rate that seeds left vegetation following entrapment across plant and seed species and by seed traits.

Results: Seed trapping rates were higher for larger-sized plants and differed among plant species but not seed species. Seed trapping and retention rates were higher for plant species with denser vegetation. Seeds with a pappus were retained less than seeds without, and we observed interactive effects between plant and seed species identity on retention rates.

Conclusions: Seed trapping and retention rates are influenced by species identities and the physical attributes of plants and seeds. Because both processes can contribute to where a seed is ultimately dispersed, seed trapping and retention may mediate species co-occurrence and further species interactions.

KEYWORDS

alpine, community assembly, community ecology, dispersal, seed retention, seed trapping, species interactions

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Species interactions and dispersal mechanisms are often inseparable among sessile organisms such as plants, fungi, and many aquatic invertebrates. Dispersal at early-life stages represents a trade-off between the potential of finding space to establish, acquiring resources, and avoiding unfavorable conditions at a place of origin and the risk of ending in a place less favorable (Janzen, 1970; Mix et al., 2006). For plants, seeds are frequently dispersed through interactions with animals (Rogers et al., 2021), including through hitchhiking (Baltzinger et al., 2019) and gut passage (Traveset, 1998), while abiotic dispersal mechanisms promote plant–plant interactions through wind, rain, snow, and gravity. In harsh environments such as desert and alpine tundra, seeds frequently depend on dispersal to establish near facilitative neighboring plants (e.g., Shreve, 1931).

Interactions between seeds and plants during seed dispersal have important consequences for species interactions and community assembly processes, including density-dependent competition (Aguiar and Sala, 1997; Bullock and Moy, 2004). Vegetation may reduce initial seed movement (seed trapping) or prevent further seed movement following entrapment (seed retention). These phenomena may result from direct physical contact between plants or indirect effects of vegetation on the environment such as alteration of wind and fluvial profiles (Lipoma et al., 2019). If seed retention causes seed death, the plant–plant interaction results in dispersal failure. Alternatively, seed trapping can influence the distance and trajectory of a dispersing seed, including by determining the outcome of secondary dispersal (i.e., seed mobility following initial dispersal from the parent plant).

Because seeds may germinate within or adjacent to the plant that traps and retains them, these interactions can promote species co-occurrence in a community. If neighboring vegetation improves resource availability or buffers microclimate conditions, as is common in many stringent environments (Callaway and Walker, 1997; Callaway et al., 2002), particularly among seedlings and juvenile plants (Miriti, 2006), then co-occurrence of the seed and trapping plant may be favored. Further, dispersal-mediated plant–plant interactions could promote species richness among interacting plants, potentially leading to increased facilitative effects (Wright et al., 2021). However, it is unclear for which contexts and species pairs dispersal-mediated plant–plant interactions are most expected (Gouws et al., 2021).

The physical properties of seeds and plants may provide a mechanism explaining variation in dispersal-mediated plant–plant interactions (Figure 1; Beckman and Sullivan, 2023). Seed size can influence seed trapping (Bullock and Moy, 2004; de Jager et al., 2019), but less is known about the contributions of other seed traits including seed shape parameters (length, width, thickness), seed mass, and pappus traits (but see Lipoma et al., 2019). Further, because seed banks (Gouws et al., 2021) and seed rain (Bullock and Moy, 2004) often vary by proximity to adult plants and by functional group (Aguiar and Sala, 1997), the traits of both seeds and adult plants may influence dispersal outcomes.

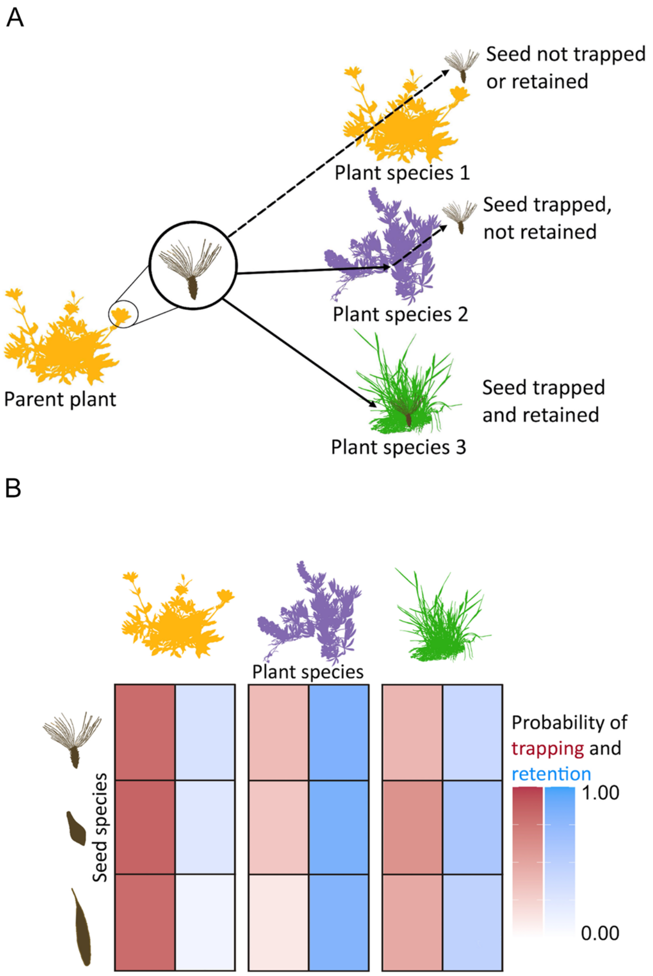

FIGURE 1 Conceptual figure. (A) Seeds dispersed from a parent plant to focal plants may either be not trapped or retained, trapped but not retained, or trapped and retained. (B) We hypothesize that due to physical attributes (i.e., size and growth form), plant species could be good trappers, but not good retainers (species 1), vice versa (species 2), or have similar trapping and retention probabilities (species 3). Plants may also trap and retain seed comparably across seed species (species 1 and 2), or trapping may vary by seed species (species 3).

There has been limited study of the influence of seed traits on the probability of being trapped or retained in vegetation and comparisons of trapping and retention for plant species with different vegetation traits have not been compared in a field setting. We are aware only of Tian et al. (2023a, b) who investigated seed–plant dispersal interactions in a laboratory setting. To explore the potential of seed trapping and retention to mediate plant–plant interactions, we therefore undertook a community study covering multiple species, enabling isolation of seed and vegetation effects in a common environment.

We conducted two experiments in an alpine tundra plant community that is frequently windy and where microclimate modification is prevalent (Ray et al., 2023). We first measured seed traits related to dispersal for six common species in the community. Then, in the first experiment, we asked (Q1) how the seed trapping rates were influenced by species identities and vegetation length. In the second experiment, we asked (Q2) how the probability of seed dispersal following entrapment (i.e., no retention) changed with species identities, seed traits, and interactions among these factors. We hypothesized that trapping and retention would vary with seed traits and predicted higher trapping and retention rates for large or heavy seeds and for seeds without a pappus. We also hypothesized that trapping and retention rates would vary with vegetative differences, with larger individuals and plant species with denser vegetation having higher seed trapping and retention rates. This experimental approach provides a proxy for the potential of seeds to be trapped or retained and enables inference about the existence of multiple dispersal-related processes and their drivers.

MATERIALS AND METHODS

Site description

We conducted seed trapping and retention experiments at a site at 3540 m a.s.l. in southwestern Colorado (38.978725° N, 107.042104° W) (Appendix S1). The alpine site is on a scree-covered southeast-facing ridgeline with limited soil development and strong winds (Appendix S2). The vegetation is patchy, highly clustered, and dominated by perennial graminoids and herbs. The snow-free season is typically from June to October.

The site for the seed trapping and retention experiments was adjacent (<150 m) to a long-term demography study (Appendix S1; Blonder et al., 2018). Nineteen species occur in the demography study, with higher species richness in the surrounding area; we studied a subset of those species. We conducted both experiments late in the growing season (trapping experiment: 1–8 August 2021; retention experiment: 29 August–11 September 2019) when most species are past flowering and seed dispersal of resident plants is common.

Focal plant species

We selected plant species (here meaning vegetation) based on abundance and morphology for both experiments. To compare trapping probabilities (Q1), we selected two common herbs that differ in vegetation density: *Heterotheca villosa* (Pursh) Shinners (Asteraceae), which has a bushy canopy, and *Lupinus argenteus* Pursh (Fabaceae), which has an open canopy (Figure 2A). For the retention experiment (Q2), we selected plant species that were abundant in the adjacent demography plot in 2018 (Appendix S3) and thus represented most potential interaction partners for seeds in the community. These plant species included perennial herbs that develop woody stems with maturation, such as *Heterotheca villosa*, *Lupinus argenteus, Eriogonum umbellatum* Torr. (Polygonaceae), perennial herbs with rosettes, *Senecio crassulus* A. Gray (Asteraceae) and *Ivesia gordonii* (Hook.) Torr. & A. Gray (Rosaceae); and a grass, *Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould (Poaceae) (Figure 2A).

Focal seed species

We selected seed species that differed from each other morphologically and had high abundance. For the trapping experiment (Q1), we used *Agoseris glauca* (Pursh) Raf. (Asteraceae), *Elymus lanceolatus*, *Eriogonum umbellatum*, *Heterotheca villosa*, and *Senecio crassulus* (Figure 2B). We quantified the trapping of *Eriogonum umbellatum* seeds in two conditions, achene with flower or achene only because seeds disperse and germinate in both conditions. In the retention experiment (Q2), we used the same seed species as in the trapping experiment, as well as *Eremogone congesta* (Nutt.) Ikonn. (Caryophyllaceae), which was too small to locate reliably in the trapping experiment (Figure 2B). Only *Eriogonum umbellatum* seeds outside of the flower were included in the retention experiment. Three seed species, *Agoseris glauca*, *Heterotheca villosa*, and *Senecio crassulus* had a pappus, the hair-like structure at the terminal end of a seed that is important for wind dispersal. Fine hairs were also present on the seed surface of *Heterotheca villosa*.

Measurement of seed functional traits

We measured five seed functional traits considered important to dispersal (length, width, thickness, pappus length, and dry mass) for six species (*Agoseris glauca*, *Elymus lanceolatus*, *Eremogone congesta*, *Eriogonum umbellatum*, *Heterotheca villosa*, *Senecio crassulus*). We measured all traits on 10 seeds from 10 plants for 100 seeds per species using the protocols of Pérez-Harguindeguy et al. (2013). For seeds with a pappus, we measured the average length of three arbitrarily chosen pappi per seed. We measured morphological traits in ImageJ (Schneider et al., 2012) from images captured using a Leica (Wexlar, Germany) dissecting microscope. Before measuring the dry mass, we removed pappi and dried seeds at 70°–80°C for at least 3 days, then individually weighed seeds to the nearest 0.001 mg.

Trapping experiment (Q1): overview

We estimated the potential trapping ability of two focal species, *Heterotheca villosa* and *Lupinus argenteus*, in the field by blowing seeds into plants using a custom-constructed wind tunnel (Figure 3A). We defined trapping as a seed remaining within or directly under a focal plant after seed-plant contact in the wind tunnel. We measured trapping on five plants per focal species from a range of sizes by measuring the length of the longest

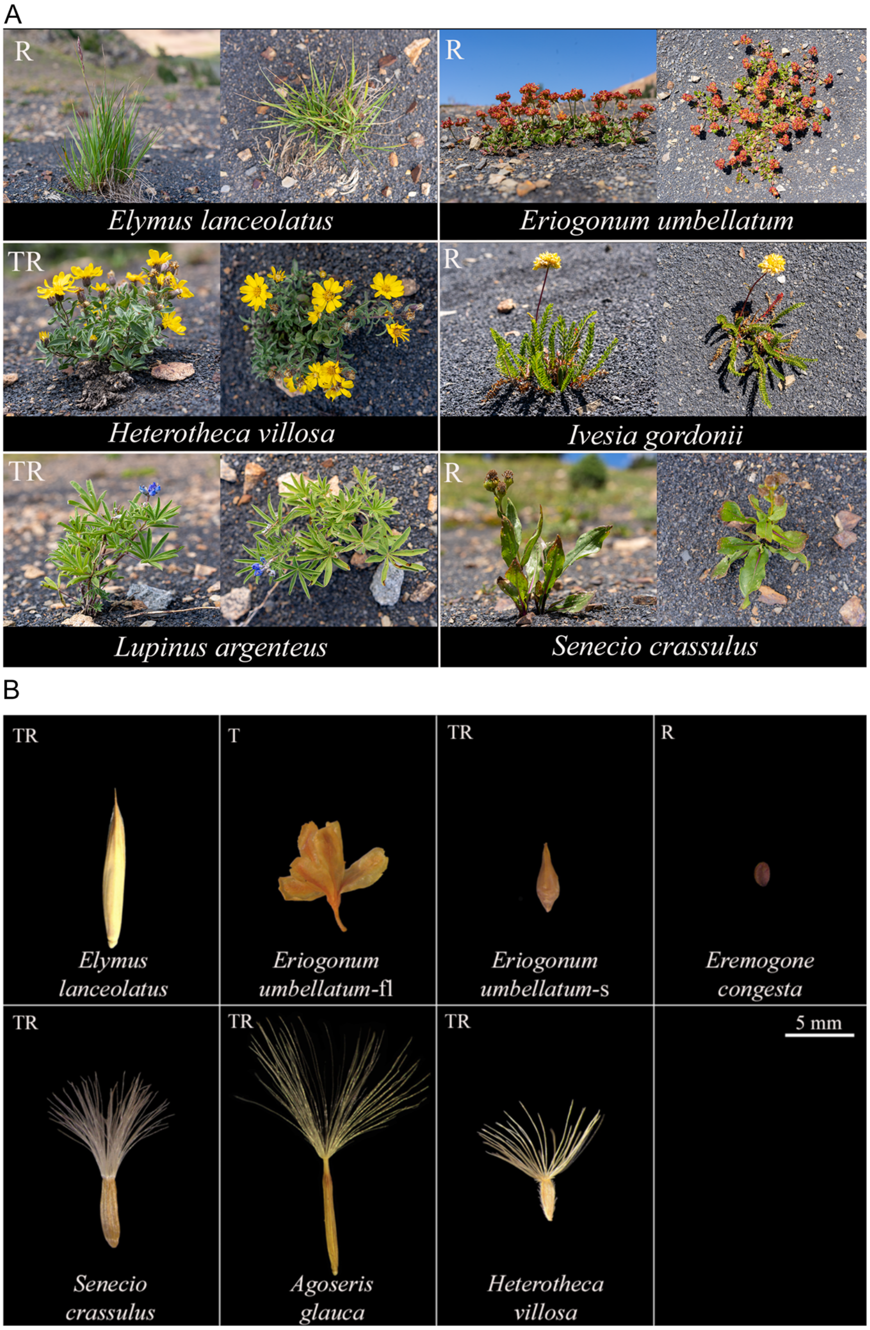

FIGURE 2 (A) Profile and aerial images of focal plant species in the trapping (T) and retention (R) experiments. Plants in these images range from ~10 to 30 cm in diameter. (B) Scaled images of the seed species used in the trapping (T) and retention (R) experiments in ascending order of mean PC1. We measured the trapping of *Eriogonum umbellatum* in two states, in flower (fl) and seed (s).

axis of each plant: *Heterotheca villosa* (length = 7–54 cm, mean = 27.2 cm, SD = 20.5 cm) and *Lupinus argenteus* (length = 4–45 cm, mean = 20.2 cm, SD = 16.9 cm) (Appendix S4). We collected focal seeds for the trapping experiment in August–September 2019 and stored them in open air as done by Pérez-Harguindeguy et al. (2013). To increase seed visibility, we dusted all seeds with UV reactive powder (GloMania, West Valley City, UT, USA) similar to the method of Schurr et al. (2005).

Trapping experiment (Q1): data collection

Wind tunnels are invaluable for comparing dispersal mechanisms and outcomes across species and environments (e.g., Zhu et al., 2019; Zong et al., 2023; Tian et al., 2023a). In this experiment, the wind tunnel consisted of the following components, from “wind source” to output: a handheld, gas leaf blower (B250 27-cc 2-cycle 205 mph 450 cfm; Craftsman, Towson, MD, USA), an intake bell, an

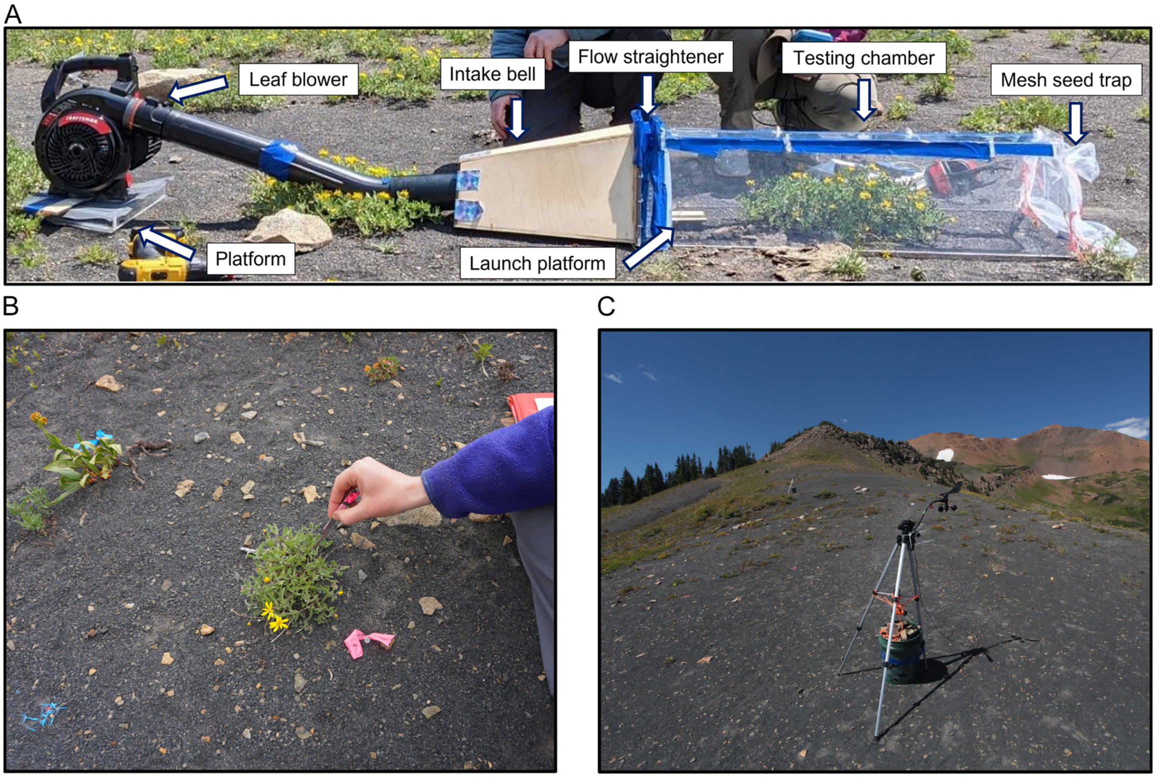

FIGURE 3 (A) Seed trapping setup. (B) The insertion of a seed into a *Heterotheca villosa* plant during the retention experiment. Blue-dyed seeds in the paired nonvegetated site are visible in the lower left corner. A second focal plant (*Senecio crassulus*, marked with blue flagging) is visible in the background. (C) A cup anemometer in the retention experiment. A second cup anemometer is visible in the background.

aluminum honeycomb flow straightener (3.18-mm cell), a testing chamber, and a rear mesh seed trap.

Through the seed trapping experiment setup, we sought to replicate the phenomenon of a seed physically contacting a plant while airborne and to determine the rate at which seeds were able to pass through plants following contact. The setup was consistent for each seed–plant comparison (Figure 3A), and trapping trials were done only under dry conditions to maintain consistency. Using the wind tunnel, we blew seeds into the path of focal plants. We considered seeds trapped if they were physically touching the focal plant or directly beneath the canopy for the entirety of the trial. Launches were considered successful if the seed contacted the plant without first touching the ground. After five successful launches, we left the blower on for 30 s. In one case, only four seeds were successfully launched for a seed–plant pair rather than five. We conducted 284 successful launches.

Inside the wind tunnel, we placed a wooden launch platform centered and adjacent to the flow straightener. Before every trapping trial, we confirmed that the launch platform was level and the focal plant was 15 cm away and centered relative to the launch platform. To avoid backflow into the tunnel, we did not face the end of the tunnel toward ambient wind. Local slopes at focal plants ranged from 0° to 15°. For one *Lupinus argenteus* on a 15° slope, we faced the output of the tunnel downhill. We placed the leaf blower on a 4.6-cm-high platform to achieve the desired air speeds.

To maintain consistency across trapping trials, we calibrated the wind tunnel to have air speeds at or near 5 m/s (11.2 mph) at the end of the launch platform. We chose to test seed trapping at 5 m/s because it was the minimum air speed at which all seeds could launch off the platform. Once air speeds were within range of 5 m/s, we individually launched seeds by placing the seed with forceps at the center edge of the launch platform, with the seed's longest axis pointed at the plant and the pappus (when applicable) pointed toward the blower. Air speeds at the launch site were 5–5.25 m/s, mean = 5.15 m/s, SD = 0.034 m/s.

Retention experiment (Q2): overview

In August 2018, we collected seeds from focal seed plants within ~500 m of the study site. Seeds were stored in open air until August 2019 and were dusted with colored fluorescent powder before deployment. In August 2019, we compared retention in different site types (i.e., focal plant species or nonvegetated areas) in a blocked experiment stratified by plant and seed species and plant lengths under natural wind regimes. We selected focal plants across the range of plant lengths (measured as the length of the longest axis) for each species (Appendix S4). To isolate the effects of plant species on retention, we avoided selecting focal plants with neighbors within 30 cm distance and multi-individual clusters.

We established a controlled comparison in a nonvegetated area adjacent to each focal plant (Figure 3B). Each nonvegetated site was 30 cm from the vegetated edge of the paired focal plant, marked with an orange nail, and did not have any other vegetation within 30 cm of it. The location of the nonvegetated site relative to the focal plant was determined by randomly selecting bearings until we identified a suitable area. Substrate characteristics, including scree size, were similar across all deployment sites, minimizing spatial edaphic effects on secondary dispersal (Chambers et al., 1991).

We recorded the average wind speed (m/s) and direction of origin (°) at 1-min intervals throughout the experiment using two-cup anemometers (Davis Cup Anemometer, Davis Instruments Corp., Hayward, CA, USA). We installed an anemometer at the upslope and downslope ends of the study site (Figure 3C). Each anemometer faced north and was 1.2 m above ground. Mean wind velocities captured by the anemometers were 10.56 m/s uphill (SD = 1.90 m/s) and 9.30 m/s (SD = 1.47) downhill (Appendix S2).

Retention experiment (Q2): data collection

To deploy seeds, we used forceps to individually place seeds on the scree surface either beneath the plant canopy or within 0–3 cm of the nail head at the paired nonvegetated area. We deployed seeds from one species (5 seeds) in the smallest plants and the seeds of up to six species (30 seeds) in the largest plants to avoid seed overlap. We deployed the same quantity and identity of seed species at the paired nonvegetated sites but with contrasting colors. We avoided similar color combinations at neighboring sites to reduce the risk of misattributed seeds. In total, we deployed 2924 seeds from 167 individuals: *Agoseris glauca* (*N* source plants = 25, *N* seeds = 579), *Elymus lanceolatus* (28, 450), *Eremogone congesta* (16, 161), *Eriogonum umbellatum* (54, 589), *Heterotheca villosa* (23, 581), and *Senecio crassulus* (21, 564). Eighty-three plants and 80 nonvegetated sites received seeds: *Elymus lanceolatus* ($N = 12$), *Eriogonum umbellatum* ($n = 14$), *Heterotheca villosa* ($N = 12$), *Ivesia gordonii* ($N = 14$), *Lupinus argenteus* ($N = 15$), and *Senecio crassulus* ($N = 16$)). In three cases, plants did not have a paired nonvegetated site due to insufficient seed availability. We deployed six seeds for one seed species rather than five in two cases. In 17 cases, we deployed four seeds due to seeds dispersing before being correctly placed. We deployed seeds at 40 sites on the first day of the experiment (29 August 2019) and completed deployment the next day.

Seeds were retained if they were under or within the focal plant's vegetation or at non-vegetated sites were within 5 cm of the nail head. We selected 5 cm as a threshold to allow for small movements by the seeds during deployment. We counted how many seeds remained at each site in three censuses after 1, 3, and 11 days. We censused plants in the same order each time to minimize variation in time between censuses across plants. Variation in census times was greater in Census 3 because rainfall reduced the visibility of the fluorescent powder and caused smaller seeds to settle beneath the scree surface. Although we attempted to locate all seeds by brushing aside scree and using a black light, detectability may have decreased.

Analyses

Seed functional traits

To assess seed functional diversity, reduce trait data dimensionality, and account for trait correlation, we calculated principal components for the seed traits using the individual plant-average trait values for each seed species. We set the average pappus length for seed species without a pappus to 0 cm and retained two principal components with eigenvalues greater than 1.

Trapping experiment (Q1)

We estimated the effect of plant species, seed species, and logged plant length on the proportion of seeds trapped in each trial using a generalized linear mixed model (GLMM) and the R package glmmTMB (Brooks et al., 2017). We used a binomial family and logit link function with the following model structure (glmmTMB/lme4 syntax):

Proportion trapped~

Plant species +
Seed species +
log(Plant length) +
(1|Plot).

The trapping proportions were weighted by the five (in one case, four) successful launches for each focal plant and seed species. Plant and seed species were factors with two and six levels, respectively. We log-transformed plant length to improve the appearance of model residuals. Plot was a factor and random effect to account for variation between the 10 focal plants. We used pairwise Tukey contrasts with $\alpha = 0.05$ in the R package emmeans (Lenth, 2025) to assess plant and seed level variation in trapping at an average log plant size of 2.8997 cm. We back-transformed the estimated marginal means to the response scale prior to contrast.

Retention experiment (Q2)

To address Q2, we assessed whether dispersal rates following entrapment (i.e., the rate that retention did not occur) differed by seed species, site type, and the interaction of those predictors using a GLMM with a binomial family and a complementary log-log (cloglog) link function. Between Census 1 and 2, we observed 51 cases of increased seed counts by 1 or 2 seeds. Between Census 2 and 3, we observed 21 cases. We assumed any seed increases were due to missed seeds in previous censuses and accounted for these “missed seeds” by adding them back to prior censuses during data cleaning. Each seed could only be dispersed once. We analyzed the data with two model structures (glmmTMB/lme4 syntax):

Probability(dispersed) ~

*Site type*Seed species +*
offset(log(Interval duration)) +
(1|Census) +
(1|Plot)

and

Probability(dispersed) ~

*Site type*Seed trait PC1 +*
*Site type*Seed trait PC2 +*
offset(log(Interval duration)) +
(1|Census) +
(1|Plot).

In the first model, site type was a factor with seven levels, one for each of the six focal plant species and one for the nonvegetated site. In the second model, we isolated the role of seed traits in dispersal rates following entrapment by including the seed traits, PC1 and PC2, as numeric predictors.

With a cloglog link, the additive models predict the log instantaneous rate of dispersal. Interval duration accounted for time in days between censuses. By including log (Interval duration) as an offset in the models, we scaled the net dispersal rate to account for different durations. We did not include plant length in these models due to the inclusion of nonvegetated sites, which lacked plant length values. Because weather and the number of seeds remaining varied between the three censuses following deployment, we included census as a factor and random effect in the model. The plot term was a unique identifier for each plant and nonvegetated site and was a factor with 161 levels. We used pairwise Tukey contrasts with $\alpha = 0.05$ to ask whether the dispersal from focal plants and nonvegetated sites differed by site type and seed species at a log interval duration of 0 (i.e., 1 day) (Q2). We back-transformed the estimated marginal means to the response scale before the contrast. We assessed the significance of the main effects using the emmeans function joint_tests. We compared model results with different site types as the intercept in the second model to assess how coefficient estimates for seed traits, PC1 and PC2 vary by site type.

We checked model fit and residuals for Q1 and Q2 using DHARMa (Hartig, 2024). R packages emmeans, ggh4x (van den Brand, 2025), and ggtext (Wilke and Wiernik, 2022) were used for estimated marginal means plots and tests. R version 4.4.0 (R Core Team, 2024) was used for all analyses.

RESULTS

Seed functional traits

In the PCA of seed functional traits, PC1 explained 67.1% of the variance, and PC2 explained 23.7% (Figure 4). Thicker, wider,

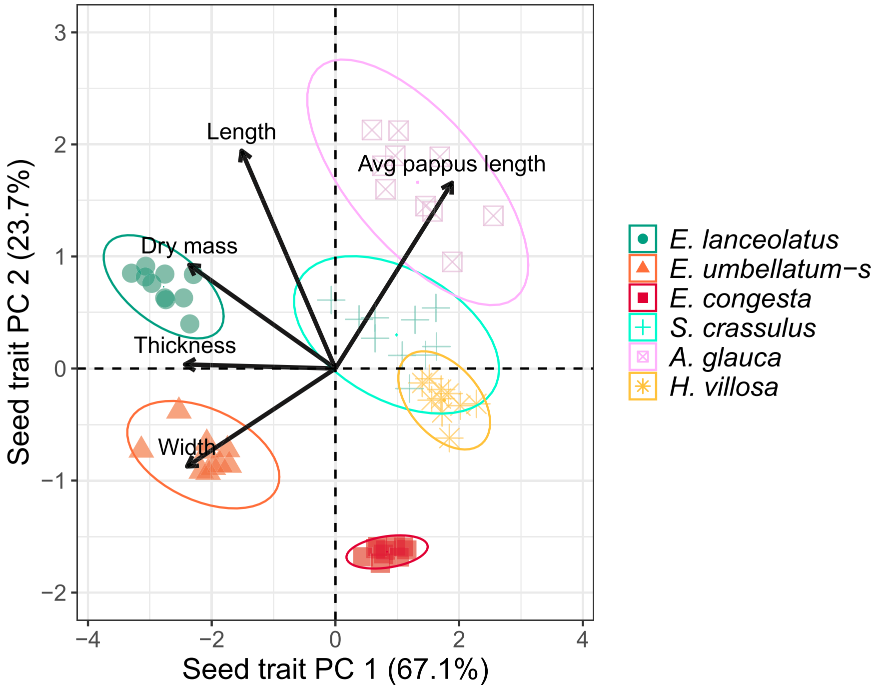

FIGURE 4 PCA biplot for five seed functional traits important for dispersal (length, width, thickness, average pappus length, and dry mass) for six alpine plant species (*Elymus lanceolatus*, *Eriogonum umbellatum*, *Eremogone congesta*, *Senecio crassulus*, *Agoseris glauca*, and *Heterotheca villosa*) with 95% confidence ellipses. Seed species are listed in ascending order of mean PC1.

and heavier seeds (*Elymus lanceolatus* and *Eriogonum umbellatum*) diverged from the pappused seeds (*Senecio crassulus*, *Agoseris glauca*, and *Heterotheca villosa*) and the non-pappused seeds of *Eremogone congesta* along PC1. Longer seeds (*Elymus lanceolatus* and *Agoseris glauca*) diverged from shorter seeds along PC2. A table of seeds traits is in Appendix S5.

Trapping experiment (Q1)

In the trapping model, the fixed effects alone explained 51.4% of the variation (marginal R^2, conditional $R^2 = 53.6\%$). Larger plants trapped more seeds (estimate [est] = 1.908, SE = 0.413, $P < 0.0001$, with *Heterotheca villosa* as the plant species and *Elymus lanceolatus* as the seed species in the intercept). *Heterotheca villosa* trapped more seeds than *Lupinus argenteus* (est = 0.098, SE = 0.045, $P = 0.03$; Appendix S6: Table S1), but we did not find a difference in trapping among seed species (all P -values > 0.05, Figure 5; Appendix S6: Table S2). We did not assess interactions because we did not have sufficient sample sizes.

Retention experiment (Q2)

In the dispersal model with seed species as predictors, the fixed effects alone explained 29.4% of the variation (marginal R^2, conditional $R^2 = 49.4\%$). Site type ($F_{6,\ \mathrm{Inf}} = 38.762$, $P < 0.0001$), seed species ($F_{5,\ \mathrm{Inf}} = 24.032$, $P < 0.0001$), and the interaction between site type and seed species ($F_{30,\ \mathrm{Inf}} = 4.078$, $P < 0.0001$) influenced dispersal.

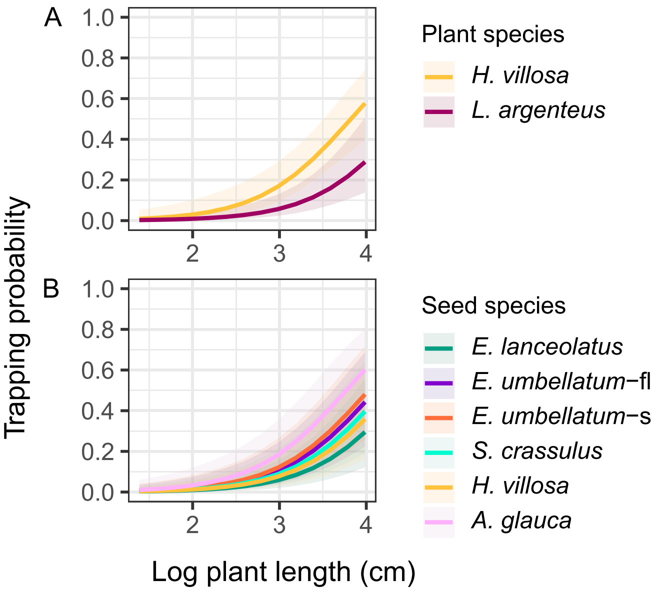

FIGURE 5 Trapping probabilities from the trapping experiment by plant length (cm) with 95% confidence bands for (A) *Heterotheca villosa* (yellow line) and *Lupinus argenteus* (purple line), and (B) across seed species. Trapping probabilities are averaged across seed species in panel A and across plant species in panel B. Seed species are in ascending order of mean PC1. Colors representing species are consistent across focal plant and seed species; *Eriogonum umbellatum* was tested in flower (–fl) and in seed (–s). We found statistically significant effects of plant species on trapping probability but not seed species.

The number of seeds dispersed in nonvegetated sites was higher than in *Elymus lanceolatus* (est = 0.203, SE = 0.067, $P = 0.0024$), *Eriogonum umbellatum* (est = 0.196, SE = 0.064, $P = 0.0024$), *Heterotheca villosa* (est = 0.177, SE = 0.058, $P = 0.0024$), and *Ivesia gordonii* (est = 0.196, SE = 0.064, $P = 0.0024$). Dispersal in nonvegetated areas did not differ from *Lupinus argenteus* or *Senecio crassulus* (Figure 6A; Appendix S6: Table S3).

Compared to seed dispersal for *Lupinus argenteus*, dispersal was lower for *Elymus lanceolatus* (est = –0.15, SE = 0.057, $P = 0.0092$), *Eriogonum umbellatum* (est = –0.143, SE = 0.055, $P = 0.0099$), *Heterotheca villosa* (est = –0.124, SE = 0.050, $P = 0.014$), and *Ivesia gordonii* (est = –0.143, SE = 0.055, $P = 0.0099$). Similarly, compared to dispersal for *Senecio crassulus*, dispersal was lower in *Elymus lanceolatus* (est = –0.162, SE = 0.061, $P = 0.0073$), *Eriogonum umbellatum* (est = –0.155, SE = 0.058, $P = 0.0078$), *Heterotheca villosa* (est = –0.137, SE = 0.053, $P = 0.01$), and *Ivesia gordonii* (est = –0.156, SE = 0.058, $P = 0.0078$).

In pairwise contrasts of seeds (Appendix S6: Table S4), *Elymus lanceolatus* dispersed less than *Eremogone congesta* (est = –0.052, SE = 0.025, $P = 0.039$), *Senecio crassulus* (est = –0.091, SE = 0.033, $P = 0.0062$), *Agoseris glauca* (est = –0.038, SE = 0.017, $P = 0.027$), and *Heterotheca villosa* (est = –0.037, SE = 0.017, $P = 0.031$), which have pappi. Similarly, *Eriogonum umbellatum* also dispersed less than *Eremogone congesta* (est = –0.071, SE = 0.030, $P = 0.017$), *Senecio crassulus* (est = –0.110, SE = 0.039, $P = 0.005$), *Agoseris glauca* (est = –0.058, SE = 0.022, $P = 0.0095$), and *Heterotheca villosa* (est = –0.056, SE = 0.022, $P = 0.01$). Among seeds with a pappus, *Senecio crassulus* dispersed more than *Agoseris glauca* (est = 0.053, SE = 0.022, $P = 0.015$) and *Heterotheca villosa* (est = 0.054, SE = 0.022, $P = 0.015$).

In the dispersal model with seed traits as predictors, the fixed effects alone explained 25.3% of the variation (marginal R^2, conditional $R^2 = 46.7\%$). Dispersal probability was influenced by seed trait PC1 ($F_{1,\ \mathrm{Inf}} = 67.138$, $P < 0.0001$), site type ($F_{6,\ \mathrm{Inf}} = 45.149$, $P < 0.0001$), the interaction between seed trait PC1 and site type ($F_{6,\ \mathrm{Inf}} = 3.348$, $P = 0.0027$), and the interaction between seed trait PC2 and site type ($F_{6,\ \mathrm{Inf}} = 6.865$, $P < 0.0001$). We did not find a significant effect of seed trait PC2 on dispersal.

Dispersal probability was higher in nonvegetated sites compared to *Elymus lanceolatus* (est = 0.202, SE = 0.069, $P = 0.0033$), *Eriogonum umbellatum* (est = 0.198, SE = 0.067, $P = 0.0032$), *Heterotheca villosa* (est = 0.181, SE = 0.062, $P = 0.0032$), and *Ivesia gordonii* (est = 0.196, SE = 0.067, $P = 0.0032$) (Appendix S6: Table S5). Dispersal probabilities were lower in several vegetated sites than in *Lupinus argenteus* and *Senecio crassulus*, which have sparse basal vegetation. Compared to *Lupinus argenteus*, we observed lower dispersal in *Elymus lanceolatus* (est = –0.142, SE = 0.055, $P = 0.01$), *Eriogonum umbellatum* (est = –0.139, SE = 0.054, $P = 0.011$), *Heterotheca villosa* (est = –0.121,

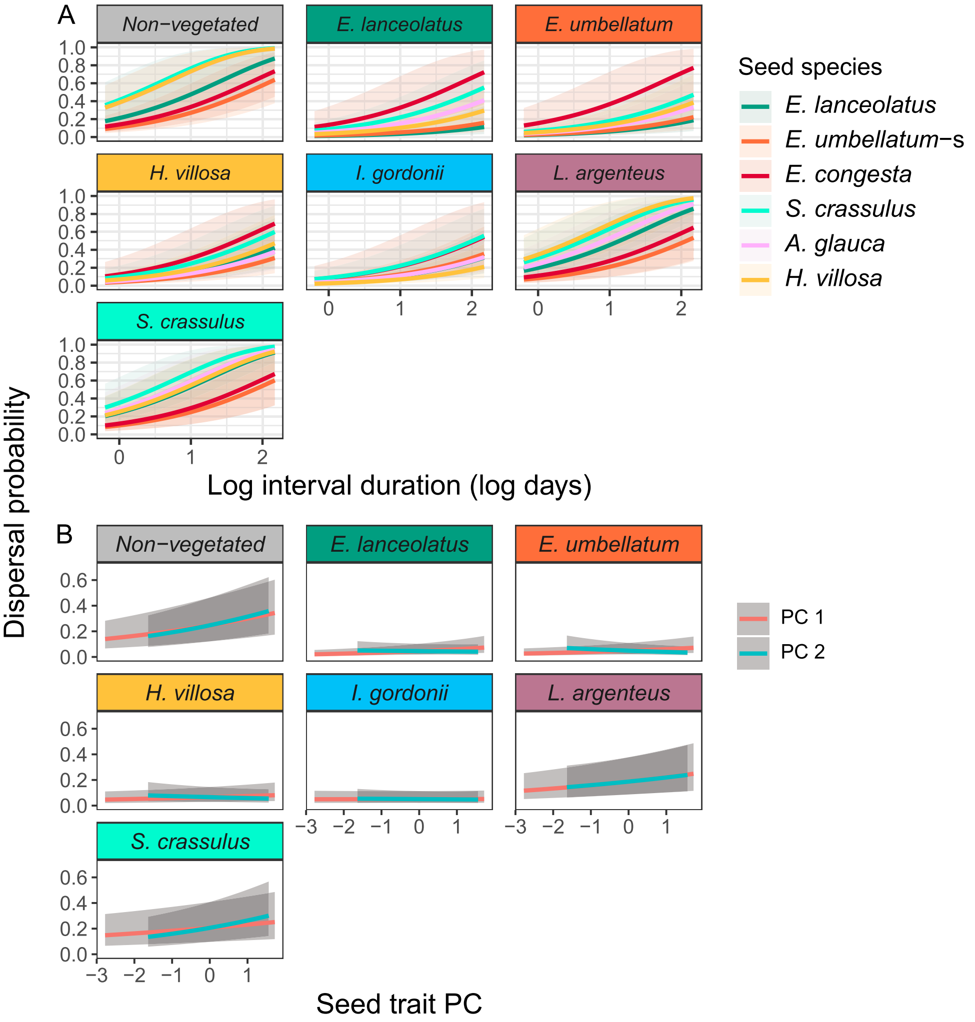

FIGURE 6 Dispersal probabilities from the retention experiment for (A) seed species at different log interval durations (log days) and (B) seed trait principal components (colored lines) after 1 day. Facets are colored by site type, and all probabilities are shown with 95% confidence bands. Seed species are listed in ascending order of mean PC1. Colors representing species are consistent across seeds and site types; *Eriogonum umbellatum* was tested in seed (–s) rather than in flower. We found statistically significant effects of site type, seed species, and seed trait PC1, including interactive effects, on dispersal probability after entrapment.

SE = 0.049, $P = 0.014$), and *Ivesia gordonii* (est = –0.137, SE = 0.054, $P = 0.011$). Similarly, compared to dispersal for *Senecio crassulus*, dispersal was lower for *Elymus lanceolatus* (est = –0.161, SE = 0.061, $P = 0.0083$), *Eriogonum umbellatum* (est = –0.157, SE = 0.060, $P = 0.0084$), *Heterotheca villosa* (est = –0.140, SE = 0.054, $P = 0.01$), and *Ivesia gordonii* (est = –0.155, SE = 0.059, $P = 0.0085$) (Figure 6B).

In comparisons of the re-leveled dispersal model with different site types as part of the intercept, greater values of seed trait PC1 (i.e., longer pappus, thinner and less-heavy seeds) increased dispersal in all site types except *Ivesia gordonii*: nonvegetated sites (est = 0.228, SE = 0.018, $P < 0.0001$), *Elymus lanceolatus* (est = 0.286, SE = 0.076, $P = 0.0001$), *Eriogonum umbellatum* (est = 0.228, SE = 0.07, $P = 0.0011$), *Heterotheca villosa* (est = 0.126, SE = 0.055, $P = 0.021$), *Lupinus argenteus* (est = 0.186, SE = 0.049, $P = 0.0001$), and *Senecio crassulus* (est = 0.131, SE = 0.044, $P = 0.0028$). Higher values of PC2 (i.e., longer length) increased dispersal in nonvegetated sites (est = 0.285, SE = 0.033, $P < 0.0001$), and plants with sparse basal vegetation, *Lupinus argenteus* (est = 0.178, SE = 0.083, $P = 0.0325$) and *Senecio crassulus* (est = 0.281, SE = 0.081, $P = 0.0006$) (Appendix S7).

DISCUSSION

Main findings

This experimental study demonstrated that seed trapping and retention potential depend differentially on the traits of the interacting partners. Trapping depended on vegetation length and plant species identity. However, retention depended on plant species identity, seed species identity, and their interaction. Thus, through trapping and retention, seed dispersal via wind could potentially generate non-random species co-occurrence and interaction outcomes similar to animal dispersal (Mack, 1995; Briggs et al., 2009) and other abiotic dispersal agents such as water (Soons et al., 2017) and snow (Matlack, 1989).

In this community, trapping and retention promoted interactions for certain seed and plant species pairs. More seeds were trapped (Q1) by *Heterotheca villosa*, which has denser vegetation, especially basally, than by *Lupinus argenteus*. Similarly, in the retention experiment (Q2), dispersal rates were highest in plants with sparser vegetation (*Lupinus argenteus* and *Senecio crassulus*) compared with plant species with denser vegetation (*Elymus lanceolatus*, *Eriogonum umbellatum*, *Heterotheca villosa*, *Ivesia gordonii*). Further, the physical attributes of plant species also influenced trapping rates. In the trapping experiment (Q1), larger plants stopped seed movement following contact with focal plants more than smaller plants did. These results suggest that dispersal promotes seed–plant interactions for plants with dense vegetation and larger sizes, which could generate downstream effects on demographic outcomes (which we will explore in future studies).

Among focal seed species, differences in trapping rates were not observed (Q1), but differences in dispersal following entrapment (i.e., no retention) were observed (Q2). Pappused seeds dispersed at higher rates following insertion into focal plants than non-pappused seeds. *Eriogonum umbellatum* seeds, which are large and non-pappused, had low dispersal probabilities compared to other seed types, including in nonvegetated sites and in plants with low vegetative densities. Thus, secondary dispersal for pappused seeds may occur over longer durations than for larger, non-pappused seeds, potentially leading to more dispersal-mediated plant–plant interactions.

Implications for community assembly

These experiments revealed a potential influence of vegetation on limiting seed movement as well as for aggregating seed rain. Because dispersal is a multistage process that begins with seed departure from the host plant and can include multiple dispersal agents and the ability of the seed to survive where it is deposited (Beckman and Sullivan, 2023), our results do not provide a full view of dispersal dynamics within this plant community; rather they provide a proxy for the potential for such processes to occur. Thus, we cannot directly assess the effect of the focal processes

on commonly measured dispersal metrics such as dispersal kernel parameters (e.g., Robledo-Arnuncio and García, 2007; Bullock et al., 2017). Nevertheless, the study is uniquely valuable in that it provides insight into the mechanisms underlying final dispersal outcomes. Further, these results also build on earlier studies showing that the physical structure of a community, including topography and distribution of other organisms, influences dispersal outcomes (Aguiar and Sala, 1997; Lipoma et al., 2019; Meysick et al., 2019).

Dispersal can strongly affect population and community dynamics (Chambers and MacMahon, 1994), with implications for species and community response to climate change (Sullivan et al., 2024). The results from the trapping and retention experiments suggest that explicitly testing for links between seed–plant interaction mechanisms and population or community shifts will benefit our understanding of community assembly processes. Because trapping and retention both depended on the identity of plant species in this community, spatial distributions and co-occurrence patterns may be strongly shaped by these processes. Further, the plant species with the highest retention rates (*Elymus lanceolatus*, *Eriogonum umbellatum*, *Heterotheca villosa*, *Ivesia gordonii*) vary in their ability to buffer temperatures and locally increase soil moisture (Ray et al., 2023). Because microclimate conditions can affect germination and recruitment, seed trapping and retention may also influence seed and seedling success.

Understanding the role of seed dispersal in community assembly and population dynamics is challenging because it is often a complex multistep process (Vander Wall and Longland, 2004; Vander Wall et al., 2005). Seeds can be trapped and retained during initial movement of the seed from the parent plant (primary dispersal) or subsequent seed movement (secondary dispersal). Further stages and mechanisms of seed dispersal may also be possible but were unexplored here. For example, in this community, *Ivesia gordonii*, *Eriogonum umbellatum*, and *Phacelia hastata* plants frequently host ant nests (*Formica* sp.). These ants are omnivorous and may transport seeds into or out of plants (potentially trapping or freeing them). Snow dispersal is also likely important in this community because regolith is reworked and transported by snow-related processes annually. Vertical seed dispersal, such as into the soil, also affects seed fates, with its likelihood varying with environmental conditions, such as wind speed, and seed traits (Liang et al., 2019). For example, heavy rainfall may push some seeds beneath the surface, which occurred most for the smallest focal seed species, *Eremogone congesta*.

CONCLUSIONS

Seed trapping and retention are dispersal-mediated plant–plant interactions shaped by the physical attributes of the interacting pair. As many plant communities shift in structure in response to global change drivers (e.g., Mod and Luoto, 2016; Carter et al., 2019; Rogers et al., 2021), including changes in plant abundance and species composition, seed trapping and retention patterns in the community may also change. Thus, increasing understanding of seed trapping and retention as mechanisms of community assembly may improve understanding of community change in systems with high occurrence of abiotic dispersal.

PERMITS

Research permits were obtained through the U.S. Forest Service via the Rocky Mountain Biological Laboratory.

AUTHOR CONTRIBUTIONS

The seed trapping experiment was designed by C.R., E.X., and B.B. C.R. and E.X. collected the wind tunnel data, which was analyzed by C.R., T.J., G.B., and E.X. measured seed functional traits. The seed retention experiment was designed by C.R., S.T., and B.B. C.R. and S.T. collected seed retention data, which were analyzed by P.d.V., C.R., and S.T. All authors contributed to writing and editing the manuscript.

ACKNOWLEDGMENTS

We thank the anonymous reviewers for their time, feedback, and guidance in improving this manuscript. For the seed trapping project, we thank Adam Hutz for helping to design and construct the wind tunnel, Michael Hensley for field assistance, Ian Breckheimer for drone imagery, and Robert Dudley for his mentorship and generosity with lab space and materials. For the seed trait and dispersal project, we thank Karla Alvarado, Emily Cruz, Victoria Delira, Deidra Johnson, Jocelyn Navarro, Susan Toepfer, and Connie Webb for their assistance in dyeing seeds and measuring traits. We are also grateful to Jennie Reithel, Rosemary Smith, and Albert Ruhi for sharing equipment. Finally, we thank Kyle Gray for his assistance with ant identification and natural history. The lands underlying this study are within the traditional homelands of the Ute people.

DATA AVAILABILITY STATEMENT

All data and code, including construction information for the wind tunnel, are freely available on Zenodo at https://zenodo.org/records/17410035.

ORCID

Courtenay A. Ray https://orcid.org/0000-0002-2276-5915
Savannah R. Troy https://orcid.org/0000-0001-5552-7289
Perry de Valpine https://orcid.org/0000-0002-8329-6796
Benjamin W. Blonder https://orcid.org/0000-0002-5061-2385

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Field site maps, including geographic, topographic, field experiment.

Appendix S2. Wind speed figures during retention experiment.

Appendix S3. Plant species abundance figure.

Appendix S4. Box plots of focal plant lengths for trapping and retention experiments.

Appendix S5. Values for focal seed traits.

Appendix S6. Summary tables of pairwise contrasts from emmeans.

Appendix S7. Figure and table of coefficient estimates for seed traits, PC 1 and PC 2, on dispersal probability by site type in the model intercept.

How to cite this article: Ray, C. A., S. R. Troy, E. V. Xie, T. M. Jenkins, G. Belfry, A. Wells, P. de Valpine, and B. W. Blonder. 2026. Wind-driven seed dispersal differentially promotes seed trapping and retention across alpine plants. *American Journal of Botany* 113: e70151. https://doi.org/10.1002/ajb2.70151