

Does the seedbank reflect the composition of the metacommunity for alpine plants?

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Abstract

Community ecology and dynamics are often only thought of in terms of the processes selection and speciation. Likewise, plants are often only considered in their immobile, germinated form. However, when it comes to plant community dynamics, seeds and the seedbank are often critical in predicting community change through the processes of drift, and dispersal. The goal of this study is to analyze the relationship between the soil seedbank and the spatial and composition patterns across an alpine plant community. Ultimately, this study found a significant correlation between local vegetation abundance and seed abundance in a given sample, meaning that vegetative community composition plays an important role in community assemblage. The exact mechanism by which seed aggregation by vegetation occurs remains unknown, however this is a subject of current study. The results also suggested possible topographical or meteorological dispersal interactions, which are the subject of planned future study.

Introduction

One long-term goal of community ecology is predicting the species composition of a given area. Doing so requires predicting the outcome of demographic processes, which are subject to physical processes like growth, or the change in an organism's size; mortality, or the rate at which individuals of a population die; recruitment, or the rate that new organisms (i.e. asexual or sexual offspring) are added to the population; and fecundity, or the rate of offspring produced per individual (Kirk, 1996).

These demographic processes in turn linked to the processes of selection, drift, speciation, and dispersal. Selection is defined as when individuals of a population exhibit varied phenotypical traits and exhibit differential reproductive success of individuals with different phenotypes. Drift is defined as stochastic changes in the population through processes such as birth rate, mortality rate, and offspring in response to environmental variation, etc. Speciation is defined as the formation of a new species through geographic, behavioral or anatomical factors. Dispersal is defined as the somewhat stochastic movement of organisms through space (Vellend, 2010). Often, community dynamics are mostly thought of in terms of speciation, however the way a community is distributed across a landscape can greatly influence how the composition and growth of a community change over time. Therefore, this study will focus on the processes of drift and dispersal, and the interplay between the each process. More specifically, this study will focus on how the dispersal and distribution plays into the assemblage and construction of plant metacommunities. The dynamics of dispersal have a strong effect on recruitment, both of which ultimately effect the growth or decline of a population.

Demography is ultimately interested in how populations change over time, and one common way to model this is through a population viability analysis. A population viability analysis (PVA) determines how a community is changing by determining whether populations are growing or shrinking, and they often rely on limited heuristics or rules of thumb (Boyce, 1992). PVAs are heavily reliant on the dynamics of the seedbank its composition, therefore a survey of the soil seedbank can provide data critical to creating accurate predictions of a population's growth rate (Salguero-Gómez, et al., 2012).

Plants, by nature, are often easier to study post-germination. With the exception of a few cases, most rooted plants do not move as adults, so it is easy to study processes including growth and mortality. However, the seed-seedling transition, from seed dispersal to germination, is quite difficult to study, because it is the most spatially dynamic aspect of a plant's life cycle. Unlike their rooted counterparts, seeds have the potential to be mobile. Most seeds are small, and methods that work for more mobile organisms like radio tagging and banding, are clearly impractical. This means, that any attempt to include seed distribution and dispersal in a predictive metacommunity model would need to be a survey or census, because individual tracking for every seed would be impractical at a community level.

Though it would be impossible to track an individual seed over the course of this process, a survey of the soil seedbank could yield a relative distribution of seeds in relation to the adult conspecifics. Soil seedbanks are often regarded as a poor proxy of a given community assemblage (Cardina & Sparrow, 1996), however seedbank study can capture the distribution and abundance of seeds of a given community.

Germinated plants, from initial seedling to senescent adult, facilitate in-depth study in the fact that they are largely immobile. That being said, it would be foolish to ignore the processes that ultimately influenced how those plants ended up there in the first place. It is likely that the seed stage of a plant's life cycle is also the stage with the highest mortality rate (Cavers, 1983). Despite the fact that most seeds do not travel further than 10 meters from the parent plant (Cain et al., 2000), some seeds have the potential to travel incredible distances (Ozinga et al., 2004), which is important in a metacommunity as it allows species to escape local density-dependent competition (Manzano & Malo, 2006). Understanding studying dispersal, and similarly soil persistence, would provide better insight into the dynamics of community ecology, namely the mechanics of recruitment of a site, the dynamics of dispersal, and the physical processes that may aggregate or further disperse seeds. Each of these in turn affect the process of recruitment in a community, and influence the assemblage and composition of a community.

The purposes of this study are to:

- 1) Understand where seeds occur in the landscape.
- 2) Determine what seeds compose the community.
- 3) Identify why seeds might be aggregated in a non-random way in the landscape.

This study could give insights into the spatial distribution of plants between seed set and germination and give an indication of the physical processes that could aggregate seeds. Knowledge of these processes would create a more complete understanding of the processes

happening in a given community, and aid in the construction of more complete models to predict community assemblage and distribution. Such models are becoming more important in the face of climate change and ecological disturbance, as they could help predict the ways communities might change over time. These models could help make more informed decisions in terms of land management in the face of global climate change, planned human interference, and unintended ecological disturbance.

Question 1: Seed Distribution

What is the spatial distribution of the seeds in a given community? Does the spatial distribution of adult plants influence the spatial distribution of seeds? In a normal setting, it would be extremely challenging to study the dispersal process, given the density and diversity of vegetation in most places. This study is an attempt to capture a snapshot in time of the distribution of seeds in a given community.

Hypothesis 1:

If the rate of long-distance dispersal is high, then the seed distribution in the soil is random and has little to do with the spatial distribution or clustering of adult plants in a community. The seeds will have a fairly homogenous spread, and the variation in distribution is due to random chance.

Question 2: External Processes Affecting Spatial Distribution

Why do seeds occur where they do in the community? What external factors drive any aggregation of seeds in the soil? It seems unlikely that the distribution of seeds found across the landscape is uniform, so another purpose of this study is to determine what might influence the distribution of seeds on the landscape.

Hypothesis 2:

A non-random aggregation of seeds could be explained by interaction with some physical factor, broken down below:

2a: A nonrandom distribution of seeds could be due to physical/structural properties of the parent plant that would catch the seeds, which could suggest interspecific interactions that structure community dynamics.

2b: Another explanation would be that most seeds simply don't disperse far from the (parent) plant (Cain et al., 2000). This phenomenon may vary depending on locale, however evidence supporting this hypothesis would not necessarily invalidate the idea that plants are physically aggregating seeds (Hypothesis **2a**), only that the seeds found in the sample were from local adults.

2c: A third explanation for non-random distribution would be that topography (and to some extent, wind) influences how seeds are dispersed on the landscape. For example, given a windy, exposed setting, it would be logical to assume that any seeds occurring in such an exposed place could simply be blown elsewhere.

Question 3: Seed Community Composition

Does the species composition of the seedbank match that of the community? Are the species present in the seedbank also represented in germinating adults and vice versa? What can the relative abundance of the species found in a survey tell us?

Hypothesis 3:

If rates of long-distance dispersal are low, the composition of the seedbank should roughly reflect that of the local adult plant community. A survey of a given community should be roughly uniform in biodiversity.

Hypothesis 4:

Given high rates of long-distance dispersal, the biodiversity of the seedbank should be higher than that of the adult plants represented in the community. A survey of a given community should also yield a roughly uniform biodiversity of species.

The Baldy Demography Plot

A dynamic, biodiverse site with high biomass would make a poor study site simply because it is difficult to study. The ideal site for testing these hypotheses would be fairly barren, with little biomass and diversity. A survey of the seedbank found at the Mt. Baldy demography plot near Gothic, Colorado could help begin to tease out the relationships between seed abundance and plant community structure.

The Baldy demography plot is a long-term alpine scree study site maintained since 2014 by the MacroSystems Ecology Laboratory. The goal of the study site is to monitor the dynamics of species composition, study the structure of alpine plant communities, and to use data gathered from the site to make falsifiable forecasts about the community composition at the site. The Baldy site is ideal for a number of reasons, the foremost of which include: thin scree soil, low biomass, and low biodiversity. The site is mostly barren, with only about 0-10% vegetation cover (Blonder et al., 2018), which allows for a fine-scale level of study not possible in a more verdant dynamic.

Given the in-depth long-term data available from this site, the data yielded by a soil survey could produce insights regarding the contribution of the soil seedbank to future generations (through the seedbank effects on recruitment and distribution) and the role of long-distance dispersal between the alpine metacommunity. This means that the data yielded by this study could be used to create more accurate models to predict future change in plant communities.

A comparison of community and seedbank structure could also establish the basis for further study focusing on the relationship between seed dispersal and distribution, the persistence of seeds in the soil and relative location to germinated individuals. The demography of a community is influenced by a myriad of factors, which means that no one study or dynamic can fully explain the change in a community, though it is clear that increasing the understanding the relationship between seed dispersal and composition in the soil would be a good starting point. Ultimately, data collected from a survey of the Baldy seedbank would help construct and strengthen PVAs that could help predict the change in the plant community at the Baldy site and beyond.

Methods

Site Description

The Baldy Demography Site is located in the Gunnison National Forest in Colorado (38.978725°N, 107.042104°W). The site is characterized by a sparsely vegetated, fine scree slope with an approximately 20% grade. The site is approximately 18 meters by 38 meters and subdivided into 50 study plots, and 40 interval plots, each measuring 2x2 meters (Blonder et al., 2018).

Mt Baldy Demography Site & Sample Plots

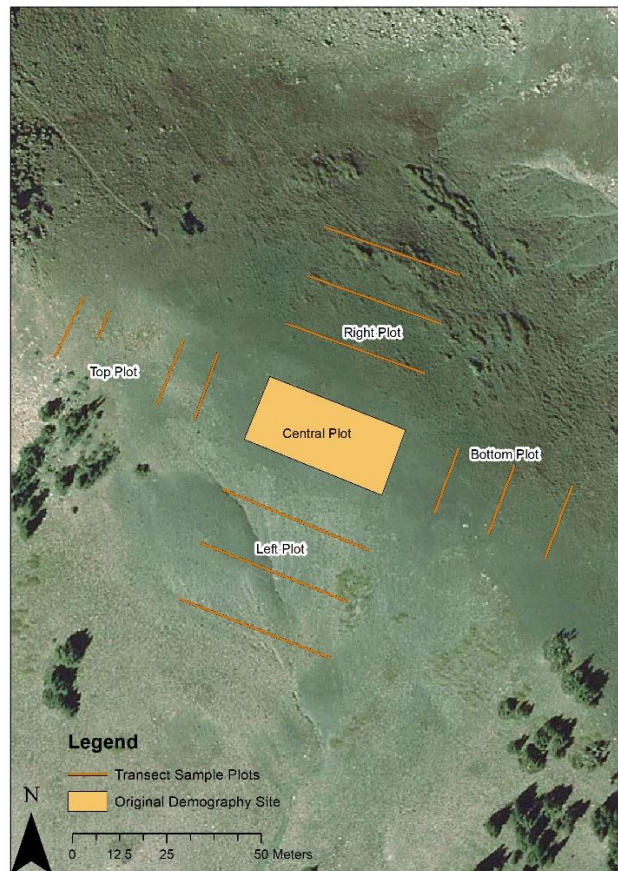


Figure 1 A map of the Baldy Demography Site and adjacent Transect Sample Plots

The Baldy site is situated on the top of a short ridge. The adjacent slopes have a much steeper grade and are more heavily vegetated with low-growing shrubs and some patchy grasses (See **Figure 2**). Above the site, the scree shifts to small talus. A large snowbank persisted through the study on the upper right side of the ridge. Below the site, the slope becomes more gentle, characterized by barren scree interspersed with patches of *Vaccinium* sp., smaller forbs, and at the extreme margins, subalpine firs.



Figure 2 a view of an adjacent slope to the study site.

Transect Plots

In addition to the central Demography site, 4 adjacent sample sites were established by creating and sampling a series of transect lines parallel to the Baldy site, creating a total of 5 sampling plots (see **Figure 1**).

The adjacent transect plots were named in their spatial relation to the original demography site when viewed from the bottom of the ridge. The northwestern plot is denoted Top, the southeastern is denoted Bottom, the southwestern is denoted Left, and the Northeastern is denoted Right (**Figure 1**).

The left and right plots were constructed with three parallel transects, each 38 meters long.¹ The transects were laid out on a 15-meter interval from the central plot, the first transect being 15 meters from the edge of the central plot, the second 30 meters, and the last transect being 45 meters from the central plot.

The Bottom plot was constructed in a similar manner to the left and right plots, but the transects were only 15 meters in length. The transects in this plot were constructed using the same 15-meter interval from the central plot.

Due to challenging topography and a persistent snowbank, the top plot was constructed with 4 transects. The first was 18 meters in length, at 15 meters from the upper edge of the center plot. The second was 18 meters long, 25 meters from the upper edge of the central plot. The third intersected with the snowbank, was 7.2 meters long and 45 meters from the edge of the central plot. The fourth transect ran just above the top of the snowbank, measuring 18 meters long and 55 meters from the central plot.

¹ All distances were measured using the horizontal distance between two points.

Sampling Procedure

A total of 115 samples were taken from the plots. The Central unit provided 40 samples (one sample taken from each of the interval units). The Left, Right, and Bottom plots yielded 6 samples per transect, with a total sample yield of 18 samples per plot. The Top plot yielded 6 samples for each full-length transect, plus 3 samples from the truncated transect, for a total of 21 samples.

Because of the extremely loose nature of the scree at the site, a traditional soil corer could not be used. Samples were taken using a small aluminum ring fashioned from a soup can, and a soup spoon. The ring was approximately 7.5 cm in diameter and 1.5 cm in height. The ring was first pushed into the soil until the upper edge is even with the surface. Then the soil inside the ring was carefully extracted using the spoon, until the soil is even with the bottom edge of the ring. The extracted soil was bagged and labeled, to be sieved following transport to the lab. Once the sample was taken, the sample location was marked with a roofing nail and flagging, and a picture was taken of the sample and surrounding soil².

Sieving Procedure

Following collection, a total of 115 soil samples were transported down to the lab in the Gothic townsite, where they were be sieved.

The soil samples were be stored in the short term in paper bags to discourage moisture buildup and fungal growth. The analysis process was as follows: The soil is poured over a 2000-micron mesh-, and then a 500 micron mesh sieve. Each fraction of the soil sample was analyzed visually for seeds, seed fragments, or cotyledons, which were recorded and separated. Following sieving, any seeds found were visually identified (utilizing resources like the Rocky Mountain Biological Laboratory Herbarium, located in Gothic), and photographed for future morphological analysis. Following this analysis the seeds were returned to their respective soil sample, and returned to the same location where they were collected³ in order to mitigate any effects caused by seed harvest on the long-term dynamics of the Baldy plot.

Photograph Analysis

Because of a suspected relationship between local plant abundance and seed abundance in soil samples, each sample site was photographed. Each sample photograph was analyzed using Image J software, via measuring percent adult plant coverage of each photo using the ellipsis tool. The percent coverage of the local area around each sample site was then found as a fraction of the total plant coverage over the total area photographed.

² Each picture was taken from a fixed height.

³ The samples will be well mixed in order to prevent unwanted dispersal of any seeds present. The soil on Baldy is so thin and dynamic that sample stratification was of little concern.

Results

Statistical Analysis

Distribution Analysis

The first step was to plot out which samples yielded seed presence (defined as whole seeds, fragments, or cotyledons found in the soil⁴), shown in **Figure 1**.

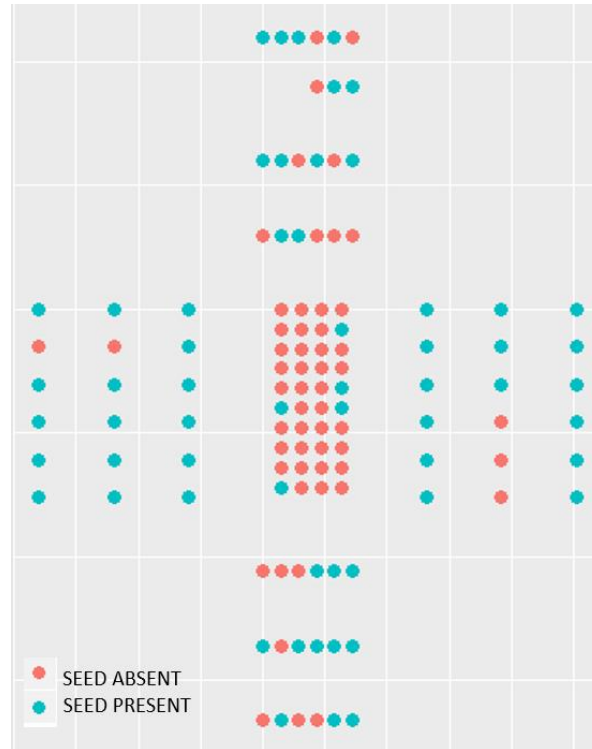


Figure 3 Spatial distribution of seed presence/absence.

The spatial distribution of seed presence is shown in **Figure 3**. There is a high spatial variation evident. **Figure 4** shows the relative abundance of seeds found in each sample, represented by a gradient from blue (high abundance) to red (low abundance).

⁴ Each of these is evidence of successful dispersal rather than successful germination. At this point in the study, it is more useful to make a distinction between dispersal/distribution and germination.

Based on the clear pattern found in **Fig. 1** a logical next step was to plot the abundance of whole seeds by sample. **Figure 2** shows the relative abundance of seeds found in each sample, represented by a gradient from blue (high abundance) to red (low abundance).

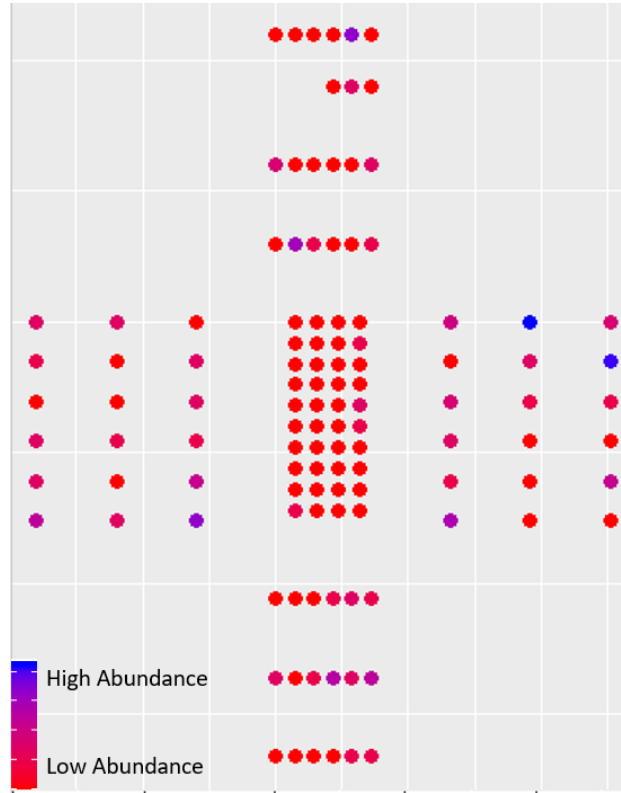


Figure 4 Relative abundance of seeds in each plot⁵.

Using Tukey's honestly significant difference test, the difference between the abundances of each plot (Top, Bottom, Left, Right, and Center), was determined (see **Figure 5**).

⁵ Note: This abundance is square root-transformed in order to normalize the data for statistical analysis.

Transect type	Difference value	p-value
Center-Bottom	-0.6861936	0.0228357
Left-Bottom	0.3646553	0.6376064
Right-Bottom	0.7534231	0.0851503
Top-Bottom	-0.3026938	0.7622624
Left-Center	1.050849	0.0000804
Right-Center	1.4396167	0.0000023
Top-Center	0.3834998	0.3937382
Right-Left	0.3887677	0.6780887
Top-Left	-0.6673492	0.0771622
Top-Right	-1.0561169	0.0035262

Figure 5 THSD test values, by plot, significant differences are marked in green⁶.

Based on the findings of the THSD, Hypothesis 1 (Given that the rate of long-distance dispersal is low, the seed distribution in the soil is random and has little to do with the spatial distribution or clustering of adult plants in a community) is unsupported. There is a clear spatial pattern in seed abundance across the community, which would indicate that there is some outside factor that is influencing the way that seeds are ultimately distributed (I.e. that the set of sub-hypotheses under Hypothesis 2 could be responsible for the pattern shown).

Based on the findings of the THSD and the spatial pattern of seed abundance, it was logical to compare seed abundance with the percent coverage of adult plants in the photographs taken at each sample site (see **Figure 6**).

⁶ Again, this abundance data was square root-transformed to normalize the dataset for analysis.

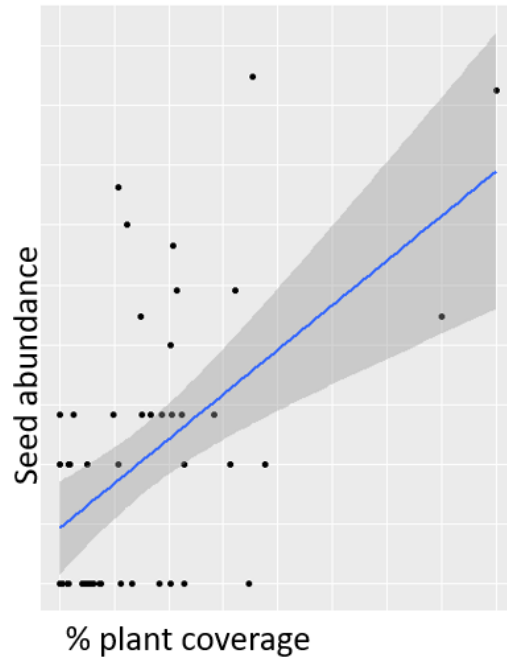


Figure 6 Percent coverage of adult plants compared to seed abundance⁷.

The linear regression in **Fig 6** would indicate that there is a positive correlation between local abundance of adult plants and abundance of seeds in a sample (inasmuch as the local abundance of plants accounts for a little less than a third of the seed abundance in each sample). This would ultimately support Hypothesis 2a and 2b, as there is a correlation between local plant abundance and seed abundance, however the exact mechanism of that relationship is unclear.

Composition Analysis

Seed degradation was an important factor in this study. The seeds were collected between late July to early August, meaning that they had spent nearly a full year in the elements of Baldy. Most were badly damaged, and most were merely fragments. Ultimately, most seeds were not good enough quality to identify with a reasonable degree of certainty. This means that based on the data collected Hypothesis 3 was neither supported nor unsupported. If this study were to be repeated, the researcher recommends collecting seeds soon after autumn seed set. This would ensure a better quality of seeds that would facilitate a higher degree of certainty in identification.

⁷ The linear regression plotted in **Fig. 4** has an R-squared value of approximately .28, and a p-value of 0.0000799.

Discussion

Interpretation of Results

Based on the environmental factors at play on Baldy, one of the most obvious explanations for the pattern in abundance over space was presence of vegetation. The THSD seemed to indicate that the Central and (to a lesser extent) Top plots seemed to be significantly different than the Left, Right, and Bottom plots in terms of seed abundance, and visually, one of the most obvious differences between these plots is how heavily vegetated they are. The central and top plots tend to be more barren and windswept whereas the other plots are covered in low-growing forbs and grasses.

Unfortunately, without further study, the actual process by which plants influence distribution of seeds cannot be determined. It is likely that a combination Hypothesis 2a and 2b could explain this relationship, however it bears repeating that at this point in time, it can only be said that approximately 28% of seed abundance can be explained by the local presence of plants. It will require future study to determine the roles of local seed set or physical aggregation in local seed aggregation.

Little could be said about the composition of the seed community, however, future study following seed set could rectify this lack of data. A study on how dispersal frequency and range across the metacommunity including the study site would also likely yield information on the composition of the seed community, at least as far as the seeds that are dispersed to the Baldy site. This would not answer any questions regarding the composition of seeds that actually persist in the soil however.

Current and Future Studies

Based on previous data collected by the Macrosystems Ecology Laboratory, it seems that seeds, wind dispersed or otherwise, tend to be concentrated near adult plants (Courtenay Ray, personal communication, July 21, 2019). The vegetation on the Baldy plot also seems to be unevenly distributed, aggregated in “mats.” These “mats” may be formed when an individual plant accumulates wind-blown seeds around its base. Over time, those seeds, when germinated, may accumulate more seeds, and form these vegetative aggregations. This is a subject of current study, and its findings could help contextualize the findings of this work.

A future study that could yield useful insights would be a comparison between the topography of the Baldy site and the abundance of seeds found. The Central and Top plots seem to be more exposed to wind and sun. It seems feasible that any seeds present in these plots is more likely to degrade or simply be blown elsewhere.

The Implications of This Study

The Baldy Demography Site is a long-term study. That being said, the Macrosystems Ecology lab is interested in using the data collected there to construct predictive integral projection models (IPMs) that would help predict change community assemblage over time. In a world faced with dynamic changes like climate change and ecological disturbance, it is important to be able to accurately predict how communities will react. Like PVAs, IPMs are extremely sensitive to the accuracy of the estimated rates of factors like community recruitment, which is a function of the soil seedbank. Given more accurate data for these models, the predictions they create will be more accurate, meaning that decisions made using these models will be better informed in the future.

This study indicates that existing vegetation plays a role in future community assemblage. This means that future study of how vegetation impacts how seed communities are distributed could be used to construct more robust models of how community assemblage is influenced by change. This makes future studies like this one very important when it comes to heavily debated topics like land management and use.

The findings of this study seem to support studies like Baker & O'Dowd's 1982 study involving plant density and seed morphology and Donohue's 1998 study on the relationship between plant traits, dispersal, and environmental factors, in the fact that environmental factors do seem to play a role in seed aggregation. The implication here is that environmental factors and the spatial and compositional patterns of a community influence the seed dispersal and ultimately the distribution and makeup of the next generations of plants. Given the data produced by this and future related studies, more accurate models can be constructed, and further understanding of the relationship between soil seedbanks and the plant metacommunities can be achieved.

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