## Introduction

## The Portal Project is a long-term research project that has so far generated 40 years of regularly-collected data on rodents, plants, and weather in the Chiricahuan Desert near Portal, AZ. The composition of the plant and rodent communities, their drivers, and the relationships between them have long been topics of interest at Portal. However, the high dimensionality of both the plant and rodent datasets has made it challenging to identify general signals of change, let alone relationships between plants and rodents, at the community rather than species level.

Recently, Christensen et al (2018) applied Latent Dirichlet Allocation - a technique adapted from text analysis - define community “types” in the rodent community, and used a change-point model to identify moments of rapid change in rodent community composition. Intriguingly, while three of the four changepoints identified in Christensen et al 2018 can be convincingly attributed to extreme weather events, the fourth cannot. This change-point occurs in the early to mid 1990s, and seems to extend over a longer period of time. It is natural to wonder whether the plant community contributed to this slower change.

Given Christensen et al’s significant progress towards distilling the rodent community into a relatively-interpretable form, it is an opportune time to attempt to simplify the plant community data. It will especially interesting to explore whether plant community dynamics predict changes in the rodent community, especially in the early 1990s.

## Methods

### The Portal data

The Portal Project consists of 20 plots, which have had various experimental treatments over the years. This project focuses on control plots, which are accessible to all rodent species. For a more complete description of Portal protocols, see the living data paper recently released by Ernest et al (2018). Briefly, we census the rodent community approximately monthly at the new moon. Sherman traps, baited with millet, are set at 49 stakes in each plot. Captured individuals are identified to species, tagged, measured and weighed, and released. We census the plant community twice a year, in the spring and late summer, because Portal has strongly differentiated winter and summer plant communities corresponding to its two wet seasons. During a census, all plants within .5x.5m quadrats (20/plot) are identified and counted.

All Portal data is freely accessible via the living data paper (Ernest et al 2018) or a GitHub repository: www.github.com/weecology/PortalData**.** In this study, I use the portalr R package to access summaries of the Portal data (Yenni 2018). The package is available on CRAN; alternatively, the scripts for this project will run without portalr as long the correct data files are in the data folder.

For this project, I used the entire rodent timeseries, standardized according to sample effort to account for incompletely-sampled census periods. Because plant censuses are annual and not monthly, I used yearly sums of rodent abundances. I used all available plant censuses, again standardized according to sample effort. I restricted the analysis to the two annual plant communities (primarily excluding some grasses and woody species better sampled at larger scales). There are 27 years with complete data: rodent censuses and a summer and winter plant census, 5 years with a summer but no winter census, and 4 years with a winter and no summer census, . There are 14 rodent species, 48 winter plant species, and 47 summer plant species.

### Analysis: Distilling the plant communities (PCoA)

The plant data do not lend themselves to current implementations of LDA for ecological data, so I used a Principle Coordinates Analysis to reduce the dimensionality of the plant communities (cmdscale in vegan, Oksanen et al 2018). The communities are known to be largely distinct, so I ran PCoA’s on summer and winter data separately. Prior to running each PCoA, I removed species that did not occur at all in the season in question. I used a Wisconsin transformation (wisconsin in vegan) on the raw abundance values, and then used a Bray-Curtis dissimilarity matrix (vegdist in vegan) for the PCoA.

For both communities, scree plots showed inflection points at approximately three axes, and three axes captured a substantial proportion of variation (Tables 1 and 2). Although we have relatively little information about the natural history of particular plant species, I explored two known features of the plant community: a general decline in large-seeded species compared to small-seeded species (Chen and Valone 2017), and the rapid establishment of the invasive *Erodium cicutarium* in the 1990s (Allington et al 2013). I used weighted scores and **regressions** (wascores in vegan and lm) to test whether seed mass predicted species’ scores on PC axes, using seed mass data from Chen and Valone 2017. I checked the weighted-average species score for *E. cicutarium* on all axes and the rank of its absolute value compared to other species scores. Because the first axis for the winter community was consistently important in the RDA analyses, I specifically examined its highest-ranking species.

### Analysis: Relating plant and rodent communities (RDA)

I used redundancy analysis to relate the first three axes of each plant community’s PCoA, as well as year, to the rodent community. Prior to analysis, I standardized rodent abundances using a Hellinger transformation (decostand in vegan). Because this is a timeseries, and year may capture a considerable portion of variation, I compared the results from a partial RDA conditioned on year and an un-conditioned RDA including year as a potential predictor (rda in vegan). I selected the most parsimonious RDAs stepwise using ordistep in vegan. I used permutation tests (anova.cca in vegan) to test the significance of the global RDAs and individual axes. For both RDAs, I used variance partitioning (varpart in vegan) to see how much variation each significant constraint axis captured.

## Results

### PCoA

Table 1: PCoA eigenvalue & proportion of variace tables

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **Summer PCoA** | | | **Winter PCoA** | | |
| **Axis** | eigenvalues | propVar | cumVar | eigenvalues | propVar | cumVar |
| 1 | 2.05087066 | 0.19608563 | 0.19608563 | 2.47912319 | 0.22814312 | 0.22814312 |
| 2 | 1.59548746 | 0.15254602 | 0.34863165 | 1.22049054 | 0.11231653 | 0.34045966 |
| 3 | 1.1032454 | 0.10548231 | 0.45411395 | 1.12113488 | 0.10317326 | 0.44363291 |
| 4 | 0.89428426 | 0.08550334 | 0.53961729 | 0.94279544 | 0.08676144 | 0.53039435 |
| 5 | 0.72033218 | 0.06887162 | 0.60848892 | 0.69744274 | 0.06418268 | 0.59457703 |

As described above, three axes captured a substantial proportion of variation for both communities (Table 1). Seed mass did not predict a species’ score for any PC axis except for axis 1 in the summer community, for which there was a positive relationship between seed mass and axis score (p = 0.015; all other p from 0.056, for winter axis 2, to 0.98.) . *E. cicutarium* had the second highest absolute value score for axis 3 in the winter community (score = -0322), and had consistently low rank absolute value scores in the other axes.

### Partial redundancy analysis

The most parsimonious partial RDA, conditioned on year, was:

rodents\_hel ~ WinterPCoAxis\_1 + WinterPCoAxis\_3 + WinterPCoAxis\_2 + SummerPCoAxis\_2

The global model was significant (p < 0.001; R2 of 0.33). Only the first two axes, winter 1 and winter 3, were significant (p < 0.001 for both; p = .41 and .94 for third and fourth axes). For variance partitioning results, see Figure 1.



Figure 1: Variance partitioning for partial RDA. Year and Winter1 share the most variation.

### Redundancy analysis (non-conditioned):

The most parsimonious RDA was:

rodents\_hel ~ WinterPCoAxis\_1 + WinterPCoAxis\_3 + WinterPCoAxis\_2 + year

The global model was significant (p < 0.001, adjusted R2 of .62). Only the first three axes, winter 1, winter 3, and winter 2, were significant (p < 0.001, < 0.001, 0.16, respectively; p for year = 0.992). For variance partitioning results, see Figure 2.



Figure 2: Variance partitioning for unconditioned RDA. Winter1 absorbs the most variation (.452)

## Exploring winter axis 1

Table 2: Ranked species scores for winter axis 1

|  |  |  |
| --- | --- | --- |
| Winter Axis 1 species scores (ranked by abs. value) | | |
| speciescode | axis1\_rank | waxis1 |
| eria.diff | 1 | -0.3654295 |
| hapl.grac | 2 | -0.3505423 |
| esch.mexi | 3 | -0.3320933 |
| step.exig | 4 | -0.3253678 |
| erig.dive | 5 | -0.322973 |
| sisy.irio | 6 | 0.32004202 |
| ambr.arte | 7 | 0.31655653 |
| sida.spin | 8 | 0.31465013 |
| amsi.tess | 9 | 0.31254431 |
| pect.recu | 10 | 0.30846961 |

The species with the highest absolute-value scores for winter axis 1 were eria.diff, hapl.grac, and esch.mexi, and are all negatively related to axis 1 (Table 2).

Plotted through time, winter axis 1 increases after the 1990s – which, intriguingly, coincides with the disappearance of banner-tailed kangaroo rats from the site and may correspond to the unknown changepoint in Christensen et al 2018 (Figure 3).



Figure 3: Values for winter axis 1 (left) and D. spectabilis abundance as a proportion of the total number of individuals of all species captured at the site (right). Red lines highlight the approximate location of the 1990 change-point.

## Discussion

The Portal plant community can be distilled into a few axes, which generally do not correspond to already-known sources of variation in the plant community – neither seed size nor the invasive *E. ciculatum* are dominant contributors to the PCoA axes that contribute the most to the RDA. The first axis of the winter community appears to be strongly related to aspects of the rodent community, including declines in the strongly-interacting *Dipodomys spectabilis* (Figure 3). It is unclear how much of its explanatory power overlaps with that of year – while, when year is treated as a constraint on an RDA, year absorbs considerable variation, in the un-conditioned RDA analysis, winter axis 1 appears to absorb that variation and render year apparently non-significant (Figures 1 and 2). A major effort in future should focus on disentangling principle axes of community variation from the effect of year.

The most important species in winter axis 1 are eria.diff, hapl.grac, and esch.mexi (Table 2). While this study is unable to tell whether changes in the rodent community drive changes in these species, plants drive rodents, or a third factor drives changes in both communities, it will be informative to further explore the relationships between these species in particular and the rodent community. A comparison in plant community dynamics between control and rodent-exclosure plots is the obvious first step. Diet analysis techniques such as DNA metabarcoding, may also be helpful in this regard.

## References

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