

# THE ROLE OF PATCH- AND LANDSCAPE-LEVEL PROCESSES IN SHAPING DESERT RODENT COMMUNITIES

## CONCEPTUAL FRAMEWORK

For much of the 20<sup>th</sup> century, community ecologists were primarily engaged in elucidating which local mechanisms allow communities of species to exist.<sup>1-5</sup> The study of communities has historically consisted of two, often independently studied, perspectives. One perspective, following from the tradition of Gause<sup>2</sup> and Lotka-Volterra<sup>1</sup>, focused on the role of local coexistence mechanisms in determining which species were able to exist in a local patch or habitat. The other perspective, based on a biogeographic slant (e.g., island biogeography<sup>6</sup>), focused on the role of large-scale processes such as colonization and extinction dynamics. In 1987, Ricklefs<sup>7</sup> seminal paper regarding the role of regional processes in shaping local communities led to a remarkable increase in research on how the structure and composition of local communities might be influenced by landscape-level processes.<sup>8-12</sup>

The concept of metacommunities—multiple communities or “localities” connected in a larger matrix through regional processes such as dispersal—emerged out of the increasing engagement with landscape patterns and processes as a way to frame community ecology through both local and regional lenses.<sup>13,14</sup> Metacommunities were initially presented as falling into one of four main paradigms.<sup>13</sup> With the realization that these paradigms are fairly restrictive not always mutually exclusive, however, the development of metacommunity theory is shifting away from the paradigms towards a more inclusive multi-scale, multi-dimensional community ecology model.<sup>13,15</sup> At its core, then, the metacommunity concept focuses on the interactions of four key processes: patch-level resource use and demographic stochasticity and landscape-level environmental heterogeneity and dispersal rates.<sup>13</sup>

Given these processes, a more generalized approach to metacommunities can broadly be conceptualized in terms of localized biotic pressures and regional, external barriers to movement. Inherent in viewing metacommunities as a multi-scale approach is a threshold at which the local pressures promoting dispersal and external barriers deterring dispersal are nearly equal and what processes affect that threshold. In my dissertation research, I will investigate how various factors—specifically system productivity, the arrival of a novel species, and potential resource partitioning—can shift such a threshold from both the local and regional perspectives.

While the theoretical development of metacommunities is moving towards a more generalized concept, it still remains highly concentrated in the effects of spatial patterns and processes. The scaffolding of the metacommunity framework, however, provides the conceptual space for incorporating temporal interactions into discussions of local and regional patterns and processes.<sup>13,14,16,17</sup> Though widely regarded as spatial processes, the four key processes associated with metacommunities are inherently temporal processes, as well.<sup>16-19</sup> For example, resource availability changes through time with seasonal and interannual variability, potentially creating environmental heterogeneity through time, colonization and extinction events can occur synchronously or asynchronously, and dispersal events can both effect and be affected by these fluctuations. Viewing metacommunities as functioning through time allows us to identify specific processes that might influence the threshold at which local or regional forces are dominant in shaping communities.

## BACKGROUND

While some work examining temporal variability in metacommunities has occurred,<sup>14,16,17</sup> it still remains uncommon. Challenges in conceptualization, analysis, and lack of appropriate data are likely contributing factors to why incorporating time into the metacommunity framework is difficult.<sup>14</sup> There are few available datasets that encompass a broad enough spatial scale to capture regional processes with enough sampling points in time. Additionally, the few studies thus far tend to focus on highly variable environments, often ones that are discontinuous (such as intermittent pools or rivers).<sup>17,20</sup> Such systems are uniquely suited to temporal studies of metacommunity processes because they naturally create patches that provide their own extinction events. In much of ecology, however, we deal in systems that tend to be more continuous, both across the landscape and through time. Expanding the temporal view of metacommunities to such systems is required to continue pushing theoretical development forward.

To ask questions about the interactions between the patch- and landscape-level processes, we can leverage time-series data. In particular, time-series data collected for multiple patches allows us to capture the spatiotemporal nature of the pivotal processes contributing to metacommunity dynamics. For my dissertation, I use data from the Portal Project, a long-term experimental site in southeastern Arizona with over four decades of small mammal capture-mark-recapture data.<sup>21</sup> The site consists of 24 50m x 50m fenced plots. Plots are designated as controls, full rodent exclosures, or kangaroo rat exclosures (only the *Dipodomys spp.*, a behaviorally dominant genus, are excluded). Rodent trapping occurs monthly year-round and plant censuses twice yearly. Climatic variables, such as temperature and precipitation, have also been recorded for the majority of the project's history.

Regardless of the scale at which we utilize the Portal data (individual patches as localities or a composite of the system as one locality), all patches experience the same abiotic conditions through time, reducing the added noise that comes from changes the physical environment. Because the Portal is located in the Chihuahuan desert, which has distinct seasons and high between-year environmental variability<sup>22,23</sup> this study site provides the ability to address the role of temporal environmental heterogeneity in determining the dynamics of metacommunities.

## RESEARCH PLAN

### Research Objectives

The primary objective of this proposal is to investigate how various factors influence the threshold at which localized pressures or regional, landscape-level processes are dominant drivers in community composition.

***Objective 1: The threshold between pressures in the patch and barriers in the landscape.***

*How does ecosystem productivity drive the distribution of transient species?*

***Objective 2. Viewing a landscape through a patchy lens.***

*How does a species' view of a patchy landscape change with spatiotemporal heterogeneity in patches?*

***Objective 3. A deeper look at local competition.***

*Do species' diet compositions indicate diet partitioning as a local coexistence mechanism in a patchy landscape?*

## Research Approach

### *Objective 1: How does ecosystem productivity drive the distribution of transient species?*

In nature, some species are common, but many species are rare. This statement is true whether the focus is on abundance of species, patterns of patch occupancy by species across space, or persistence of species at a single location through time.<sup>24-27</sup> Generally, ecologists assume that the processes influencing community composition impact all species in a community equally. Magurran and Henderson,<sup>26</sup> however, demonstrated that species in a community can be separated into two groups based on patterns of temporal occupancy in the system; core species are those which are persistent throughout the time-series, and transient species are those which are present intermittently. The core-transient distinction is the temporal analog of Hanski's<sup>28</sup> well-established core-satellite hypothesis; while the core-satellite hypothesis refers to the spatial occupancy of species at a given snapshot in time, the core-transient hypothesis focuses on species' presence in a time series at one site.<sup>29-31</sup>

Studies have shown that the richness of core and transient species is driven by different processes operating at varying scales.<sup>30,32,33</sup> For example, Coyle and colleagues<sup>30</sup> found that core species richness was best predicted by local environmental factors while species richness for transients was best predicted by regional landscape factors. There is also accumulating evidence that these two groups of species might also have varying life-history traits.<sup>31</sup>

While we have ideas about what drives transient richness, we still have little understanding of why regional processes are better predictors of transient species richness. A recent metapopulation study, however, has shown that periods of increased productivity can allow increased dispersal between patches.<sup>19</sup> Thus, increased prevalence of transients may be expected after resource pulses in the system, especially in desert systems.<sup>22,23,34</sup> Dispersal, however, is a high-risk activity;<sup>28,35-37</sup> increased connectivity in the landscape may not reduce risk enough to drive increased dispersal. Additional factors, such as local pressure due to high population densities in patches, may also be required to overcome the risk of dispersing beyond a known habitat. I propose that during an increase in productivity, external barriers to movement should decrease; local pressures likely will not increase either, as carrying capacity temporarily increases. As the productivity in the system decreases after a resource pulse, however, we expect both landscape-level barriers and local pressures to increase. At some point, the per capita dispersal rate will necessarily increase when local pressures are higher than the landscape-level barriers to dispersal, resulting in a pulse of transients in the system.

Using the rodent-abundance and NDVI time series from Portal, I will examine the potential relationship between transient dynamics in the desert and resource pulses. Preliminary data explorations have shown that the abundance of transient species at Portal often increases after a peak in NDVI, a proxy for system productivity;<sup>38,39</sup> not all peaks of NDVI are followed by such

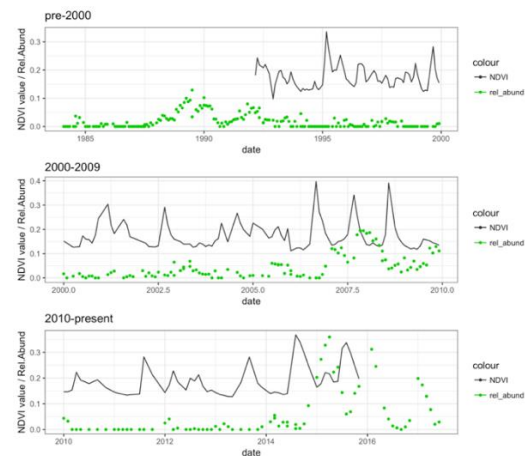


Figure 1. Time series of NDVI and relative abundance of transient species during three phases of community dynamics at Portal. Phases were determined through Christensen and colleagues<sup>49</sup> analysis of rapid ecological transitions in Portal.

an increase, however (Figure 1). Does the maximum productivity, the duration of increased productivity, or a combination of the two inform which pulses lead to an influx of transient species? To address this question, I will perform a canonical correlation analysis with all of these factors and relative transient abundance at differing lag times to see if which aspects of NDVI drive increased transient presence in the system.

**Objective 2:** *How does a species' view of a patchy landscape change with spatiotemporal patch heterogeneity?*

Metacommunity paradigms, particularly the patch dynamics archetype, suggest that an organism's perspective on the quality of a patch can depend solely on the local competitive environment.<sup>4,14</sup> Across landscapes, however, shifts in species composition often co-occur with shifts in habitat, making it difficult to disentangle the role of competitors and environment on assessments of patch quality. Using Portal data, we can observe how both spatial *and* temporal patch heterogeneity affect species and how they view the landscape. With multiple treatment types, the system at the Portal project essentially establishes multiple patches within a more-or-less continuous landscape.<sup>21</sup> In this case, the patch heterogeneity is due primarily to species composition rather than habitat and the environment. Therefore, we are able to separate responses to changes in species competition from those resulting from differences in habitat.

In the mid-1990s, a species of large pocket mouse (*C. baileyi*) that was known to exist in the regional species pool made its first appearance at the site. Within a few years, *C. baileyi* had completely infiltrated the site, and it remained one of the most abundant species at the site for over two decades. Though some *C. baileyi* individuals were found on control plots with kangaroo rats, the majority of *C. baileyi* were on kangaroo-rat exclosure plots. Our study focuses on a small congeneric of *C. baileyi*, *C. penicillatus*, which has been found at the site consistently throughout the majority of the time series. The arrival of *C. baileyi* into the system from the regional pool created a natural experiment for examining how changes in species composition in areas experiencing the same environmental conditions can affect perception of patch quality.

My results demonstrate that *C. penicillatus*'s view of the landscape has, in fact, changed in response to the arrival of *C. baileyi* (Fig. 2). Initially, *C. penicillatus* was found primarily on kangaroo-rat exclosures, as *Dipodomys* were its main competitors. With the invasion of *C. baileyi*, *C. penicillatus* became disproportionately more abundant on control plots (Fig. 2B). Population metrics of *C. penicillatus*, including immigration of new individuals, apparent survival, and transition probability between plot types, were all affected by the arrival of *C. baileyi*. Previous research has shown that the arrival of *C. baileyi* also had profound effects on ecosystem functioning in the kangaroo rat exclosures, which had previously never greater than 33% of the energy use by *Dipodomys sp.* on control plots.<sup>40</sup> After *C. baileyi* came into the system, however, the ratio of biomass between kangaroo-rat exclosures and control got much closer to equal, which might also explain *C. penicillatus*'s initial preference for kangaroo-rat exclosures seems to disappear as *C. baileyi* becomes abundant. Together, our results suggest that even though all patches are experiencing the same extrinsic environment, the intrinsic heterogeneity of patches—in this case, driven by differences in the dominant competitor in the patch types—can influence a species' patch selection.

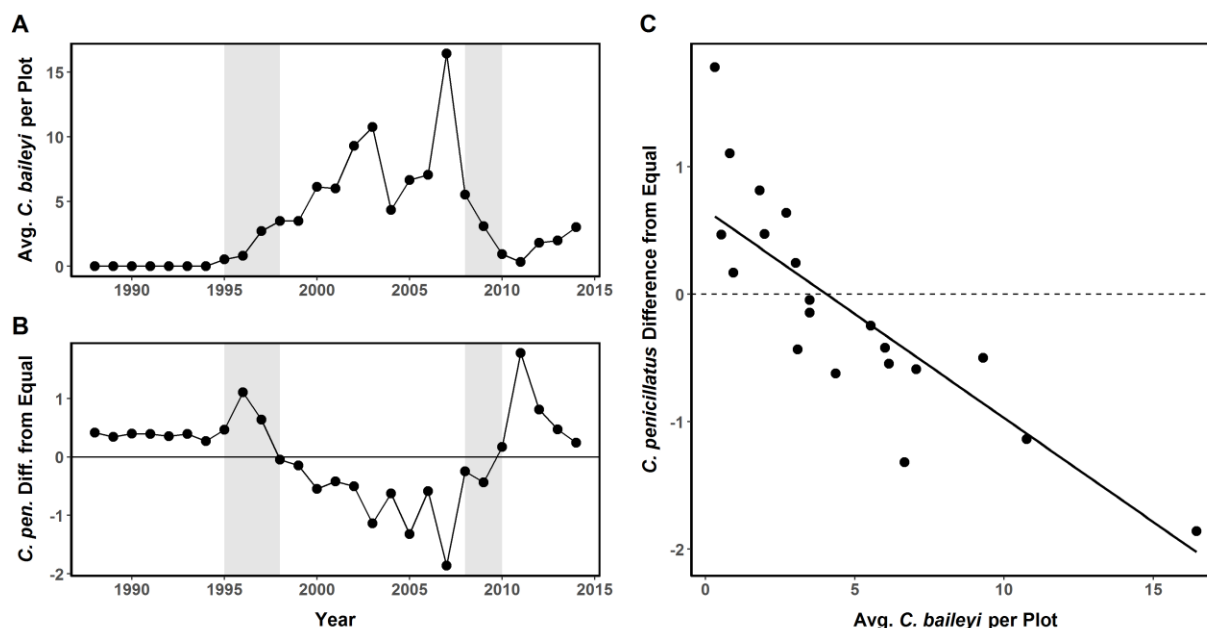


Figure 2. Relationship between mean *C. baileyi* and *C. penicillatus* plot preferences through time. (A) Mean *C. baileyi* individuals per plot through time. (B) The difference between mean *C. penicillatus* individuals per treatment type through time. The zero line indicates equal numbers of *C. penicillatus* on both treatments. Points are residuals from a linear model run against a 1:1 line of mean *C. penicillatus* on kangaroo-rat exclosures (y-axis) against control plots (x-axis). Above the zero line (positive residuals) indicates higher mean *C. penicillatus* individuals on kangaroo-rat exclosures than equal; below the line (negative residuals) are higher mean *C. penicillatus* on controls plots. In plots (A) and (B), grey bars indicate the period of arrival and infiltration (1995-1998) and subsequent decline (2008-2010) of *C. baileyi*. (C) Generalized least squares regression of *C. penicillatus* differences from equal (y-axis from (A)) against mean *C. baileyi* individuals per plot per year (y-axis from (B));  $y = -0.163x + 0.662$ ,  $df = 20$ ,  $RSE = 0.48$ ,  $p < 0.05$ ). As mean *C. baileyi* abundances increase, the mean abundance of *C. penicillatus* shifts from more individuals on kangaroo-rat exclosures to more on control plots.

**Objective 3: Do species' diet compositions indicate diet partitioning as a local coexistence mechanism in a patchy landscape?**

Both experiments and mathematical models show that similar species sharing the same limiting resource cannot coexist.<sup>1,2</sup> Theoretically, coexistence is most likely to occur when intraspecific competition is stronger than interspecific competition.<sup>41</sup> Resource partitioning between species, which decreases interspecific competition, is a commonly invoked mechanism facilitating long-term coexistence in similar species.<sup>3-5,42</sup> One way of partitioning resources is spatially, as discussed in Objective 2. In addition to landscape shifts in population-level responses to the spatial distribution of competitors, species can also adjust their diet overlap with interspecific competitors.<sup>43,44</sup> This can result in differences across the landscape in a species' diet depending on the presence of competitors.

While resource partitioning is foundational in most species coexistence models, it is difficult to quantify diet overlap in animals.<sup>45,46</sup> Metabarcoding, or the simultaneous identification of multiple species in a single sample, is a new genetic analysis technique that offers an efficient and effective way to determine diet content without intensive observation or fatal sampling.<sup>44-46</sup> It has been used successfully to study diets in a variety of animals, including rodents and other granivores.<sup>44-48</sup> Using this technique at Portal opens a window into how diet

partitioning might play a role in local species coexistence and whether there is an interaction between diet partitioning and spatial partitioning.

To assess diet partitioning across a patchy landscape, I collected fecal samples from two *Dipodomys spp.* and *C. penicillatus* in control and kangaroo rat enclosure plots at the Portal site in three separate sampling efforts, once in 2016 and twice in 2017. The experimental manipulation of the system allows me to assess how diet changes when the behaviorally dominant competitors, *Dipodomys spp.*, are not present in a patch, a rare opportunity in resource partitioning studies. Additionally, I created a plant reference database by collecting DNA samples and voucher specimens for species at the site, which are being identified at the Univ. of Arizona Herbarium. This reference library contains voucher specimens and DNA samples for nearly 80% of the species known to be found at the Portal site; all abundant species are included.

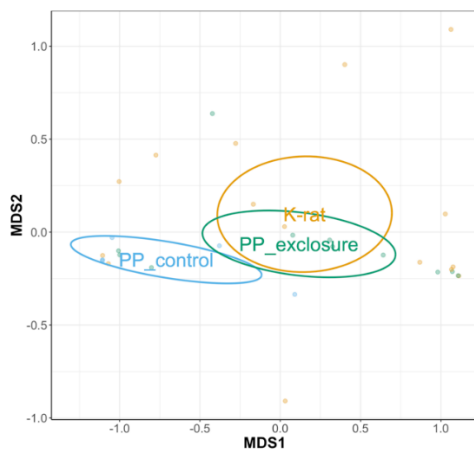


Figure 3. NMDS plot of rodent diet composition, grouped by species and plot type. The *Dipodomys* species and *C. penicillatus* found on the kangaroo rat enclosure plots show high levels of overlap in diet composition. The *C. penicillatus* that are found on control plots (with kangaroo rats present), however, show a shift in diet composition from the kangaroo rats, suggesting diet partitioning as a possible mechanism promoting coexistence.

Results from the high-frequency throughput analysis indicate that we do have the ability to successfully detect plants through rodent feces, though with varying levels of specificity. I am currently in the process of synthesizing results from two different primer sequences to enhance our ability to identify the presence of plants down to the most resolute taxonomic level possible. Once the sequences in each fecal sample are fully identified in the reference library, I will be able to utilize this as presence/absence data in diet composition. I can potentially also calculate frequency of occurrence and relative read abundance for comparison between individuals or groups of the same species<sup>44,48</sup> Preliminary analysis of data collected during the spring of 2016 suggest that *C. penicillatus* may, in fact, be shifting its diet due to the presence of kangaroo rats (Figure 3).

## INTELLECTUAL MERIT

In order for the theoretical framework of metacommunities to move forward, we must conceptually integrate temporal and spatiotemporal changes in novel and creative ways. My objectives above can be thought of a case-studies identifying just a few of the many facets through which we can begin investigating spatiotemporal patterns and processes that contribute to the metacommunity. By incorporating data from both the local and regional scales as well as studies that examine combinations of the four major processes that make up metacommunities, we can begin to form a more complete picture of what affects the threshold at which local or regional processes dominant the community patterns we see.

## TIMELINE

<b>Year</b>	<b>Research/Training Goals</b>	<b>Dissemination of Results</b>
<b>2018</b>	<ul style="list-style-type: none"><li>• Finish writing manuscript for Objective 2</li><li>• Run CCA for Obj. 1</li><li>• Continue development of pipeline for Obj. 3</li><li>• Co-teaching class with Morgan</li></ul>	<ul style="list-style-type: none"><li>• Presented results of Obj. 2 at ESA</li><li>• Submit Obj. 2 manuscript</li></ul>
<b>2019</b>	<ul style="list-style-type: none"><li>• Complete analysis for Obj. 3</li><li>• Continue conceptual development and subsequent analyses for Obj. 1</li></ul>	<ul style="list-style-type: none"><li>• Submit manuscript for Obj. 3</li><li>• Present research at national conference</li></ul>
<b>2020</b>	<ul style="list-style-type: none"><li>• Complete analysis and manuscript for Obj. 1</li><li>• Complete dissertation</li><li>• Graduate in May or August 2020</li></ul>	<ul style="list-style-type: none"><li>• Submit manuscript for Obj. 1</li><li>• Present research at conference</li></ul>

## LITERATURE CITED

- <sup>1</sup> Lotka, A. H. 1932. The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences* 22: 461-469.
- <sup>2</sup> Gause, G. F. 1934. *The Struggle for Existence*. Hafner, New York, New York, USA.
- <sup>3</sup> MacArthur, R. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39(4): 599-619.
- <sup>4</sup> Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93(870): 145-159.
- <sup>5</sup> Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185(4145): 27-39.
- <sup>6</sup> McArthur, R., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- <sup>7</sup> Ricklefs, R. 1987. Community diversity: relative roles of local and regional processes. *Science* 235(4785): 167-171.
- <sup>8</sup> Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65(1): 169-175.
- <sup>9</sup> Cornell, H. V. and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61(1): 1-12.
- <sup>10</sup> Ricklefs, R. E., and D. Schluter, editors. 1993. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, USA.
- <sup>11</sup> Cornell, H. V., and R. H. Karlson. 1996. Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology* 65(2): 233-241.
- <sup>12</sup> Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177-192.
- <sup>13</sup> Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt, J. Shurin, R. Law, and D. Tilman. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.
- <sup>14</sup> Leibold, M. A., and J. M. Chase. 2018. *Metacommunity Ecology*. Princeton University Press, Princeton, New Jersey, USA.



- <sup>15</sup> Logue, J. B., N. Moquet, H. Peter, and H. Hillebrand. 2011. Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution* 26:482-491.
- <sup>16</sup> Padial, A. A., F. Ceschin, S. A. J. Declerck, L. De Meester, C. C. Bonecker, F. A. Lansca-Toha, L. Rodrigues, L. C. Rodrigues, S. Train, L. F. M. Velho, L. M. Bini. 2014. Dispersal ability determines the role of environmental, spatial, and temporal drivers of metacommunity structure. *PLoS ONE* 9(1): e111227.
- <sup>17</sup> Datry, T., N. Bonada, and J. Heino. 2015. Towards understanding the organization of metacommunities in highly dynamic ecological systems. *Oikos* 125(2): 149-159.
- <sup>18</sup> Ernest, S. K. M., J. H. Brown, K. M. Thibault, E. P. White, and J. R. Goheen. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. *American Naturalist* 172(6): E257-E269.
- <sup>19</sup> Fernandez, N., J. Roman, and M. Delibes. 2016. Variability in primary productivity determines metapopulations dynamics. *Proceedings of the Royal Society B* 283: 20152998.
- <sup>20</sup> Ochoa-Ochoa, L. M., and R. J. Whittaker. 2014. Spatial and temporal variation in amphibian metacommunity structure in Chiapas, Mexico. *Journal of Tropical Ecology* 30: 537-549.
- <sup>21</sup> Brown, J. H. 1998. The granivory experiments at portal. In W. J. Resetarits and J. Bernardo, editors. *Experimental ecology: issue and perspectives*. Oxford University Press, New York, New York, USA.
- <sup>22</sup> Ernest, S. K. M., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88(3): 470-482.
- <sup>23</sup> Lima, M., S. K. M. Ernest, J. H. Brown, A. Belgrano, and N. C. Stenseth. 2008. Chihuahuan desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. *Ecology* 89(9): 2594-2603.
- <sup>24</sup> Fisher, R. A., A. S. Corbet, and C. B. Willaims. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* 12: 42-58.
- <sup>25</sup> Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* 29: 254-283.
- <sup>26</sup> Magurran, A. E., and P. A. Henderson. 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature* 422:714-716.
- <sup>27</sup> McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornales, B. J. Enquist, J. L. Green, F. He, A. H. Hurlbert, A. E. Magurran, P. A. Marquet, B. A. Maurer, A. Ostling, C. U. Soykan, K. I. Ugland, E. P. White. 2007. Species abundance

distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10(10): 995-1015.

<sup>28</sup> Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210– 221.

<sup>29</sup> White, E. P., S. K. M. Ernest, P. B. Adler, A. H. Hurlbert, and S. K. Lyons. 2010. Integrating spatial and temporal approaches to understanding species richness. *Phil. Trans. Royal Society B* 365: 3633-3643.

<sup>30</sup> Coyle, J. R., A. H. Hurlbert, and E. P. White. 2013. Opposing mechanisms drive richness patterns of core and transient bird species. *American Naturalist* 181:E83–90.

<sup>31</sup> Supp, S. R., D. N. Koons, and S. K. M. Ernest. 2015. Using life history trade-offs to understand core-transient structuring of a small mammal community. *Ecosphere* 6(10): 187.

<sup>32</sup> Belmaker, J. 2009. Species richness of resident and transient coral-dwelling fish responds differently to regional diversity. *Global Ecology and Biogeography* 18:426–436.

<sup>33</sup> Henderson, P. A., and A. E. Magurran. 2014. Direct evidence that density-dependent regulation underpins the temporal stability of abundant species in a diverse animal community. *Proceedings of the Royal Society B* 281:20141336.

<sup>34</sup> Brown, J. H., and S. K. M. Ernest. 2002. Rain and rodents: complex dynamics of desert consumers. *BioScience* 52(11): 979-987.

<sup>35</sup> Murray, B. G. 1967. Dispersal in Vertebrates. *Ecology* 48(6): 975–978.

<sup>36</sup> Waser, P. M. 1985. Does competition drive dispersal? *Ecology* 66:1170–1175.

<sup>37</sup> Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* 15(3): 469-476.

<sup>38</sup> Paruelo, J. M., H. E. Epstein, W. K. Lauenroth, I. C. Burke. 1997. ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* 78(3): 953-958.

<sup>39</sup> Xu, C., Y. Li, J. Hu, X. Yang, S. Sheng, and M. Liu. 2012. Evaluating the difference between the normalized difference vegetation index and net primary productivity as the indicators of vegetation vigor assessment at landscape scale. *Environmental Monitoring and Assessment* 184(3): 1275-1286.

<sup>40</sup> Ernest, S. K. M., and J. H. Brown. 2001. Delayed compensation for missing keystone species by colonization. *Science* 292:101–104.

<sup>41</sup> Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-358.

- <sup>42</sup> Pianka, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53-74.
- <sup>43</sup> Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* 19:281-307.
- <sup>44</sup> Kartinzel, T. R., P. A. Chen, T. C. Cloverdale, D. L. Erickson, W. J. Kress, M. L. Kuzmina, D. I. Rubenstein, W. Wang, and R. M. Pringle, 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences* 112(26): 8019-8024.
- <sup>45</sup> Valenti, A. C. Miquel, M. A. Nawaz, E. Bellemain, E. Coissac, F. Pompanon, L. Gielly, C. Cruaud, G. Nascetti, P. Wincker, J. E. Swenson, and P. Taberlet. 2009. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the trnL approach. *Molecular Ecology Resources* 9(1): 51-60.
- <sup>46</sup> Pompanon, F., B. E. Deagle, W. O. C. Symondson, D. S. Brown, S. N Jarman, and P. Taberlet. 2012. Who is eating what: diet assessment using next generation sequencing. *Molecular Ecology* 21(8): 1931-1950.
- <sup>47</sup> Soininen, E. M., A. Valenti, E. Coissac, C. Miquel, L. Gielly, C. Brochmann, A. K. Brysting, J. H. Sonstebo, R. A. Ims, N. G. Yoccoz, and P. Taberlet. 2009. Analysing diet of small herbivores: the efficiency of DNA barcoding couple with high-throughput pyrosequencing for deciphering the composition of complex plant mixtures. *Frontiers in Zoology* 6(1): 1-9.
- <sup>48</sup> Iwanowicz, D. D., A. G. Vandergast, R. S. Cornman, C. R. Adams, J. R. Kohn, R. N. Fisher, C. S. Brehme. 2016. Metabarcoding of fecal samples to determine herbivore diets: a case study of the endangered Pacific pocket mouse. *PLoS ONE* 11(11): 1-23.
- <sup>49</sup> Christensen, E. M., D. J. Harris, and S. K. M. Ernest. 2018. Long-term community change through multiple rapid transitions in a desert rodent community. *Ecology* 99(7): 1523-1529.