Reports

An experimental test of the response of macroecological patterns to altered species interactions

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Abstract. Macroecological patterns such as the species–area relationship (SAR), the species-abundance distribution (SAD), and the species–time relationship (STR) exhibit regular behavior across ecosystems and taxa. However, determinants of these patterns remain poorly understood. Emerging theoretical frameworks for macroecology attempt to understand this regularity by ignoring detailed ecological interactions and focusing on the influence of a small number of community-level state variables, such as species richness and total abundance, on these patterns. We present results from a 15-year rodent removal experiment evaluating the response of three different macroecological patterns in two distinct annual plant communities (summer and winter) to two levels of manipulated seed predation. Seed predator manipulations significantly impacted species composition on all treatments in both communities, but did not significantly impact richness, community abundance, or macroecological patterns in most cases. However, winter community abundance and richness responded significantly to the removal of all rodents. Changes in richness and abundance were coupled with significant shifts in macroecological patterns (SADs, SARs, and STRs). Because altering species interactions only impacted macroecological patterns when the state variables of abundance and richness also changed, we suggest that, in this system, local-scale processes primarily act indirectly through these properties to determine macroecological patterns.

Key words: community ecology; macroecology; species-abundance distribution; species–area relationship; species–time relationship.

INTRODUCTION

Macroecology treats individuals, populations, and species as ecological particles, and uses patterns in these particles to understand ecological systems (Brown 1995). Macroecological patterns such as the species abundance distribution (i.e., distribution of abundance across species; SAD), the species–area relationship (i.e., accumulation of species across space; SAR), and the species–time relationship (i.e., accumulation of species through time; STR) are commonly used to quantify and compare community structure (Brown 1995). These patterns are often used to infer local-scale ecological processes and to inform management decisions. For example, SADs are often used to investigate questions of commonness and rarity (e.g., Magurran and Henderson 2003, Dolan et al. 2009), SARs are used to make

predictions concerning species' extinctions as habitat area declines (e.g., Brooks et al. 1999, Thomas et al. 2004), and STRs have been used to test the dynamic predictions of ecological theories (e.g., Adler 2004).

Despite important applications to ecology and conservation, determinants of macroecological patterns remain poorly understood. Decades of empirical research show that biotic interactions can impact the abundance and distribution of species (Colwell and Fuentes 1975, Chase and Leibold 2003, Clark 2009), leading many ecologists to assume that patterns such as the SAD reflect small scale community structuring processes (e.g., competition for resources, dispersal limitation [MacArthur 1960, Hubbell 2001]). Alternatively, recent work suggests that macroecological patterns may be relatively insensitive to the details of species interactions and other biological processes per se because the patterns are proximally determined primarily by a small number of community-level state variables (e.g., species richness [S] and total abundance [N] [Harte et al. 2008, 2009, McGill 2010, Harte 2011, White et al.
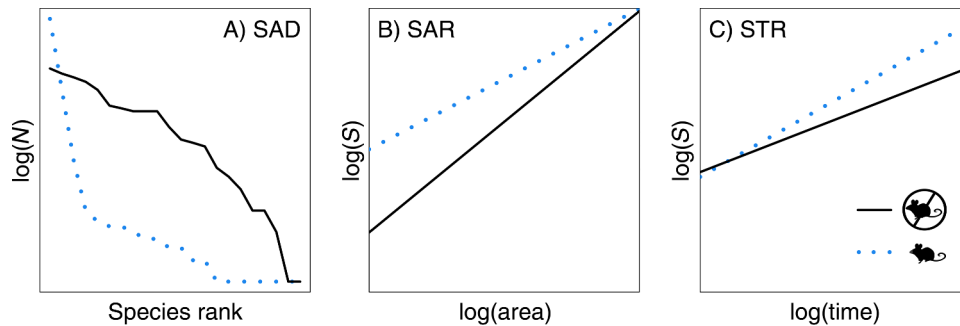
FIG. 1. Possible responses of three macroecological patterns to manipulated seed predation assuming that the manipulation has no effect on species richness (S) and total abundance (N): (A) the species–abundance distribution (SAD), (B) the species–area relationship (SAR), and (C) the species–time relationship (STR). The blue dotted line indicates response in the presence of a seed predator; the solid black line shows the response in the absence of a seed predator. Please note that each macroecological pattern varies with manipulations that impact species composition (blue dotted line) despite fixed S and N. For each pattern, the abundance for each ranked species is allowed to differ between communities, as long as the abundances still sum to the same total N (SAD; $\log(N)$ for each rank can differ), spatial turnover at scales below the whole community may differ (SAR; S is fixed at the largest scale, the whole community), and temporal turnover may differ between communities even when total S remains invariant (STR; S is fixed at the intercept, the whole community in one year).

2012]). While macroecological patterns are inherently influenced by the values of the state variables, fully defining these patterns requires not only S and N but also evenness, aggregation (spatial and temporal), and potentially spatial and temporal species turnover. As such, it is possible for patterns to change even when S and N are fixed (Fig. 1). In effect, state variable theories hypothesize that evenness, aggregation, and turnover are related in some specific manner to S and N, and are therefore not free to vary independently of changes in the state variables. If this is true, then the key to understanding at least some macroecological patterns lies in understanding the processes that generate variation in state variables such as S and N (McGill 2010).

Here we ask the question: do biological interactions *directly* influence macroecological patterns of community structure or is their influence *indirect* through the impacts of biological interactions on S and N? If biotic interactions directly impact macroecological patterns, independently of the state variables, then the shapes of these relationships should be sensitive to the removal of biotic interactions that have a strong impact on species composition. This should be true even when S and N are unaffected by altered biotic interactions because there is substantial room for variation in each of the macroecological patterns for a given combination of S and N (Fig. 1; He and Legendre 2002, White et al. 2012). However, if these patterns are proximally determined largely by state variables such as species richness and total abundance, then manipulating important biotic interactions should only have indirect effects on the shapes of these patterns that emerge when altered biotic interactions also affect the species richness and total abundance of the community.

To address our question, we used 15 years of experimental data (1995–2009) from a long-term site in the Chihuahuan desert near Portal, Arizona. We examined the response of two temporally distinct annual plant communities (summer and winter) to a sustained manipulation of an important biotic interaction: seed predation by rodents, the dominant seed predators in this system (Reichmann and Price 1993). Plant communities experience one of three different levels of seed predation: (1) unmanipulated controls (all rodents present), (2) kangaroo rat removals (dominant seed predators, *Dipodomys* spp., removed), and (3) total rodent removals.

The study site and experimental design are ideal for addressing whether the structure of biotic interactions directly influence macroecological patterns because altering seed predation is known to impact the composition of the plant community (Brown and Heske 1990, Samson et al. 1992, Guo and Brown 1996), and the response of plant species richness and total abundance differs among seasons and seed predator manipulations (see Plate 1). Because one of the two plant communities exhibited only compositional responses to treatments and the other community exhibited both compositional responses and changes in richness and abundance, this system provides a unique opportunity to examine the responses of macroecological patterns to altered biotic interactions.

We assess the impact of biotic interactions on macroecological patterns by examining three widely studied patterns (SAD, SAR, and STR) to determine whether they respond to the biotic manipulation alone, or only when that manipulation also impacts species richness and total abundance. Using local-scale experiments to study macroecology is a powerful, but little used, approach for directly assessing mechanisms underlying macroecological patterns (see Marquet et al. 1990, Wootton 2004, Hurlbert 2006).

Materials and Methods

Study site

Data were collected at the Portal Project field site, located in the Chihuahuan Desert near Portal, Arizona, USA. The Portal Project consists of 24, 0.25-ha, fenced plots. Four gates cut into each side of the fenced plots allow passage of rodents into and out of plots. Since kangaroo rats (*Dipodomys* spp.) have enlarged auditory bullae, plots with a smaller gate size ($n = 8$) selectively exclude these species. Total rodent removal plots have no gates ($n = 6$), while control plots have relatively large gates that allow all species unimpeded access ($n = 10$). Plots are trapped monthly to maintain experimental treatments (Brown 1998).

A bimodal precipitation pattern (October–April and May–September) generates two distinct annual plant communities with effectively no species overlap. Twice annually, once each for the summer and winter communities, the number of stems per species were counted on 16 permanent and evenly spaced 0.25-m^2 quadrats on each experimental plot. We excluded data that were compromised due to changes in the experimental treatment or high abundances of unidentifiable individuals (Appendix A). For additional details on study site and experimental design see Brown (1998). For data, see Ernest et al. (2009).

Composition analysis of annual plant communities

Compositional differences among rodent treatments were characterized with partially constrained correspondence analysis (pCCA) and permutational significance tests were used to determine significance of the pCCA axes (R package vegan; *available online*).[2] We square root transformed the abundance data and controlled for the effect of year. All statistical analyses were conducted in R 2.12.2 (R Development Core Team 2011).

Macroecological pattern construction

Total richness (S), total abundance (N), and all macroecological patterns were characterized for each plot in each year, with the exception of the STR, which is characterized once for each plot using data from all years of the study (Appendix B). Our measures of S and N were determined at the level of the whole plot, not the individual quadrat. Years when plot-level $S < 5$ were excluded from analysis because of the difficulty of characterizing macroecological patterns precisely when S is small.

Species-level abundance data were used to construct SADs for each plot in each year using package vegan (see footnote 2). We characterized the SAD using the Poisson log-normal (Bulmer 1974) distribution, which is one of the most common characterizations of the pattern (McGill et al. 2007). The maximum likelihood (MLE) of the Poisson log-normal parameters, μ (mean)

and σ (standard deviation), were estimated with R function poilogMLE from package poilog (*available online*).[3] Since μ took both positive and negative values, we used its exponentiated form, $\exp(\mu)$, which roughly represents the geometric mean of the abundances, as the response variable to facilitate later transformation in order to meet the assumptions of our statistical analyses (Appendix D: Table D1). The log-series distribution, which in some cases provided a better fit to the SAD, could not be used because the maximum likelihood estimate of its parameter is determined entirely by S and N (Evans et al. 2000), thus inappropriately constraining this pattern to only respond to changes in S and N.

SARs were generated for each year by calculating the species richness for groups of neighboring quadrats within a plot representing five spatial scales (1, 2, 4, 8, and 16 quadrats). For spatial scales where multiple replicates existed (e.g., species richness counts for 16 different quadrats at the smallest scale within a plot) mean species richness across replicates at that spatial scale was used for our analyses. For STRs, we used a temporal moving window approach to count mean species richness in every possible timespan (i.e., species richness averaged over 1 year, 2 years, and so on, up to the maximum time length) in each plot. Summer annual STRs were restricted to 1999–2009 due to high abundance of unidentifiable individuals in 1997 and 1998 (Appendix A). SARs and STRs were characterized using power-laws, a common form for both patterns (White et al. 2006, Dengler 2009). For the log-transformed SARs, both the slope and the intercept can fluctuate for given values of S and N (Fig. 1B). However, for the STR the intercept is mathematically constrained to be nearly equal to S because S is measured at the plot level, which is the same scale as the intercept of our STRs (Fig. 1C). Therefore, we searched for differences in the slope and intercept of SARs but only the slope of the STRs.

Statistical approach

Statistical analyses were performed on five macroecological parameters (SAD $\exp(\mu)$ and σ, SAR slope and intercept, STR slope), as well as plot-level total richness (S) and total abundance (N) to test the effect of treatments on macroecological patterns. We tested whether parameters differed significantly among paired treatments while controlling for other random effects. For S, N, SAD, and SAR we used linear mixed-effect models (lmer) in the R package lme4 (*available online*),[4] which analyze the fixed effects of treatment while controlling for the random effects of plot, year, and treatment–year interaction. *P* values were calculated using the function pvals.fnc (in the package languageR; *available online*).[5] Because STRs lack the temporal (i.e.,

[2] http://CRAN.R-project.org/package=vegan

[3] http://CRAN.R-project.org/package=poilog
[4] http://CRAN.R-project.org/package=lme4
[5] http://CRAN.R-project.org/package=languageR
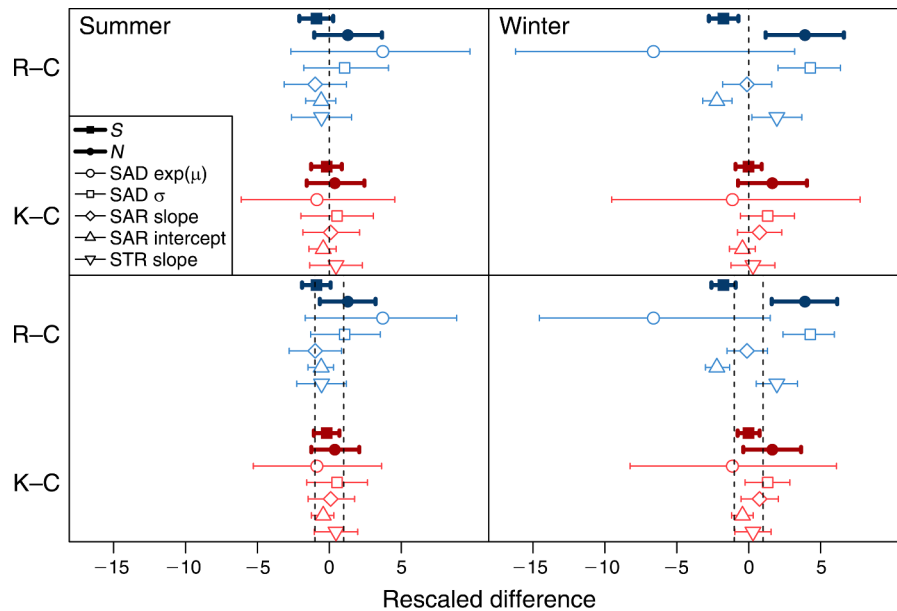
Reports

FIG. 2. Statistical differences among the parameters were only detected in the winter annual community when experimental manipulation (C, control; K, kangaroo rat removal; R, total rodent removal) also impacted species richness and total abundance. Top panels display results from standard statistical tests (linear mixed effects models for SAD and SAR, ANOVA for STR) for significant differences, and lower panels display results from equivalence tests. Symbols represent the mean difference in parameter estimation between two treatments, and whiskers indicate 95% confidence intervals (CI; top) and 90% CI (bottom) of the difference in parameter estimates. Because parameter estimates differ in magnitude for different patterns, all values and their CIs are standardized with respect to their designated range of equivalence in both the upper and lower panels for better visualization.

variable year) component, they were analyzed with traditional ANOVA. All response variables were transformed to meet assumptions of normality and homoscedasticity (Appendix D: Table D1). We used false discovery rate control (FDR; Benjamini and Hochberg 1995, Garcia 2004) to correct for multiple statistical tests within each seasonal community. We also used equivalence tests to examine if macroecological patterns were significantly similar across treatments (Dixon and Pechmann 2005; see Appendix C for details). SAD, STR, and SAR are interrelated measures of community structure (Storch et al. 2008). The five variables are not strictly independent measures, but neither are they strictly dependent on one another. Code for conducting the analyses and generating the figures in this paper is available in the Supplement.

RESULTS

In accordance with earlier studies at the site (Brown and Heske 1990, Samson et al. 1992, Guo and Brown 1996), significant differences in plant species composition among treatments were observed in both seasons in response to both the removal of kangaroo rats and of all granivorous rodents (pCCA permutation test, summer, $R^2_{CCA} = 0.02$, $P = 0.005$; winter, $R^2_{CCA} = 0.05$, $P = 0.005$).

Changes in S and N in response to the removal of seed predators occurred only in the winter community and only in response to the removal of all rodents, which showed an increase in total abundance (lmer, $P = 0.014$;

Appendix D: Table D2) and a decrease in species richness (lmer, $P = 0.001$; Table D2). In contrast to the community-level changes observed in the winter annual community, the summer annual community exhibited no detectable response in S or N to the removal of rodents (Table D3).

Despite differences in species composition, the macroecological patterns showed no significant changes in response to altered seed predation, except when plant S and N were influenced by rodent removal. In the summer annuals, no significant differences in the macroecological patterns were detected among treatments (Fig. 2, Appendix D). However, in the winter annual community, total rodent removals exhibited significant differences in the standard deviation of SADs (σ) and the intercept of SARs in comparison to controls or kangaroo rat removals after controlling for the rate of false discovery (FDR [Benjamini and Hochberg 1995, Garcia 2004]; Fig. 2; Appendix D). These differences corresponded with the observed changes in S and N described in the last paragraph. The difference in the slope of STRs was significant before controlling for FDR, but insignificant after controlling for FDR, while the mean of SADs ($\exp(\mu)$) and the slope of SARs were not affected by the manipulations (Fig. 2, Appendix D).

In addition to traditional statistical tests, which can determine if treatments differ but not if they are meaningfully similar, we conducted equivalence tests.

PLATE 1. A view along the plot-19 fence line, which selectively removes kangaroo rats (*Dipodomys* spp.). The photo demonstrates differing annual plant species composition inside the plot versus outside the plot, a consequence of altered seed predation. Plants to the right of the fence are inside the plot, and plants to the left of the fence are outside the plot. Photo credit: S. R. Supp.

Results pertaining to SADs, SARs, and STRs were inconclusive (i.e., we failed to reject the null hypothesis that the parameters differed) for both communities after controlling for FDR (Appendix D) using our prespecified equivalence ranges. Sensitivity analyses, however, indicate that modest increases in the similarity range in SARs and STRs from ±5% to ±12% result in significant similarity between kangaroo rat removal plots and control plots in the summer annuals (Appendix C). Nonetheless, we cannot conclude that patterns that do not significantly differ are also biologically meaningfully similar (Appendix C). More research is necessary to understand the generality of these results and whether the lack of similarity is a statistical issue or a biological signal indicating a more subtle influence of biotic interactions on macroecological patterns.

DISCUSSION

Our results show a mechanistic pathway through which biotic interactions may indirectly impact patterns at higher levels of organization. Manipulations of granivorous rodents had a direct and significant effect on plant community composition in both seasons. However, responses of macroecological patterns to these changes in seed predation were only observed when the changes in biotic interactions impacted S or N, which only occurred in the winter community when the entire granivorous rodent guild was removed. Our results provide empirical support for the state variable approach to macroecology and

for the idea that biological interactions affect the shapes of macroecological patterns indirectly through their impacts on state variables. To be clear, our results only apply to macroecological patterns, not to the importance of processes operating in the system. In fact, our results show that in all cases, manipulating biotic interactions directly impacted the composition of the plant community.

Understanding how biotic interactions influenced the state variables at our site, and therefore the macroecological patterns, requires examining how the different manipulations of seed predation impacted the plant community. Despite the fact that kangaroo rats are considered dominant keystone species with important cascading effects on ecological interactions across multiple trophic levels (Brown and Heske 1990, Ernest and Brown 2001, Valone and Schutzenhofer 2007), macroecological patterns did not respond to the removal of kangaroo rats alone. Although kangaroo rats exert a significant influence on plant species composition, this does not result in changes in S and N. While control and kangaroo rat removal plots differ in rodent and plant composition, compensatory dynamics in the rodent community resulted in nearly equivalent seed consumption on controls and kangaroo rat removal plots (Ernest and Brown 2001, Thibault et al. 2010). In contrast, consumption pressure was substantially reduced on total rodent removal plots. This reduced consumption likely caused the total plant abundance to increase due to

Reports

an increase in the number of seeds available to germinate, and S to decline in response to the elevated prevalence of the competitively dominant large-seeded species preferred by granivorous rodents (Samson et al. 1992, Guo and Brown 1996). Thus, changes in macroecological patterns occurred when changes in trophic or competitive interactions were such that they strongly impacted the community-level state variables S and N.

If the state variable view of macroecology is correct, it may explain why using macroecological patterns such as the SAD to distinguish among different mechanistic models has been so problematic (McGill et al. 2007). If state variables determine macroecological patterns, then any model will do well at predicting those patterns if the model also predicts realistic values of state variables (McGill 2010, White et al. 2012). More broadly, if the indirect effect of biotic interactions on macroecological patterns is general, then these patterns may be unsuitable for determining the detailed biological processes operating in specific ecosystems. Communities with similar values of S and N could be dissimilar in the structure of their biotic interactions, ecological and evolutionary history, and other processes. The potential value of macroecological patterns being determined only indirectly by specific biological processes is that it makes it easier and more generalizable to use them for building ecological theories, and apply them to accomplish important tasks like scaling diversity estimates for reserve design, hotspot analysis, and future climate scenarios (e.g., Brummitt and Lughadha 2003, Thomas et al. 2004, Diniz-Filho et al. 2005, Harte 2009) and estimating abundance from occupancy (e.g., He and Gaston 2000, Harte 2011). Because only the impacts of biological processes on S and N are important, and not the details of the biological interactions themselves, the same approaches can potentially be applied across diverse ecosystems and taxonomic groups (McGill 2010, Harte 2011, White et al. 2012).

Our results support the state variable framework linking biotic and abiotic interactions indirectly to macroecological patterns through the constraints imposed by community-level properties (Harte et al. 2008, 2009, McGill 2010, Harte 2011). However, our results are only for a single community, and a single set of ecological interactions, and more research is necessary before drawing general conclusions. In addition to validating these results in more systems, there are underlying assumptions in this approach that need to be explored. Specifically, we need to evaluate how variables such as spatial aggregation, species turnover, and evenness are related to S and N. State variable approaches assume that changes in species composition will not impact these measures independently of changes in S and N. This is an important assumption that remains untested. Our results suggest that state variables are important for understanding macroecological patterns, and that combining experimental approaches with macroecological analyses can improve our understanding of the linkages between pattern and process.

LITERATURE CITED

Adler, P. B. 2004. Neutral models fail to reproduce observed species–area and species–time relationships in Kansas grasslands. Ecology 85:1265–1272.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B Statistical Methodology 57:289–300.

Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conservation Biology 13:1140–1150.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. H. 1998. The desert granivory experiments at Portal. Pages 71–95 *in* W. J. Resetarits, and J. Bernardo, editors. Experimental Ecology: Issue and Perspectives. Oxford University Press, New York, New York, USA.

Brown, J. H., and E. J. Heske. 1990. Control of a desert–grassland transition by a keystone rodent guild. Science 250:1705–1707.

Brummitt, N., and E. N. Lughadha. 2003. Biodiversity: where's hot and where's not. Conservation Biology 17:1442–1448.

Bulmer, M. G. 1974. On fitting the Poisson lognormal distribution to species-abundance data. Biometrics 30:101–110.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.

Clark, J. S. 2009. Beyond neutral science. Trends in Ecology and Evolution 24:8–15.

Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics 6:281–310.

Dengler, J. 2009. Which function describes the species–area relationship best? A review and empirical evaluation. Journal of Biogeography 36:728–744.

Diniz-Filho, J. A. F., R. P. Bastos, T. F. L. V. B. Rangel, L. M. Bini, P. Carvalho, and R. J. Silva. 2005. Macroecological correlates and spatial patterns of anuran description dates in the Brazilian Cerrado. Global Ecology and Biogeography 14:469–477.

Dixon, P. M., and J. H. K. Pechmann. 2005. A statistical test to show negligible trend. Ecology 86:1751–1756.

Dolan, J. R., M. E. Ritchie, A. Tunin-Ley, and M. D. Pizay. 2009. Dynamics of core and occasional species in the marine plankton: tintinnid ciliates in the north-west Mediterranean Sea. Journal of Biogeography 36:887–895.

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

Ernest, S. K. M., T. J. Valone, and J. H. Brown. 2009. Long-term monitoring and experimental manipulation of a

Chihuahuan Desert ecosystem near Portal, Arizona, USA. Ecology 90:1708.

Evans, M., N. Hastings, and B. Peacock. 2000. Logarithmic series distribution. Pages 121–123 *in* M. Evans, N. Hastings, and B. Peacock, editors. Statistical distributions. Third Edition. John Wiley and Sons, New York, New York, USA.

Garcia, L. V. 2004. Escaping the Bonferroni iron claw in ecological studies. Oikos 105:657–663.

Guo, Q., and J. H. Brown. 1996. Temporal fluctuations and experimental effects in desert plant communities. Oecologia 107:568–577.

Harte, J. 2011. Maximum entropy and ecology: a theory of abundance, distribution, and energetics. Oxford University Press, New York, New York, USA.

Harte, J., A. B. Smith, and D. Storch. 2009. Biodiversity scales from plots to biomes with a universal species–area curve. Ecology Letters 12:789–797.

Harte, J., T. Zillio, E. Conlisk, and A. B. Smith. 2008. Maximum entropy and the state-variable approach to macroecology. Ecology 89:2700–2711.

He, F., and K. J. Gaston. 2000. Estimating species abundance from occurrence. American Naturalist 156:553–559.

He, F., and P. Legendre. 2002. Species diversity patterns derived from species–area models. Ecology 83:1185–1198.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hurlbert, A. H. 2006. Linking species–area and species–energy relationships in *Drosophila* microcosms. Ecology Letters 9:287–294.

MacArthur, R. 1960. On the relative abundance of species. American Naturalist 94:25–36.

Magurran, A. E., and P. A. Henderson. 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422:714–716.

Marquet, P. A., S. A. Navarrete, and J. C. Castilla. 1990. Scaling population density to body size in rocky intertidal communities. Science 250:1125–1127.

McGill, B. J. 2010. Towards a unification of unified theories of biodiversity. Ecology Letters 13:627–642.

McGill, B. J., et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10:995–1015.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Reichmann, O. J., and M. V. Price. 1993. Ecological aspects of heteromyid foraging. Pages 539–574 *in* H. H. Genoway and J. H. Brown, editors. Biology of the Heteromyidae. Special publication no. 10. American Society of Mammalogists. http://www.biodiversitylibrary.org/bibliography/39570

Samson, D. A., T. E. Philippi, and D. W. Davidson. 1992. Granivory and competition as determinants of annual plant diversity in the Chihuahuan Desert. Oikos 6:61–80.

Storch, D., A. L. Šizling, J. Reif, J. Polechová, E. Šizlingová, and K. J. Gaston. 2008. The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. Ecology Letters 11:771–784.

Thibault, K. M., M. S. K. Ernest, and J. H. Brown. 2010. Redundant or complementary? Impact of a colonizing species on community structure and function. Oikos 119:1719–1726.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Valone, T. J., and M. R. Schutzenhofer. 2007. Reduced rodent biodiversity destabilizes plant populations. Ecology 88:26–31.

White, E. P., P. B. Adler, W. K. Lauenroth, R. A. Gill, D. Greenberg, D. M. Kaufman, A. Rassweiler, J. A. Rusak, M. D. Smith, J. R. Steinbeck, R. B. Waide, and J. Yao. 2006. A comparison of the species–time relationship across ecosystems and taxonomic groups. Oikos 112:185–195.

White, E. P., K. M. Thibault, and X. Xiao. 2012. Characterizing species-abundance distributions across taxa and ecosystems using a simple maximum entropy model. Ecology 93:1772–1778.

Wootton, J. T. 2004. Field parameterization and experimental test of the neutral theory of biodiversity. Nature 433:309–312.

SUPPLEMENTAL MATERIAL

Appendix A

Additional methodology on data restriction (*Ecological Archives* E093-235-A1).

Appendix B

Figures for all the data and the functions used to characterize the macroecological pattern parameters (*Ecological Archives* E093-235-A2).

Appendix C

Details on the methods and results of equivalence testing (*Ecological Archives* E093-235-A3).

Appendix D

Tables showing the transformations applied to each variable and the *P* values for the conventional and equivalence statistical tests comparing parameters between the control plots and each of the experimental treatment plots (*Ecological Archives* E093-235-A4).

Supplement

Code for conducting the analyses and generating the figures in this paper (*Ecological Archives* E093-235-S1).