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Local and Regional Drivers of Biodiversity: From Life-History Traits to System-Level Properties

Sarah R. Supp

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LOCAL AND REGIONAL DRIVERS OF BIODIVERSITY: FROM LIFE-HISTORY TRAITS TO SYSTEM-LEVEL PROPERTIES

by

Sarah R. Supp

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Ecology

Approved:

S. K. Morgan Ernest Major Professor	Peter B. Adler Committee Member
David N. Koons Committee Member	Michael E. Pfrender Committee Member
Ethan P. White Committee Member	Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah
2013

ABSTRACT

Local and Regional Drivers of Biodiversity: From Life-History Traits to System-Level Properties

by

Sarah R. Supp, Doctor of Philosophy

Utah State University, 2013

Major Professor: S. K. Morgan Ernest
Department: Biology and the Ecology Center

Biodiversity research aims to understand and predict the occurrence, abundance, and distribution of species and the diversity of species traits, body sizes, and functional roles in a community. Ecologists lack a comprehensive understanding of the interplay between processes driving biodiversity at differing spatiotemporal scales, hindering the ability to predict response to change. A crucial challenge facing ecologists is to incorporate knowledge of the regional dynamics and temporal stability of communities in biodiversity research. This dissertation investigates the role that species traits and system-level properties play in determining biodiversity at local sites and evaluates biodiversity response to change.

Local and regional processes may regulate biodiversity via their different influences on core (common, temporally persistent) and transient (rare, temporally intermittent) species. In Chapter 2, we tested the hypothesis that core vs. transient species have fundamentally different life-history traits that are associated with survival strategies targeted at local vs. regional habitat use. Using long-term mark-recapture data from a rodent community, we found that core species generally had high ecological specialization, high survival, low dispersal rates, and low reproductive effort compared to transient species. Life-history trade-offs may correspond to differing roles in maintaining species richness and responses to environmental change.

Macroecology describes patterns of biodiversity in communities without respect to species identities or traits. Diversity patterns (i.e., species-abundance distribution-SAD, species-area relationship-SAR, species-time relationship-STR) are well-studied, but drivers of these patterns are poorly understood. In Chapter 3, we tested the hypothesis that local-scale interactions influence the form of SADs, SARs, and STRs using long-term data from annual plant communities. Our results suggest that patterns are directly influenced by system-level properties (species richness, total abundance) and respond indirectly to local-scale processes. In Chapter 4, we analyzed data from a global-span database and found the SAD and species richness generally resilient to environmental change.

This work suggests that local processes are important determinants of species composition and abundance and may set an upper limit to species richness, but that regional processes are responsible for maintaining richness and community structure. This insight may partially explain why many biodiversity metrics are often invariant under environmental change scenarios.

(178 pages)

PUBLIC ABSTRACT

Local and Regional Drivers of Biodiversity: From Life-History Traits to System-Level Properties

by

Sarah R. Supp

Biodiversity research includes the study of where species occur, the commonness and rarity of species, the number of species, and the diversity of life-history traits that occur in a single location, or community. Research is increasingly recognizing that a combination of local and regional scale processes influence community dynamics over ecological and evolutionary time-scales. However, ecologists currently lack a comprehensive understanding of the mechanisms driving biodiversity in different systems and at different spatial scales. This presents a critical problem because without understanding the important mechanisms that determine and maintain biodiversity, it is difficult to accurately predict community response to environmental change. This dissertation investigates the role that species traits and system-level properties have in determining biodiversity at local sites and evaluates biodiversity response to change.

Our results suggest that species traits are related to local vs. regional survival strategies and that partitioning communities into the two groups utilizing each strategy (core and transient, respectively) may help ecologists better understand and predict the impacts of environmental change on species composition and species richness. Our work also suggests that system-level properties (species richness and total abundance) are the main determinants of macroecological diversity patterns and that patterns are generally insensitive to environmental change. These findings suggest that species richness and macroecological diversity patterns should not be used as indicators for fundamental shifts within a system and imply that regional processes may be largely responsible for maintaining system-level properties.

Bailey’s pocket mouse (*Chaetodipus baileyi*) in the grass. Photo taken at a cattle tank just off-site from the Portal project, October 2012. Photo by S. R. Supp.

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Sarah R. Supp

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CHAPTER 1

INTRODUCTION

The study of biodiversity is a broad field usually focused at the community-ecosystem interface. Biodiversity research includes understanding and predicting the number of species, the abundance of species, community structure (*i.e.*, evenness, commonness and rarity, the scaling of species richness across space and time), and the diversity of traits, body sizes, and functional roles species exhibit (Magurran 2004, Magurran and McGill 2011). Despite a long history of research studying the drivers of biodiversity, new studies often seem to yield more questions than answers. Ecologists have suggested a multitude of mechanisms that predict biodiversity and community structure including intra- and inter-specific competition (Chesson 2000), resource partitioning (Tilman *et al.* 1997), dispersal (Hubbell 2001), and information entropy (Harte 2011). One important way that suggested mechanisms differ is their focus on regional vs. local processes as the principal driving force for biodiversity. Traditionally, ecology has studied only one process or one spatial scale at a time, but current research aims to understand the interaction of local and regional processes as drivers of biodiversity at and to determine which processes are *necessary* for accurate forecasting.

Although a large body of work demonstrates the importance of species interactions on the distribution and abundance of particular species (Colwell and Fuentes 1975, Chase and Leibold 2003, Clark 2009), recent work suggests that understanding the detailed biotic and abiotic interactions at a particular site is not necessary to predict patterns of diversity (e.g., species-abundance distribution, species-area relationship) at a site (McGill 2010, Harte 2011, White *et al.* 2012). In fact, these theories suggest that all that is needed to predict diversity patterns and community structure, including spatial aggregation and body size distributions, is knowledge of the system-level properties species richness (the number of species) and abundance (the total number of individuals, summed over the species). If this is true, then a central unanswered goal for ecologists moving forward is to determine if there is a general theory for what processes generate variation in richness and abundance (McGill 2010).

While some aspects of biodiversity may not directly depend on understanding detailed biotic interactions (e.g., species-abundance distribution, species-area relationship), other aspects of biodiversity may be strongly tied to the specific biotic interactions occurring at a site (e.g., species composition, species richness, total abundance). For example, the species-abundance distribution is a well-studied macroecological diversity pattern that universally demonstrates communities to have a small number of very common species and a large number of very rare species (Magurran 2004, McGill *et al.* 2007, Ulrich *et al.* 2010). The pattern can be easily predicted across taxonomic groups, continents, and ecosystems using neutral models that do not require knowledge of the identity of species (McGill *et al*. 2007). However, the number of species and the number of individuals at a site may not be as easily predicted without understanding variation in regional species pool richness (Magurran *et al*. 2011), regional environmental heterogeneity (Belmaker 2009, White and Hurlbert 2010, Coyle *et al.* in press), or resource availability in the system (Chase and Leibold 2003). In an era of rapid global-scale environmental change (*e.g.,* Thomas *et al.* 2004, Brummit and Lughada

2004), it is increasingly important to consider new approaches to study biodiversity, including synthesizing across scales and theoretical-empirical boundaries.

Ecology increasingly requires a multi-scale approach where both local-scale and regional processes are needed to understand the structure and diversity of communities. Understanding biodiversity and community structure at multiple scales requires an understanding of local and regional processes, but also mechanisms capable of linking across scales (Fisher *et al.* 2010). To address how local and regional processes influence community structure in continuous landscapes, I have combined field research with global-scale data. The aim of this dissertation is to evaluate the role that species traits and system-level properties play in determining community structure and biodiversity at local sites, and to evaluate biodiversity response to environmental change. In Chapters 2 and 3 I use rodent and plant community data from a long-term experimental manipulation, the Portal Project, located in the Chihuahuan desert in southeastern Arizona. At this site, experimental plots have been used since 1977 to manipulate and monitor the granivorous rodent community each month. Data on plant response to the experimental manipulations are collected biannually (Brown 1998, Ernest *et al.* 2009). In Chapter 4, I use my own global-span database of manipulated terrestrial animal communities from the literature to assess biodiversity and community structure response to ecological change.

In Chapter 2, I evaluate the differing role that local and regional processes play in regulating biodiversity in the Portal rodent community. Specifically, I partitioned the community into two groups: core species, which are temporally persistent and locally abundant, and occasional species, which are temporally intermittent and locally rare

(Magurran and Henderson 2003). A high degree of temporal species turnover in the occasional species of the rodent community suggests that dispersal is an important structuring mechanism at our site. In turn, this implies that transient species are governed more strongly by regional environmental heterogeneity and regional species pool dynamics than core species. Transient species that rely on dispersal as part of a regional survival strategy are expected to have evolved associations with life history traits that mitigate the mortality cost associated with dispersal (*e.g.*, high reproductive investment, resource generalism). Core species that rely on persisting at a specific site are expected to have evolved strong associations with traits that enable coexistence with competing species and persistence through periods of low resource availability (*e.g.*, high self-investment, resource specialization). We use individual-level trap data at the site to evaluate dispersal and survival probabilities and reproductive effort of core vs. transient rodent species.

In Chapters 3 and 4, we combine experimental data with a macroecological approach to evaluate the response of biodiversity patterns to ecological change. Macroecological patterns (i.e., species abundance distribution – SAD, species-area relationship – SAR, species-time relationship – STR) are typically generated at regional to continental scales (Brown 1995), and the ability of local-scale processes to influence patterns at small scales is poorly understood. The annual plant communities (summer and winter) experience differing levels of seed predation at our experimental site which influences plant species composition and are an ideal system in which to test the hypothesis that local-scale interactions (*e.g.*, seed predation) influence the form of SARs, SADs, and STRs. We examined the response of the SAD, SAR, and STR to sustained rodent manipulations and evaluated whether shifts in patterns were related to changes in the details of biotic interactions to changes in system-level properties (species richness and total abundance). In Chapter 4, we use a global-span database of local-scale terrestrial animal communities to assess biodiversity response (species composition, species richness, total abundance, evenness, SAD) to artificial and anthropogenic manipulations.

The goal of this dissertation is to disentangle the roles that local and regional scale processes play in regulating biodiversity and community structure, to determine if local vs. regional habitat use is related to life history trade-offs and temporal permanence, and to evaluate the unknown response of biodiversity metrics to environmental change. The conceptual framework emerging from this dissertation, linking local and regional scale processes with community structure, suggests novel research directions for the study of macroecology and global change biology.

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CHAPTER 2

LIFE-HISTORY TRADE-OFFS AMONG CORE AND TRANSIENT SPECIES REGULATE LOCAL DIVERSITY AND STRUCTURE IN A SMALL MAMMAL COMMUNITY[1]

Abstract

The connection between biodiversity and the commonness and rarity of species is a major research focus in ecology. A recent conceptual framework aims to understand biodiversity by partitioning communities into core species that are abundant and temporally persistent and transient species that are rare and temporally intermittent. Core and transient species have been shown to differ in spatiotemporal turnover, diversity patterns, and importantly, survival strategies targeted at local vs. regional habitat use. We suggest that if core and transient species have local vs. regional survival strategies, and consequently differ in population-level spatial structure and gene flow, they should also exhibit different life-history strategies. Specifically, core species should display relatively low dispersal rates, low reproductive effort, high ecological specialization and high survival rates compared to transient species. We present results from 10 years of capture-mark-recapture data in a diverse rodent community evaluating the linkages between temporal permanence, local abundance, and trade-offs between/among life-history traits. Core and transient species at our site generally supported our hypotheses, differing in

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[1] This chapter is co-authored by Sarah R. Supp, David N. Koons, and S. K. Morgan Ernest.

ecological specialization, survival and dispersal probabilities, and reproductive effort. We suggest that trait associations among core-transient species may be similar in other systems and will correspond to differing responses to environmental change in the two groups.

Introduction

Ecologists have long observed that assemblages are universally characterized by a small number of common species and a large number of rare species. Recent research has suggested that common and rare species at a site may also be common and rare across time (Magurran and Henderson 2003). The insight that species abundance may also be related to temporal persistence suggests that the structure and diversity of ecological communities may be better understood when the community is partitioned into two groups: core species, which are usually more abundant and display high temporal persistence, and transient species, which are usually less abundant and display low temporal persistence (Magurran and Henderson 2003). The core-transient framework is potentially important for understanding the processes that regulate biodiversity because it suggests that the spatial and temporal scale of processes governing species richness in the two groups differ (*e.g.,* Ulrich and Ollik 2004, Dolan *et al.* 2009, Coyle *et al. in press*).

One of the key insights from the core-transient framework is that core and transient species may significantly differ in the ecological and evolutionary drivers determining their occurrence, abundance and species richness (Magurran and Henderson 2003, Dolan *et al.* 2009). Core species that are strongly governed by local ecological processes may experience strong local co-evolutionary pressures with their biotic and abiotic environment (McCauley 2007). Limited gene flow among populations enhances the role of local natural selection and adaptation for core species (McPeek and Holt 1992, Kisdi 2002, Urban *et al.* 2008). Core species experiencing high levels of local adaptation may partially explain the observation that common species often play an important functional role in a community (*e.g.*, keystone species; Dolan *et al.* 2009, Gaston 2010). Transient species that are strongly governed by regional ecological processes and dispersal limitation likely have relatively high levels of gene flow among populations. High dispersal may impact the evolutionary dynamics of transient species if: 1) high gene flow homogenizes gene pools and inhibits local adaptation (Urban *et al.* 2008) or 2) intermediate gene flow increases the capacity for local adaptation in unstable habitats via novel gene subsidies from the regional gene pool (Urban and Skelly 2006, Loeuille and Leibold 2008). Both the high gene flow and intermediate gene flow scenarios suggest that on average transient species should be less adapted to local biotic and abiotic conditions than core species and are therefore at a competitive disadvantage, except for the ability to exploit novel conditions in unstable environments. Given the eco-evolutionary constraints imposed by local versus regional habitat use, core and transient species likely maintain different survival strategies targeted at local vs. regional habitat use, respectively

An important expectation that emerges from the core-transient framework that has never been assessed is that patterns of abundance and persistence among core and transient species may be linked to population dynamics and life history evolution. Local versus regional survival strategies require different life-history strategies to cope with the different evolutionary pressures. If core species depend on a local survival strategy that requires them to successfully compete in and adapt to their biotic and abiotic environment, then core species should be strongly associated with traits that enable them to compete for local resource constraints and cope with local environmental stressors. Local adaptation strategies should also result in a lower probability of long-distance dispersal since movement away from a local environment is more likely to result in dispersal into an unsuitable environment (McPeek and Holt 1992, Kisdi 2002). Conversely, if transient species depend on a regional survival strategy that requires the ability to track suitable environmental conditions and survive in heterogeneous landscapes, then transient species should be strongly associated with traits that enable them to survive traversing non-ideal habitat patches and to colonize new suitable habitat patches (McCauley 2007). This implies that dispersal may be an important trait distinguishing core and transient species. Dispersal may be related to an individual's ability to find suitable habitat or mates, but is also often associated with an increased mortality risk and increased time and energetic cost (Murray 1967, Waser 1985, Rousset and Gandon 2002). Variation in adult risk-taking among species leads to trade-offs in apparent survival and the proportion of resources allocated towards reproduction (*e.g.*, Clutton-Brock 1991, Stearns 1992). Therefore, species that disperse long distances may have decreased adult survival (few future breeding opportunities) and display a strategy of high reproductive investment (Charlesworth 1980). To offset the potentially high costs of dispersal, transient species may have evolved associations with other life-history traits such as resource generalism, high fecundity, and early age of primiparity. Core species that generally do not disperse, or only disperse short distances, likely have increased adult survival (many future breeding opportunities) and employ strategies geared towards self-investment, thereby decreasing reproductive investment (Ghalambor and Martin 2000). The trade-offs and relationships among traits could have important implications for predicting the cascading impacts of environmental change on species loss, community structure, biodiversity, and ecosystem function (Suding *et al.* 2003).

Using a 10 year mark-recapture study of desert rodents, we test the hypothesis that core and transient species have fundamentally different life history strategies associated with local vs. regional habitat use. From the core-transient framework, we predict that core species will be associated with relatively low dispersal rates, low fecundity, high resource specialization and high survival rates. We predict that transient species will be associated with relatively high dispersal rates, high fecundity, low resource specialization, and low survival rates (Fig. 2-1). We also predict that trait differences between core and transient species may explain the observed stability of species richness through time, despite high compositional turnover at our site.

Materials and Methods

Study site and data

We evaluated the relationship between traits and core-transient status at our site using 10 years (2000-2009) of capture-mark-recapture data from a long-term experimental site in the Chihuahuan desert in southeastern Arizona. The small mammal community at our study site includes a diverse set of species (n = 21), spanning several feeding guilds (4), and a wide range of body sizes (approximately 4 – 270 g) that can be partitioned into core and transient groups. At our site, species in the two groups also have divergent evolutionary histories, leading to differing levels of adaptation to the arid environment, which results in them being differently suited to local and regional survival strategies. Since the small mammal community includes species representing a suite of different feeding guilds and survival strategies (n = 4, Table 2-1), our site is ideal for investigating the traits associated with core and transient species and their potential role in determining biodiversity and community structure at the site.

Data were collected at the Portal Project field site, a long-term experimental manipulation located in the Chihuahuan Desert near Portal, Arizona (Ernest *et al.* 2009). The study site consists of 24, 0.25 ha fenced plots (50 m X 50 m). Each month, year-round, plots are trapped on a grid consisting of 49 evenly spaced permanent stakes to survey the rodent community and to maintain experimental treatments. Four gates cut into each side of the fenced plots allow free passage of rodents in and out of plots. Large-bodied and behaviorally dominant kangaroo rats (*Dipodomys spp.*) have enlarged auditory bullae that make it possible to selectively exclude them from plots that have a smaller gate size (n=8). Total rodent removal plots have no gates (n=6), while control plots (n=10) have relatively large gates that allow all species access (Brown 1998). Upon capture, each individual is marked with a permanent, subcutaneous passive integrated transponder (PIT) tag that allows it to be uniquely identified upon capture. For each captured individual, we recorded species, sex, reproductive status, hind foot length, weight, and individual PIT tag. When applicable, we right-censored data from individuals after the point that they were captured on total rodent removal plots, or from kangaroo rat individuals captured on kangaroo rat removal plots because these individuals were subsequently removed from the study site.

We used data from species that were present and sufficiently abundant during 2000-2009 to conduct statistical analyses (n=13). This allowed us to compare movement and survival of rodent species in 4 main feeding guilds: granivores in the family *Heteromyidae* (n=5), granivores in the family *Cricetidae* (n=3), folivores (n=3) and carnivores (n=2). We analyzed data for individuals where there was no discrepancy in recorded species or sex across captures. During 2000-2009, individuals were marked with PIT tags, but previously, ear and toe tags were used extensively. Recaptured ear and toe tagged individuals were excluded from analysis due to uncertainty in potential duplicate tags that make it difficult to accurately track individuals.

Core and transient species designation

Since core and transient species designation is related to abundance as well as temporal persistence, status was assigned using the proportion of years that each species was present and the average rank of each species on the control plots in our sample (1 - most abundant, 13 - least abundant). In order to have a large enough species-level sample size for our analyses we did not include species in the analysis that were present in fewer than half of the years. Species omitted in this study that were present in 2000-2009 include: *Baiomys taylori, Peromyscus leucopus, Chaetodipus intermedius, Dipodomys spectabilis, Reithrodontomys montanus,* and *R. fulvescens*.

Life-history trait analyses

To assess reproductive effort for each species, we tracked the reproductive history for captured individual females within each calendar year. We considered females with enlarged and/or red nipples or who were pregnant (researcher could feel embryos) to be actively reproducing. If a female was marked in reproductive condition during consecutive trapping periods, we considered it to be one reproductive event. Reproductive condition recorded for an individual across non-consecutive trapping periods was considered as multiple reproductive events. We used data from females because males display reproductive signals for a much larger portion of the year, and male reproductive status is not necessarily indicative of recent copulation or reproductive success.

Using individual-level recapture data, we assessed movement trends for each species. Locations of the permanently marked trap stakes were recorded in 2010 using ProMark3 GPS Units with an error of < 2cm. We recorded the distance traveled in meters between trapping stakes among chronologically ordered capture histories for each individual. For each species, we binned the individual movement data by 6 meter increments that roughly represent the distance between stakes (with bin 1 representing distance 0-3 meters, or recapture at the same stake), and plotted the data in histograms. For each species, we calculated the mean + standard deviation of the log (Y+1) transformed data to determine a benchmark at which each movement distribution transitions into long-distance movements. We chose this transformation to meet the assumptions of normality and because there are many 0 m movements (Sokal and Rohlf

2012). For a given species, these histograms provide insight into the frequency at which individuals move short vs. long distances.

To more thoroughly evaluate life-history relationships between dispersal and survival, conditional on recapture probability, we used a multistate capture-mark-recapture (CMR) modeling approach in Program Mark version 7.0 (White and Burnham 1999, White and Cooch 2012) through the R programming environment 2.15.2 (R Core Development Team 2012) and package RMark (Laake *et al.* 2012, Laake and Rexstad 2008). To address our questions of if core and transient species differ in traits including survival (S), recapture (p), and dispersal probabilities (Psi), we used a two-state model that partitioned species movements into two states: state 1 (near) indicates that an individual did not move or moved a relatively short distance, and state 2 (far) indicates a relatively long-distance movement away from the previous trap location. Using the combined individual movement distances of the core granivorous species, we set the mean + one standard deviation of log(Y+1) transformed data as our benchmark defining a short movement (state 1) vs. a long distance movement (state 2) for all species. This two-state CMR design allowed us to estimate the probability of remaining near the previous capture and release location (1→1 or 2→1) versus the probability of dispersing to a distant location (1→2 or 2→2), conditional on apparent survival and recapture probabilities. We defined apparent survival probability as the probability that an individual alive in trapping period *i* survived and did not emigrate from the study area by trapping period *i*+1. We defined recapture probability at *i*+1 as the probability that a live individual on the study area was recaptured in a trap. All probabilities were measured over a time scale of approximately one month, the time between trapping events. To address inconsistencies in the data, we controlled for omitted trap periods (when trapping did not occur or the site was only partially trapped) by fixing recapture probability to zero for those instances. It should be noted that we cannot differentiate between permanent emigration and death, which may bias our survival estimates. Therefore, low apparent survival probabilities may be indicative of low actual survival, high permanent emigration off the study area, or both. We used a species-level model in RMark to generate survival, recapture, and transition probabilities separately for species, but we also evaluated support for guild, core-transient, and null models using AICc weights (White and Cooch 2012). For further details on our RMark analysis, please refer to our code, which is maintained online in a public GitHub repository along with the data (https://github.com/weecology/portal-rodent-dispersal) and is available in the online supplement.

Results

Core-transient species designation

During the 10-year study period, we captured 7,238 individuals from the 13 species included in the analysis (Table 2-1). Based on temporal occupancy and abundance, we categorized species into three groups: Core (*Dipodomys ordii, D. merriami, Chaetodipus baileyi, C. penicillatus,* and *Onychomys torridus*), transient (*Perognathus flavus, Permyscus maniculatus, Sigmodon hispidus, S. fulviventer, and O. leucogaster*), and intermediate species (*P. eremicus, Neotoma albigula, and*

Reithrodontomys megalotis). Core species were present in all years of the study and were consistently abundant (mean rank < 5) (Fig. 2-2 upper left). Transient species were present in a subset of the years and were consistently rare, indicating a potentially important role for dispersal from the regional species pool (Fig. 2-2 lower right) whereas intermediate species were present in all years, but were consistently rare (Fig. 2-2, upper right), and difficult to otherwise classify.

Reproduction

All species in *Heteromyidae* demonstrated a similar pattern where the majority of captured females were never recorded in reproductive condition (Fig. 2-3a). However, despite their much lower abundance, nearly 50% of *Peromyscus eremicus* and *P. maniculatus* were recorded in reproductive condition (Fig. 2-3b) at least once per year. Among folivores, *N. albigula* females were often found in reproductive condition, as opposed to *Sigmodon* females that were almost never recorded as reproductive (Fig 2-3c). The lack of observed reproduction may suggest that *Sigmodon* rarely reproduce at the site or could be a sampling error due to the low number of females captured. *Onychomys* females were rarely recorded as reproductive, but data suggest that *O. torridus* may reproduce multiple times per year (Fig 2-3d).

Dispersal and survival

Among the core species, movement distances between recaptures are strongly unimodal and left-skewed, excluding *O. torridus*, which has a secondary mode suggesting long-distance movements are not uncommon. Transient and intermediate species generally have a much longer tail on their movement distributions and most include a secondary mode, suggesting more long-distance movements, larger home ranges, and possible emigration off-site (Fig. 2-4, Table 2-1). *N. albigula, S. hispidus* and *Perognathus flavus* are transient species that show very few long-distance movements, which may be attributed to increased mortality, low detectability, or both. For *N. albigula*, the short movement distances likely reflects an individual's strong association to its midden, which is energy-intensive to build and maintain (Hoffmeister 1986). Among granivores, core species had a much lower probability of moving a relatively far distance away from the previous trap location (mean = 30.70 m) than intermediate (mean = 83.67 m) or transient species (mean = 61.21 m; Table 2-1). Among carnivores, the core species *O. torridus* generally moved much shorter distances than the transient species, *O. leucogaster* (movement benchmark, Table 2-1; Psi, Table 2-2).

We used data from the species model in Mark to compare survival, recapture, and dispersal probabilities among core and transient species. Differences were most apparent among core granivores versus transient and intermediate granivores (Table 2-3). On average, core granivores had a much lower probability of moving a long distance (means 0.11 vs. 0.40) and a much higher recapture probability (means 0.61 vs. 0.28) than transient and intermediate granivores. Differences among core and non-core granivore survival were less strong (means 0.79 vs. 0.72), but suggested slightly higher survival among core species. Among carnivorous species, the transient species showed a much higher probability of moving a long distance (Table 2-3), consistent with results from the histograms, but survival probabilities were opposite our expectations, with the transient species having a higher survival probability (core = 0.64, transient = 0.84). Recapture probability was indistinguishable among the two carnivorous species. Survival, recapture and dispersal probabilities among transient and intermediate folivore species were variable (Table 2-3). Model comparison using AICc weights strongly supported the species-level model (weight=1 for species model vs. 0 for all other models). Since the guild model groups species differing in temporal permanence and the core-transient model groups species differing in their feeding guild, relatively low support for these models is unsurprising given patterns across species presented above.

Discussion

We expected that core and transient species would exhibit different life-history strategies associated with utilization of local or regional resources and habitats. Based on temporal persistence and average ranked abundance over time, we felt confident in our ability to partition the rodent community into core, transient, and intermediate species. Our analysis of the reproductive, survival and movement data indicated that core species tend to have higher survival probability and move shorter distances than transient species. Because it is difficult to study individual behavior and reproduction in small mammals, we do not have fine-scale data on reproductive effort and success. Therefore, we had to rely on coarse signals of female reproduction that were difficult to interpret. For example, low levels of observed reproductive investment for a species could indicate low reproductive rates across individuals, changes in behavior that decrease capture probability while pregnant or nursing, or that reproduction is occurring off-site. Despite these limitations, patterns in female reproductive investment across species suggest that there may be differences among core-transient granivorous species that are consistent with our hypothesis (Table 2-1, Fig. 2-3), with transient and intermediate species reproducing more often; perhaps to offset the risk of moving more regularly. In addition, data from the literature support the idea that core granivore species at our site generally have low reproductive effort, reproducing fewer times per year and having smaller litter sizes than intermediate and transient granivore species (Table 2-3; Hoffmeister 1986).

Life history traits may help explain the local commonness and rarity of certain species, which in turn, leads to important insights into the maintenance of diversity and community structure at a given site. Core taxa are abundant, present in the majority of years, and have traits that enable them to successfully exploit most of the available resources in a local system (Magurran and Henderson 2012). Strong local-scale evolutionary pressures may explain why core species often have traits that enable them to play a unique, important functional role (Grime 1998, Gaston 2010, Gibson *et al*. 2011). For example, core species at our site were arid-adapted specialists that showed a low signature of movement relative to other species in their feeding guild. Kangaroo rats (*Dipodomys* spp.) are behaviorally dominant (Reichmann and Price 1993) and have cascading impacts on rodent and plant communities (Brown and Heske 1990; Heske *et al.* 1994; Valone and Schutzenhofer 2007), pocket mice (*Chaetodipus* spp.) become dominant in the absence of kangaroo rats (Ernest and Brown 2001), and the southern grasshopper mouse (*O. torridus*) may be uniquely able to survive periods of extreme drought (McCarty 1975) compared to the northern grasshopper mouse (*O. leucogaster*).

Core species may thus be responsible for much of the ecosystem functions at a site (*e.g.,* nutrient cycling, biomass production) and may set an upper limit to local diversity (Belmaker *et al.* 2008, Belmaker 2009), but transient species are likely a key component in the maintenance of species richness over time (Magurran *et al*. 2011). Transient species are generally less abundant, less specialized, and may arrive at a site stochastically or in response to temporary resource fluctuations, requiring strong dispersal abilities to do so (McCauley 2007, Magurran and Henderson 2012). Life history data at our site support the idea that transient and intermediate species are generally inferior competitors that temporarily colonize in response to resource pulses and density dependence at other locations, both of which could create a source-sink dynamic over time (Heske *et al.* 1994, Thibault *et al.* 2004). For example, *Sigmodon* and *Reithrodontomys* are prairie-adapted species which usually arrive during years where climatic conditions lead to higher than normal grass cover (Webster and Jones 1982, Thibault *et al.* 2004). Additionally, during the period of our study these species had relatively low abundance and are rarely recorded in reproductive condition – strong evidence that our site represents a habitat sink for these populations. Interestingly, the species that we identified as 'intermediate' have features of both groups (e.g., habitat specialization [Hoffmeister 1986, Whitford and Steinberger 2010], arid-adaptation, high fecundity [Hoffmeister 1986], and resource generalization [Dial 1988]). Life history trade-offs may explain why species richness at our site has remained remarkably consistent over time (Brown *et al.* 2001). As long as the regional pool contains species with a wide range of environmental tolerances, transient species will re-colonize local sites during periods of suitable conditions or when resources become available after local extinction events. At our site, colonization-extinction dynamics are compensatory within the granivorous guild, suggesting that species richness is maintained by supplements of transient species from the regional metacommunity (Goheen *et al.* 2005),

If transient species play a large role in maintaining species richness at local sites, it could help to explain why few sites experience large temporal shifts in species richness, including sites undergoing manipulation (*e.g.,* Chapin *et al.* 2000, Hillebrand *et al.* 2008). While the abundance of transient species may fluctuate independently of one another (Magurran and Henderson 2010, Magurran *et al*. 2011), as long as there are no major changes in the size of the regional species pool or in the isolation of the local community, then changes in individual species demographics cancel each other out at the local scale (Cottingham *et al.* 2001). Transient species are limited by the supply of colonists from the surrounding region, and transient species richness may thus remain relatively constant over time, but exhibit a high magnitude of compositional turnover (Goheen *et al.* 2005, Belmaker 2009, Coyle *et al. in press*). By crediting transient species with maintaining species richness, the core-transient framework also suggests a way to predict what kinds of ecological change lead to shifts in system-level properties.

Major changes in species richness may be relatively rare in systems (*e.g.*, Chapin *et al.* 2000, Hillebrand *et al.* 2008) but could have cascading effects on other system level properties (Isbell *et al.* 2011) and inability to predict the magnitude of change in species richness in response to disturbance represents a critical problem for conservation biology. Core and transient species should respond differently to environmental change because they are expected to differ in their life-history traits, amount of gene flow among populations, and their ability to immigrate to suitable habitat. Therefore, changes that alter surrounding regional habitat, but not local conditions, may eliminate transient species from local sites by increasing dispersal limitation among habitat patches, without having a large immediate impact on core species. In turn, the site may experience a decrease in overall species richness. Environmental changes that alter local conditions long-term (*e.g.* temperature, resource availability) may have catastrophic effects on core species that lack adequate gene flow for adaptation or the ability to track shifts in the location of suitable habitats, but may have relatively small effects on transient species that are less strongly associated with specific habitat characteristics, have high levels of gene flow enabling local adaptation, or can emigrate more readily. Since core species often have unique functional roles in a community (Gaston 2010) and utilize most of the resources in a system (Magurran and Henderson 2012), changes in the richness of this group may have cascading impacts on other species, trophic groups, and ecosystem function. The recognition that environmental change will impact core and transient species in different ways may enable ecologists to better predict how changes will impact long-term maintenance of species richness or continued ecosystem function at local sites.

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Species	**Guild**	**Specialist**	**Status**	**N**	**Mean body mass (g)**	**Estimated yearly reproductive effort**	**Species-level movement benchmark (m)**
Dipodomys merriami	Granivore	Yes	Core	728	43.60	0.50	32.64
D. ordii		Yes	Core	546	48.47	0.49	28.36
Chaetodipus baileyi		Yes	Core	1848	31.95	0.41	25.57
C. penicillatus		Yes	Core	2159	17.01	0.40	36.22
Perognathus flavus		Yes	Occ	192	7.41	0.34	29.12
Peromyscus eremicus	Granivore	Yes	Int	300	21.42	0.53	93.05
P. maniculatus		No	Occ	118	23.23	0.48	93.30
Reithrodontomys megalotis		No	Int	345	10.60	0.23	74.29
Sigmodon hispidus	Folivore	No	Occ	220	94.31	0.09	37.02
S. fulviventer		No	Occ	122	68.54	0.06	65.84
Neotoma albigula		No	Int	74	186.29	0.68	41.08
Onychomys torridus	Carnivore	No	Core	540	23.45	0.54	75.55
O. leucogaster		No	Int	46	32.66	0.44	134.14

Table 2-1 Species-level trait details summarizing feeding guild, core-transient status, ecological specialization, total number of individuals tracked through the study (N), mean body mass across all recorded weights, mean yearly reproductive effort, and species-level benchmarks defining where each movement distribution transitions into long-distance movements. Yearly reproductive effort was estimated by taking weighted average of the number of individual females marked as reproductive 0-4 times per year.

Species	**Status**	**Litter size**	**Mean litter size**	**Number of litters per year**	**Typical breeding months**
*Dipodomys ordii**	Core	2-3	2.37	1-2	February-July
*D. merriami**		2-3	2	1-2	March-October
*Chaetodipus baileyi**		1-6	3.6	--	April-August
*C. penicillatus**		2-8	4.72	1	April-August
Onychomys torridus		2-5	3.45	--	March-October
*Peromyscus eremicus**	Intermed.	1-4	2.53	--	Year-round
Neotoma albigula		1-4	1.95	≥ 1	Year-round
*Reithrodontomys megalotis**		--	3.6	1-10	Year-round
*Perognathus flavus**	Transient	1-6	4	1	April-August
Sigmodon hispidus		2-10	5.6	1-9	Year-round
S. fulviventer		--	--	--	Year-round
P. maniculatus		1-6	4.29	--	Year-round
O. leucogaster		3-5	4	--	March-September

Table 2-2. Summary of reproductive life history traits from Hoffmeister (1986). Dashes (--) indicate no data. Species marked with an asterisk (*) are directly competing for resources in the granivore feeding guild.

Species	**Status**	**S**	**LCL**	**UCL**	**p**	**LCL**	**UCL**	**Psi**	**LCL**	**UCL**
*Dipodomys ordii**	Core	**0.76**	0.74	0.78	**0.73**	0.70	0.88	**0.09**	0.07	0.10
*D. merriami**		**0.78**	0.76	0.79	**0.69**	0.67	0.72	**0.13**	0.11	0.15
*Chaetodipus baileyi**		**0.80**	0.79	0.81	**0.74**	0.73	0.75	**0.08**	0.07	0.08
*C. penicillatus**		**0.81**	0.80	0.82	**0.27**	0.26	0.28	**0.14**	0.13	0.16
Onychomys torridus		**0.64**	0.57	0.70	**0.37**	0.29	0.47	**0.31**	0.22	0.42
*Peromyscus eremicus**	Intermed.	**0.67**	0.62	0.71	**0.28**	0.23	0.34	**0.48**	0.39	0.56
Neotoma albigula		**0.46**	0.36	0.56	**0.25**	0.15	0.38	**0.17**	0.09	0.32
*Reithrodontomys megalotis**		**0.81**	0.75	0.85	**0.25**	0.19	0.33	**0.23**	0.14	0.35
*Perognathus flavus**	Transient	**0.76**	0.74	0.78	**0.44**	0.41	0.48	**0.49**	0.45	0.53
Sigmodon hispidus		**0.74**	0.69	0.78	**0.20**	0.15	0.25	**0.14**	0.08	0.22
S. fulviventer		**0.54**	0.45	0.62	**0.45**	0.32	0.58	**0.52**	0.39	0.65
P. maniculatus		**0.62**	0.55	0.69	**0.13**	0.09	0.18	**0.41**	0.30	0.53
O. leucogaster		**0.84**	0.78	0.88	**0.36**	0.28	0.45	**0.63**	0.51	0.73

Table 2-3. Table summarizing results from Mark model evaluating species-level survival (S), recapture (p), and transition probability (Psi). Probabilities are measured over time scales representing approximately one month. Species marked with an asterisk (*) are directly competing for resources in the granivore feeding guild.

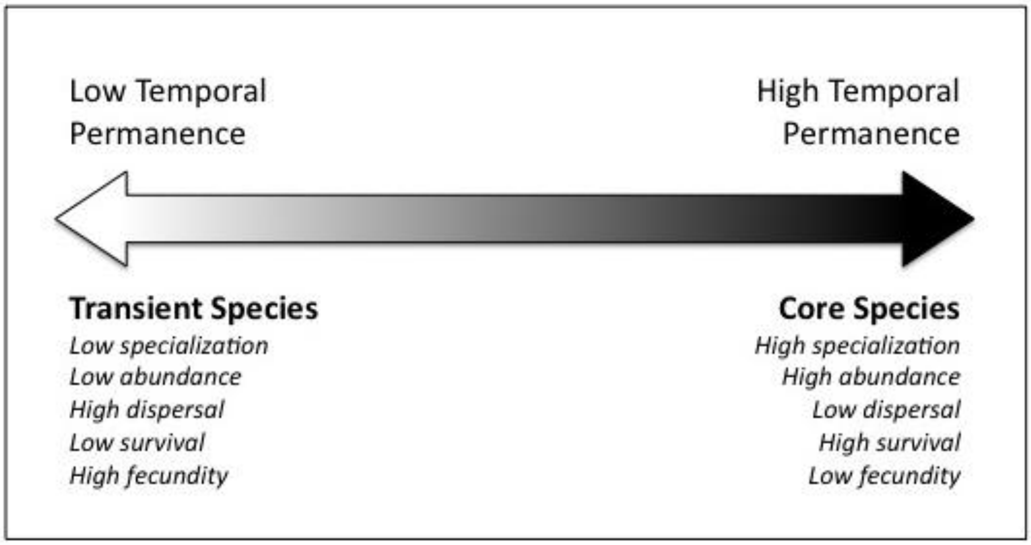

Figure 2-1. Hypothesized relationships between core-transient status and life history trade-offs.

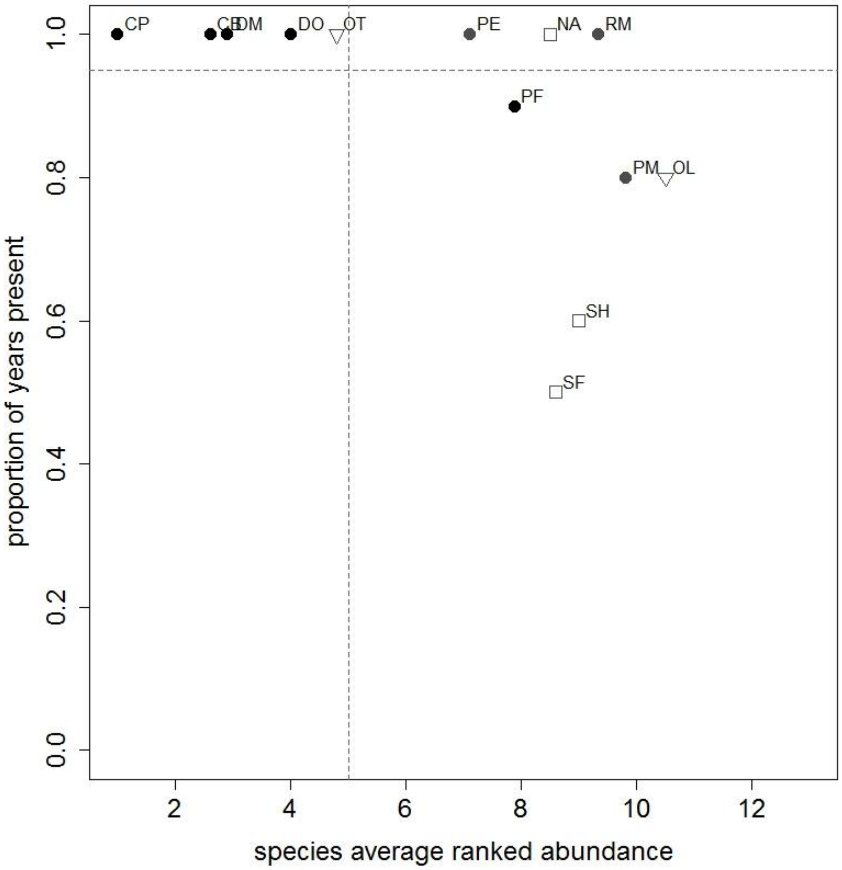

Figure 2-2. Species average rank in abundance on control plots (which represent the unmanipulated whole community) plotted against the proportion of years in 2000-2009 which the species was present. Dashed lines show that species can be broken into three main groups: core (present in all years and consistently abundant), transient (present in some years and consistently rare), and intermediate (present in all years, but consistently rare). Filled dots are granivores (*Heteromyidae* = black, *Cricetidae* = gray) and open points are folivores (square) and carnivores (triangle).

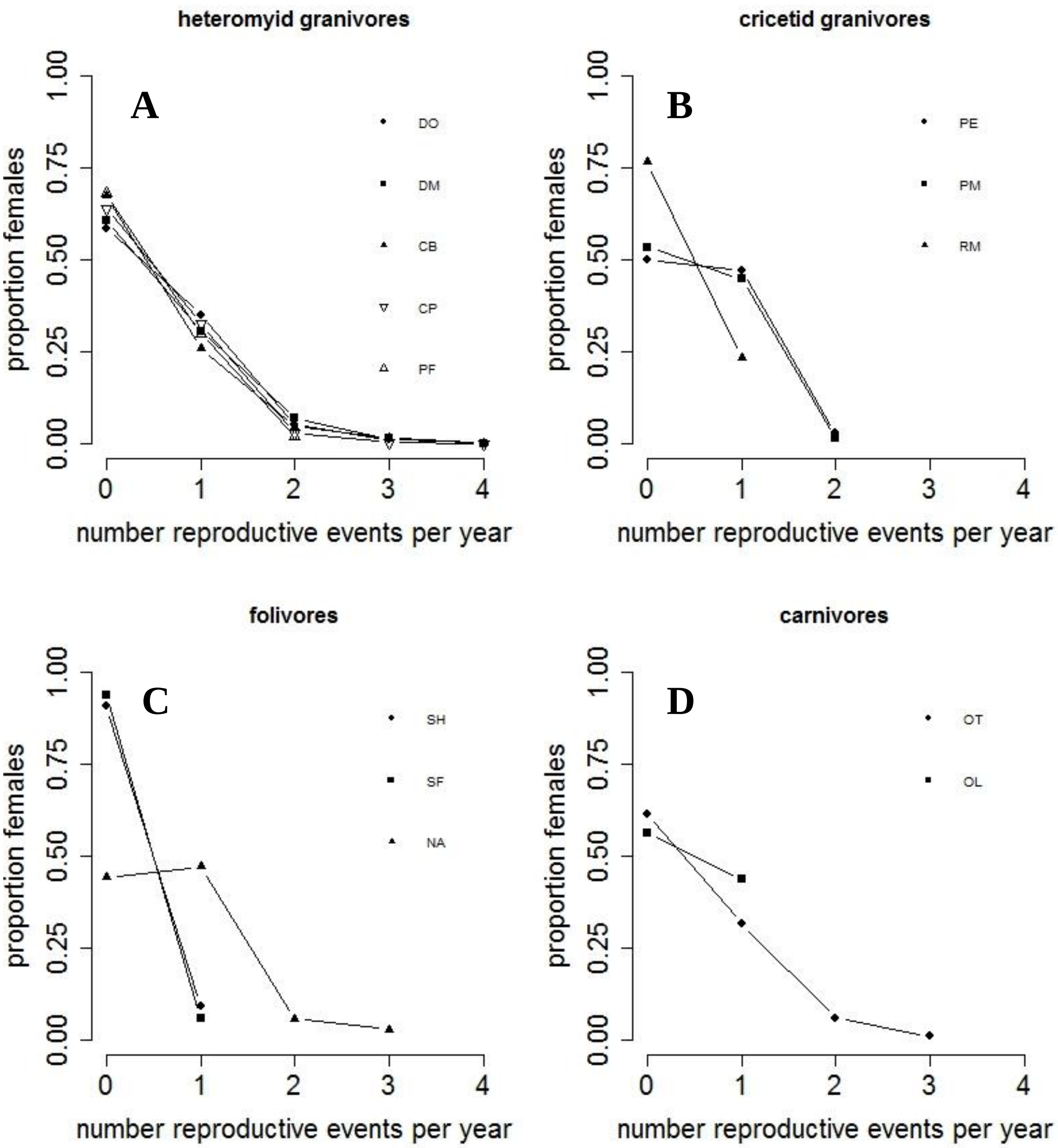

Figure 2-3. Yearly reproductive effort for individuals of each species. The y-axis represents the proportion females that we tracked that were recorded in reproductive condition 0-4 times per calendar year.

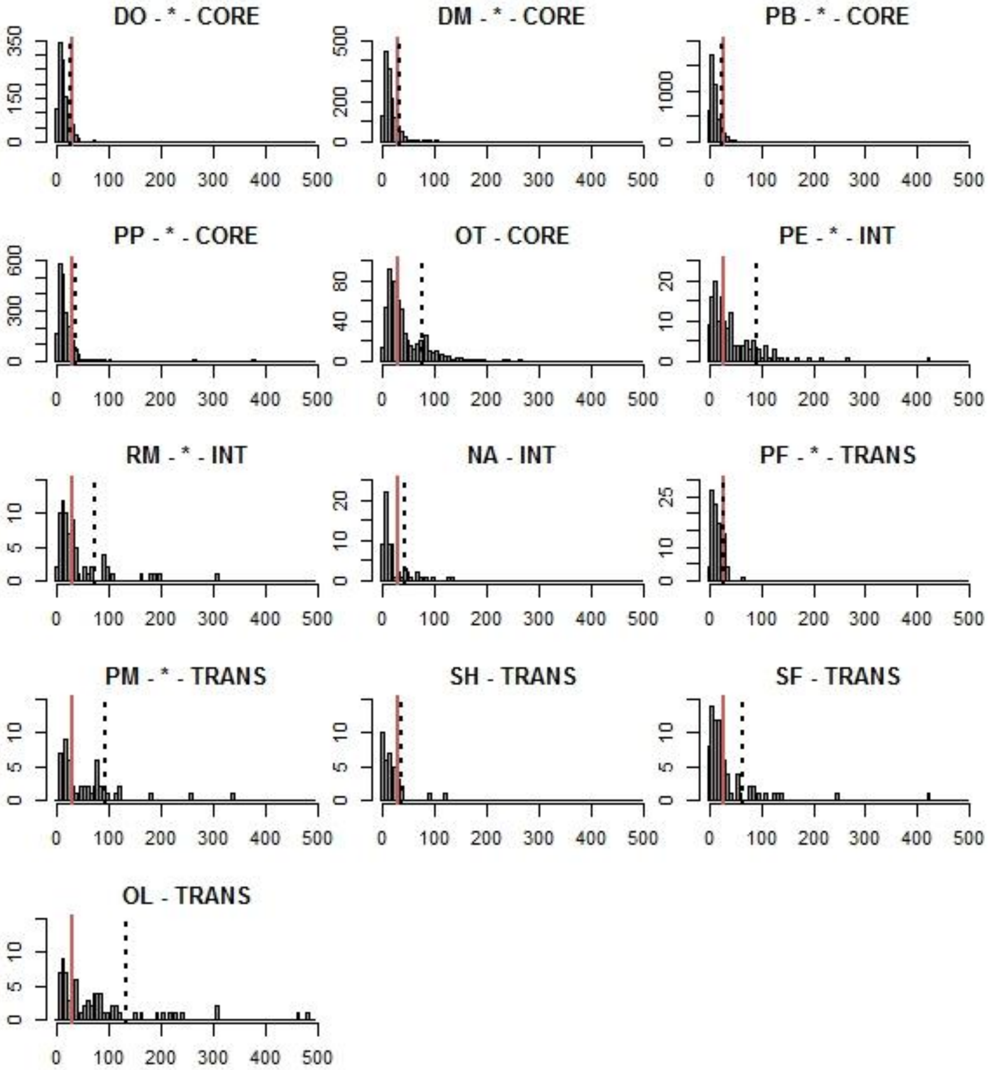

Figure 2-4. Histograms for all estimated individual movements (meters) of each species. The red vertical line is the benchmark for transition between near and far movements (29.52 m) based on data from core granivorous species (*D. ordii, D. merriami, C. baileyi,* and *C. penicillatus*). Note that the x-axis (distance in meters) is on the same scale for all species but the y-axis (frequency of movements) varies depending on total number of recaptures for a species.

CHAPTER 3

AN EXPERIMENTAL TEST OF THE RESPONSE OF MACROECOLOGICAL PATTERNS TO ALTERED SPECIES INTERACTIONS1[2,3,4]

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

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[2] This chapter is co-authored by Sarah R. Supp, Xiao Xiao, S. K. Morgan Ernest, and Ethan P. White.

[3] Permission to include this manuscript as part of the dissertation has kindly been given by all the co-authors.

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(SADs, SARs, and STRs). Because altering species interactions only impacted macroecological patterns when the state variables of abundance and richness also change, we suggest that, in this system, local scale processes primarily act indirectly through these properties to determine macroecological patterns.

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.* 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. 3-1). 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 (Figure 3-1, 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. 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; Oksanen *et al.* 2010) and permutational significance tests were used to determine significance of the pCCA axes. We square root transformed the abundance data and controlled for the effect of year. All statistical analyses were conducted in R 2.13.1 (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 was < 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” (Oksanen *et al*. 2010). 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" (Grøtan and Engen 2008). Since μ took both positive and negative values, we used its exponentiated form, exp (μ), 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 (Table S1). 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 5 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, etc. 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. 3-1, middle). 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. 3-1, right). 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, SADs and SARs we used linear mixed effect models (lmer) in R package “lme4” (Bates *et al.* 2011), 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 function “pvals.fnc” (languageR; Baayen 2010). Because STRs lack the temporal (i.e., variable year) component, they were analyzed with traditional ANOVA. All response variables were transformed to meet assumptions of normality and homoscedasticity (Table D-1). 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 inter-related 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.

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; Table D-2) and a decrease in species richness (lmer, p = 0.001; Table D-2). 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 D-3).

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 3-2, 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 3-2; Appendix D).

These differences corresponded with the observed changes in S and N described above. 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(μ)) 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. 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 pre-specified 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 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 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 *et al.* 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.

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Supplemental Material

Appendix A. Additional methodology on data restriction.

Appendix B. Figures for all the data and the functions used to characterize the macroecological pattern parameters.

Appendix C. Details on the methods and results of equivalence testing.

Appendix D. Data and Code to replicate the analyses.

Appendix E. Details on the computational analyses needed to replicate the results.

Plate 3-1. A view along the plot-19 fence line, which selectively removes kangaroo rats (*Dipodomys* spp.). Annual plant species composition differs inside the plot vs. outside the plot, a consequence of altered seed predation. Plants to the right of the fence are inside, and plants to the left of the fence are outside the plot. Photo credit: S. R. Supp.

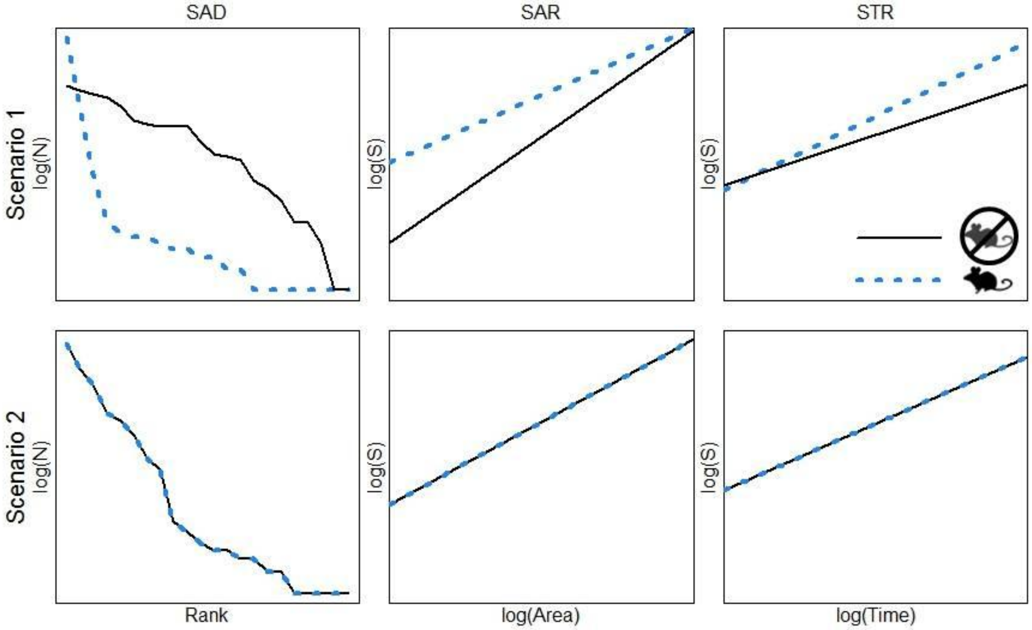

Figure 3-1. Possible responses of three macroecological patterns to manipulated seed predation assuming that the manipulation has no effect on species richness (S) and total abundance (N). Please note that each macroecological pattern varies with manipulations that impact species composition (blue dotted line) despite fixed S and N.

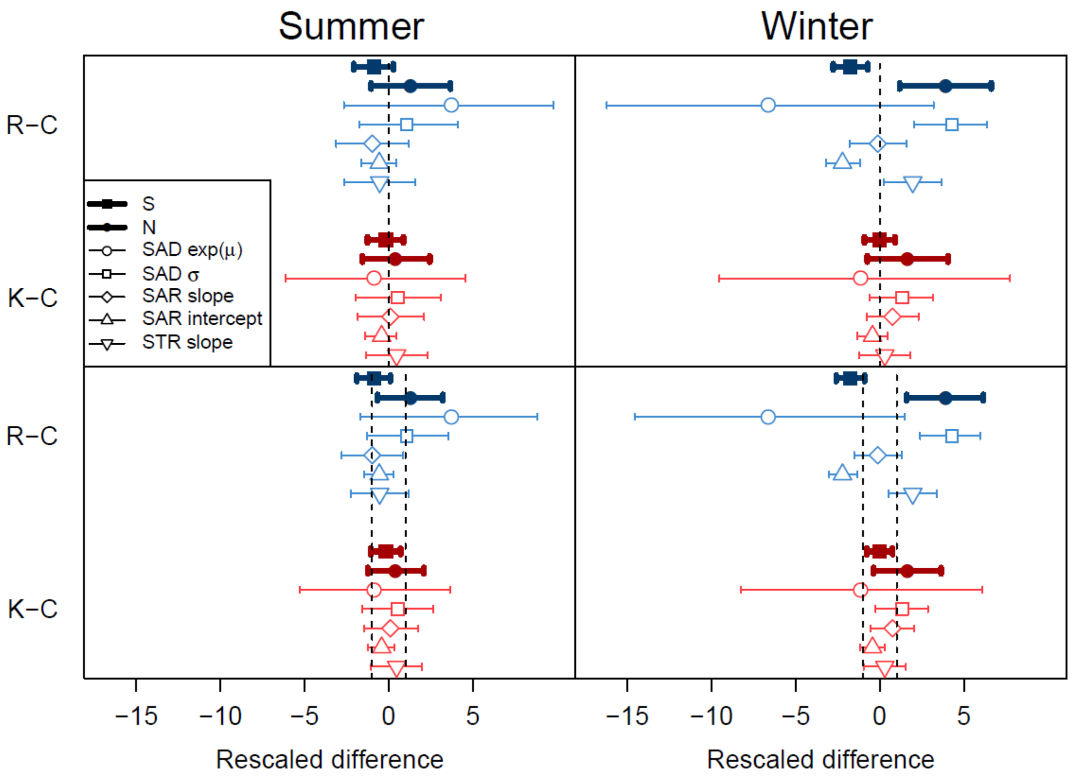

Figure 3-2. Statistical differences among the parameters were only detected in the winter annual community when experimental manipulation (C = control, K = kangaroo rat removal, R = total rodent removal) also impacted species richness and total abundance. Top panels display results from standard statistical tests (linear mixed effects models - SAD, SAR; ANOVA – STR) for significant differences and lower panels display results from equivalence tests. Points represent the mean difference in parameter estimation between two treatments, and whiskers indicate 95% confidence intervals (CIs; 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.

CHAPTER 4

BIODIVERSITY AND THE SPECIES ABUNDANCE DISTRIBUTION: DO SYSTEM LEVEL PROPERTIES RESPOND TO ENVIRONMENTAL CHANGE? [5]

Abstract

Macroecology studies the abundance and distribution of species, typically at large spatial scales. While it is increasingly clear that researchers will need to forecast changes in biodiversity, macroecology currently lacks a framework for understanding if and how biodiversity patterns will respond under environmental change scenarios. The species abundance distribution (SAD) is a key macroecological pattern that incorporates biodiversity metrics of species richness, abundance, and evenness. SADs are heavily studied because they can be predicted by mechanistic models and represent a potentially powerful tool for describing and predicting biodiversity across ecosystems and taxonomic groups. Currently, their sensitivity to global changes is unknown. Using global-span data from small-scale terrestrial animal communities, we show that the SAD and species richness are generally resilient under a suite of artificial and natural manipulations. In contrast, species composition and abundance responded readily to manipulation. Our results suggest that the SAD is a poor indicator of change and that this pattern is not strongly influenced by changes in the biotic structure of communities. Evaluating macroecological patterns in an experimental context represents a novel framework by which researchers can simultaneously clarify the mechanisms underlying patterns and determine the unknown ability of patterns to respond to environmental change.

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[5] This chapter is co-authored by Sarah R. Supp and S. K. Morgan Ernest

Introduction

A central goal of ecology is to understand and predict the abundance and distribution of species (*e.g.*, Hubbell 2001, Magurran and Henderson 2003, Logue *et al.* 2011). Macroecology is a potentially powerful approach which uses patterns of species diversity, typically at large spatial and temporal scales, to understand ecological systems (Brown 1995). Because macroecological patterns exhibit regular behavior across taxonomic groups, ecosystems and continents, they represent a potentially powerful tool for describing and predicting biodiversity structure in various systems (*e.g.,* Thomas *et al.* 2004, Harte 2011). However, recent reflection on the state of macroecology has identified several challenges in moving forward, including the need to explicitly consider the influences of local-scale processes on patterns and to better predict patterns under global change scenarios (Fisher *et al.* 2010, Beck *et al.* 2012; Keith *et al.* 2012).

It is increasingly clear that ecology needs to do more than quantify biodiversity for a snapshot in time. Ecology must also be able to forecast changes in biodiversity for systems in flux (Araujo and Rahbek 2006, Dawson *et al*. 2011). Disturbance itself may play a fundamental role in driving biodiversity patterns (Dornelas *et al*. 2011), but the effects of disturbance on macroecological patterns remains poorly understood (Fisher *et al.* 2010, Beck *et al.* 2012, Keith *et al.* 2012). The lack of a comprehensive understanding of if and how these patterns should be expected to respond to environmental change hinders the usefulness of macroecology for predicting impacts of environmental changes on biodiversity.

The species abundance distribution (SAD) is a well-studied macroecological pattern that describes patterns of commonness and rarity (*e.g.*, Magurran and Henderson 2003). Communities are universally represented by a few very common species and many rare species (McGill *et al.* 2007, Magurran 2004). Since the SAD incorporates biodiversity metrics of species richness, abundance, and evenness, it has been the focus of intense ecological study (McGill *et al.* 2007, Ulrich et al. 2010). Models describing the SAD have focused on a variety of mechanistic explanations including statistical (logseries, Fisher *et al.* 1943; lognormal, Preston 1948; maximum entropy, Harte 2011), niche division (*e.g.,* Tokeshi 1990), ecological drift (Hubbell 2001), population dynamics (He 2005), and spatial distribution (*e.g.,* Magurran and Henderson 2003). Attempts to determine which mechanistic model is correct have met with difficulty (McGill *et al.* 2007), which may explain why there is no existing framework to understand the dynamic response of these patterns under environmental change scenarios (Fisher *et al.* 2010). Evaluating how the SAD responds to environmental stressors could simultaneously clarify the mechanisms most important in determining SAD form and determine the unknown ability of SADs to respond to ecological challenges relevant to conservation and management.

Using a compilation of experimentally manipulated community-level data of terrestrial animal taxa from the published literature (Table S1), we evaluated if SADs and related biodiversity metrics of species composition, total abundance (N), and species richness (S), respond to environmental change. This approach allows us to specifically address 1) whether community perturbations cause changes in the shape of the SAD and 2) if community-level biodiversity-metrics exhibit similar sensitivities to perturbations.

Materials and Methods

Database compilation

We conducted a literature search using Google Scholar October 2011 – February 2012. Peer-reviewed articles which included data tables that reported species-level abundance for a control community and at least one manipulated community were recorded. Published data was often summed or averaged over replicates, rather than reporting abundance separately for each replicate. The data were recorded from a wide variety of sites including manipulated, artificial experiments (i.e., caged exclosures, habitat modules, nutrient addition) and human-mediated "natural" experiments (i.e., controlled burn, silvicultural treatment, grazed plots). Sites represent all continents except Antarctica, and widely varying terrestrial animal taxa (e.g., zooplankton, arachnid, mammal, bird). The data were recorded in linked tables describing the reference, site, experiment, and community details (Appendix F).

Data selection

For analysis, we eliminated communities where > 10% of individuals were not identified to the species level or where the area sampled for paired control – experiment communities was unequal. We used data where raw abundance was reported as a summed total for each species or where mean abundance was reported across the replicates, excluding percent cover, biomass, and presence-only data. In rare cases where mean abundance was reported using less than symbols (*e.g.* < 0.01) we assumed the value was at the top of that bin. SADs are difficult to characterize when the number of species or total abundance is very low, so we included only communities with $S \geq 5$ and $N \geq 30$. We compared pairs of communities at sites that were sampled at the same spatial scales and at similar temporal scales (*e.g.*, we did not compare data from different seasons or across a time-series) to avoid complications due to differences in sampling intensity or timing (Gotelli and Colwell 2001, Magurran 2004). Data meeting the criteria was comprised of 62 control and 114 experiments (4 sites were compared both as control and experiment), representing 119 paired control-experiment comparisons from 41 published papers. Species richness ranged 5-189 and total abundance ranged 30-6,483.

Characterizing and comparing paired communities

For each paired community, we compared the relative rank abundance distributions (RAD), species composition, total abundance, and species richness (*for plots of all comparisons*, Appendix G). RADs are an alternate visualization to SADs where the relative abundance of each species in the community is ordered from most abundant to least abundant. The RAD uses relative abundances and thus minimizes the impacts on the distribution caused primarily by change in total abundance, and also minimizes the information lost using histogram binning methods, especially in smaller communities (McGill *et al.* 2007).

We used the Bray-Curtis dissimilarity metric (BC) to quantify differences between controls and experiments for each of our biodiversity metrics (vegan, function vegdist; Oksanen *et al.* 2010). Bray-Curtis dissimilarity is a semi-metric index that provides a dissimilarity measure ranging from 0 (two communities are the same) to 1 (completely different). It is commonly used to examine similarity of ecological communities. When used to examine species composition or the RAD, it takes into account the presence/absence of a given species or rank across the two communities, but also the relative abundance of each species or rank. We also characterized RADs using Simpson's evenness (J), which describes how similar species are in their abundances and is somewhat independent of S and N (Magurran 2004, McGill 2011; vegan, function diversity; Oksanen *et al.* 2010). For other biodiversity metrics, S and N, we calculated the BC dissimilarity and percent difference for each control-experiment community pair.

This research is not focused on which model fits empirical distributions best, but we compared the performance of the log-series to the Poisson lognormal distribution, which is often considered a superior model for describing SADs (Preston 1948, McGill *et al*. 2007, Ulrich *et al.* 2010) compared to the log-series, an alternate model (Fisher *et al.* 1943, Harte 2011). We used methods following White *et al*. (2012) to indicate the relative probability that one distribution best describes each empirical abundance distribution.

Statistical analysis

To compare measures of relative abundance at each rank (a proxy for the shape of the rank abundance distribution), Simpson's evenness, total abundance, and species richness, we calculated fit of values to the 1:1 line (R^2), which represents no change in values from control to experimental manipulation (Fig. 4-1). We also calculated root mean squared error (rmse) which is used to obtain the standard deviation of model prediction error, where lower values indicate better performance. Here, we used the control data as our "observed" and the experimental data as our "predicted" data in order to determine the degree of change, or variance between N, S, and evenness at paired sites (package hydroGOF, function rmse; Zambrano-Bigiarini 2011).

To determine the explanatory influence of species composition and community-level S and N on observed variation in the form of paired rank abundance distributions, we standardized all the data to make it compatible for statistical analysis and used standardized parameters in a variance-partitioning framework with multiple regression (Legendre and Legendre 2012) to determine the relative importance of composition and of community-level S and N in explaining the observed variation among paired RADs. We analyzed the data using both standardized BC dissimilarity in S and N and standardized absolute percent difference in S and N to avoid bias in the metric of difference chosen, since there is not a well-recognized way to characterize differences in S and N across disparate communities. We performed the analysis using all the data (Table 4-1), and using a smaller subset of the data including only communities with N >= 300 (n = 53, pairs = 37) to avoid bias by including communities which were more likely to be under sampled (McGill 2003), by including experimental type and taxonomic group as predictors for observed variation in the rank abundance distribution (Appendix H). Data and all necessary code for replicating the results are available online[6] and in the Supplement (Appendix J).

Results

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[6] https://github.com/weecology/experimental-rads

All communities experienced compositional differences when comparing manipulated sites with control sites (Fig 4-2a; BC values ranged 0.105-0.994). Many communities experienced a change in total abundance (Fig 4-1a, Fig 4-2b; $R^2 = 0.428$, rmse = 1004.453; BC values ranged 0-0.795). Few communities experienced large changes in the number of species (Fig 4-1b, Fig 4-2c; $R^2 = 0.771$, rmse = 15.281, BC values ranged 0-0.484). Changes in the abundance at each rank for paired RADs was small (Fig4-1d, Fig 4-2d; $R^2 = 0.805$, rmse = 0.033, BC values ranged 0.054-0.502) as well as differences in RAD evenness (Fig4-1c; $R^2 = 0.534$, rmse = 0.121).

Although we were not explicitly testing RAD fit to a specific model, we found that nearly all our communities were best described by the log-series (n = 147), rather than the lognormal, distribution (n = 7). Communities reporting mean abundance could not be weighted using our function (n = 18). Although fit to lognormal distribution may indicate that that a community has been well-sampled (Preston 1948, McGill *et al*. 2007, Ulrich *et al.* 2010), other models predict the log-series distribution (Fisher *et al.* 1943, Harte 2011). Our finding is consistent with White *et al.* (2012), who also found that log-series was a good descriptor of communities across a wide range of taxonomic groups and ecosystems.

Variance partitioning analysis suggested that composition and community-level S and N explained little of the observed variation among paired RADs; results were qualitatively similar for both metrics of S and N change used. Results were qualitatively similar when the analysis was restricted to only communities with N >= 300 (Table C-1).

Taxonomic group and experiment type were relatively uninformative for predicting RAD response to change (Table C-2).

Discussion

Across a wide range of taxonomic groups, ecosystems, and experimental treatments, measures of community structure, especially the rank abundance distribution and species richness, demonstrated little response to disturbance. Perhaps unsurprisingly, species composition responded readily to disturbance, with total abundance following close behind. These results support the idea that the species abundance distribution does not respond readily to environmental change and that it is relatively un-influenced by the exact structure of biotic interactions occurring within a community (Hubbell 2001, Harte 2011).

The small magnitude of changes observed in the rank abundance distribution suggests that this pattern is relatively insensitive to disturbance, including those that most ecologists would agree constitute as "major" changes to a system (*e.g.*, wildfire, clear-cuts). Although disturbance often has an important influence on the identity, abundance and distribution of species (*e.g.*, Chase and Leibold 2003, Clark 2009), even large changes in species composition and abundance often had little or no influence on species richness or on the shape of the abundance distribution. Since changes in species composition may influence the kind of diversity in which land managers are interested (e.g., functional diversity [Prinzig *et al*. 2008, Tilman *et al.* 1997], phylogenetic diversity [Mace *et al*. 2003, Webb *et al.* 2002] and ecosystem function [Flynn *et al.* 2011, Hooper and Vitousek 1997]) while having little effect on SAD shape, we suggest that the SAD is not a good indicator for change within a system or of escalating disturbance impact.

Our results also suggest that species richness, one of the most commonly used diversity metrics for quantifying the influence of disturbance on a community or ecosystem (Dornelas *et al*. 2011), may not be a good indicator of ecosystem change. Decades of diversity experiments have manipulated species richness to understand the impacts of species gain or loss on ecosystems (*e.g.* Naeem *et al.* 1995, Hector *et al.* 1999, Reich *et al.* 2012), but ecologists still generally lack an understanding of the existing background variability of species richness at natural sites, the magnitude of changes that occur in response to disturbance, or how much change in species richness is *biologically* significant. Our results and others (*e.g.*, Chapin *et al.* 2000, Hillebrand *et al.* 2008) suggest that species richness is often surprisingly insensitive to the changes applied to a system. In our analysis, only one site experienced more than a twofold change in species richness. This raises the important question of what diversity experiments actually tell us about ecological response to disturbance if the magnitude of species richness change that is studied in these systems is often much larger than what is empirically observed.

Critical conservation decisions for threatened areas are often made based on continuing function of ecosystem services (*e.g.*, Chan *et al.* 2006, Nelson *et al.* 2009), which in turn are often dependent on maintaining specific biological interactions. As such, the details of biotic interactions are often quite important. If, in fact, the SAD contains little information related to the details of biotic interactions (McGill *et al.* 2007, Harte 2011, White *et al*. 2012), then it also has little promise for informing conservation policy and management decisions for ecosystems that are in flux. However, because the SAD appears to be fairly resilient to many disturbances, we suggest that cases in which detectable shifts in the form of the SAD *do* occur may indicate fundamental changes in specific processes within a system that warrant further study and attention. Since the SAD can be accurately predicted using models that do not depend on knowing biological details (*e.g.*, Hubbell 2001, McGill *et al.* 2007, Harte 2011), the pattern may yet play a valuable role in conservation biology as a static descriptor of community structure in systems where it is logistically difficult or impossible to thoroughly sample the community.

A major challenge facing macroecological advancement is to bridge the existing gap between basic and applied ecological research. Using experiments to study macroecological patterns such as the species abundance distribution represents a little-explored but potentially powerful approach for exploring the drivers of macroecological patterns and for evaluating their sensitivity to environmental change (See Chapter 3, Keith *et al*. 2012). We believe that this represents an open and interesting research avenue for moving macroecological study forward. Future research evaluating empirically observed changes in macroecological patterns related to energy flux or body size (e.g., individual size distributions, species-energy relationships) may respond more readily to disturbance and may provide an important way to link macroecology to predictive forecasting and conservation goals.

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Supplemental Material

Appendix F. Metadata and data for the communities included in the analysis.

Appendix G. Figures for all the paired community data represented as rank abundance distributions.

Appendix H. Additional results from the variance partitioning analyses.

Appendix I. Locations of all of the manipulated communities used in the analysis.

Appendix J. Details on the computational analyses needed to replicate the results.

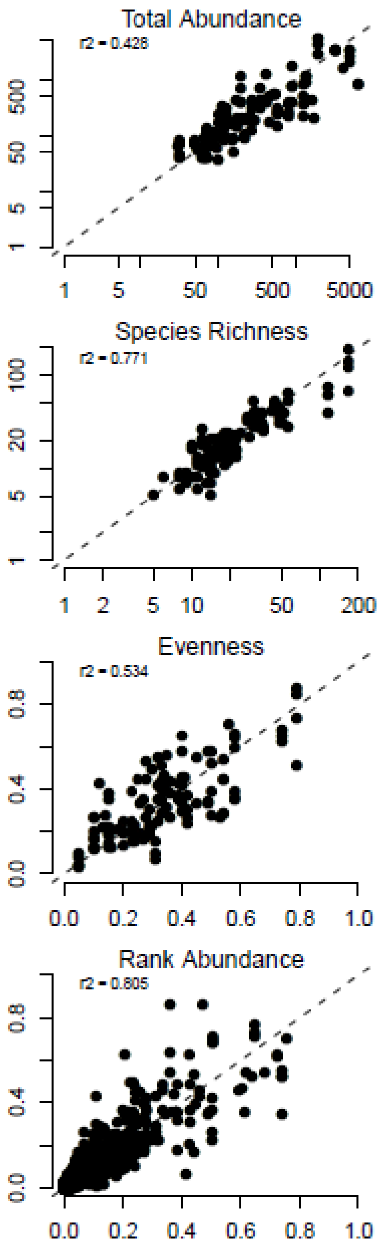

Figure 4-1. Panel of 1:1 plots with R2 for a) total abundance, b) species richness, c) Simpson’s evenness, and d) relative abundance at each rank of the RAD. Control data is on the x-axis and experimental data is on the y-axis. Fit to the 1:1 line (red-dashed line) suggests no change in the parameter among the paired control-experiment comparison.

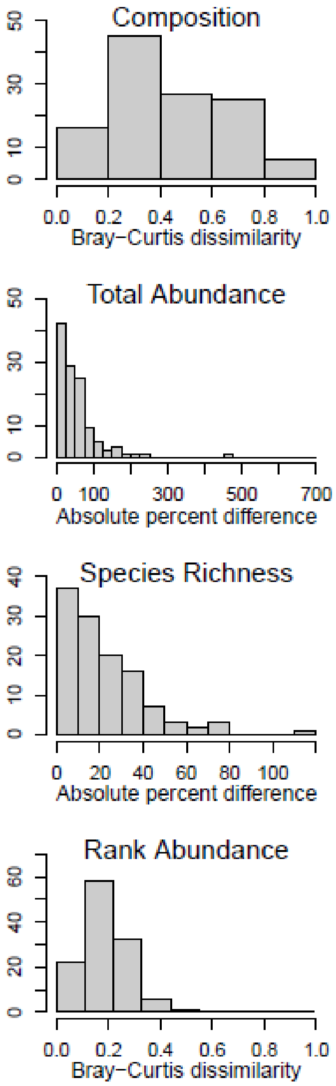

Figure 4-2. Panel showing the change in the four parameters among the paired control-experiment sites: a) Bray-Curtis dissimilarity in species composition, b) absolute percent change in total abundance, c) absolute percent change in species richness, d) Bray-Curtis dissimilarity of the relative abundance at each rank for compared RADs.

Model	Full Model R^2	Composition R^2	S and N R^2	Composition variance explained	SandN variance explained
A) Bray-Curtis dissimilarity model: composition + N + S + N * S	0.2838	0.1811	0.1618	0.1221	0.1027
B) Percent difference model: composition + %N + %S + %N * %S	0.2987	0.1811	0.1784	0.1203	0.1175

Table 4-1. Table showing results from variance partitioning analysis. Since we used both Bray-Curtis dissimilarity and absolute percent difference to characterize change in species richness (S) and total abundance (N) between compared sites, we used two models in the variance partitioning analysis: A) We tested the explanatory power of Bray-Curtis dissimilarity of species composition, S, and N , and the interaction between Bray-Curtis dissimilarity in S and N (since they are somewhat related measures) on the observed Bray-Curtis dissimilarity of rank abundance distributions. B) We tested the explanatory power of Bray-Curtis dissimilarity of species composition, absolute percent difference in S, and N , and the interaction between absolute percent difference in S and N on the observed Bray-Curtis dissimilarity of rank abundance distributions.

CHAPTER 5

CONCLUSION

Ecologists are increasingly aware that biodiversity results from the complex interplay of local and regional –scale processes (Holyoak *et al.* 2005, Magurran and McGill 2011) and that studying systems as if they are static entities is problematic (Fisher *et al.* 2010). Lack of knowledge of the mechanisms regulating biodiversity across spatiotemporal scales inhibits ecologists' ability to forecast changes in biodiversity for systems in flux or to make accurate predictions (Dawson *et al.* 2011, Araujo and Rahbek 2006). The aim of this dissertation was to disentangle the roles that local and regional scale processes play in regulating biodiversity and community structure and to determine the unknown response of biodiversity metrics to environmental change.

A recent conceptual framework suggests that the processes that regulate biodiversity differ among core and transient species. Core and transient species have been shown to differ in spatiotemporal turnover (Belmaker 2009), diversity patterns (Magurran and Henderson 2003), and in local vs. regional survival strategies (Coyle *et al.* in press). In Chapter 2, we hypothesized that due to differing local vs. regional survival strategies and therefore evolutionary dynamics, core and transient species should also differ predictably in important life-history traits including degree of specialization, dispersal ability, survival, and reproductive effort. We used 10-years of capture-mark-recapture data (2000-2009) from the Portal Project (Ernest *et al.* 2009) to evaluate temporal permanence, local abundance, and life-history traits of species in the rodent community. Our results support the hypothesis that core species generally have high ecological specialization, high survival, low dispersal rates, and low reproductive effort compared to transient species in the same feeding guild. Core species may be responsible for much of the function at a site (e.g., biomass production, nutrient cycling) and may set an upper limit for diversity (Magurran and Henderson 2010), but transient species may be primarily responsible for maintaining species richness via subsidies from the regional species pool (Magurran *et al.* 2011, Belmaker 2009). These results suggest that trait associations differ among core-transient species and will correspond to differing responses to environmental change.

In Chapter 3, we evaluated the response of local-scale macroecological patterns to manipulated seed predation. Macroecological patterns, including the species abundance distribution (SAD), species-area relationship (SAR), and the species-time relationship (STR), exhibit regular behavior across ecosystems and taxa (Brown 1995), and are increasingly being used to make predictions about biodiversity (Thomas *et al.* 2004, Diniz-Filho *et al.* 2005, Dolan *et al.* 2009). We used data from 15 years of the rodent removal experiment at the Portal Project (1995-2009) to evaluate the response of the SAD, SAR, and STR to two levels of manipulated seed predation (kangaroo rat removal and total rodent removal). Seed predator manipulations significantly impacted plant species composition in all cases, but did not impact species richness, community abundance, or macroecological patterns in most cases. Since macroecological patterns were only influenced when species richness and community abundance were also altered, we suggest that local scale processes primarily act indirectly through these properties to determine macroecological patterns. Regional scale processes that maintain the regional species pool may regulate species richness by maintaining a diverse supply of propagules that enable compensation dynamics in the system.

In Chapter 4, I used a broad-scale approach to investigate the unknown ability of the SAD and related biodiversity metrics (composition, species richness, total abundance, evenness) to respond to ecological change. While it is increasingly clear that researchers will need to forecast changes in biodiversity (Araujo and Rahbek 2006, Dawson *et al.* 2011), macroecology currently lacks a framework for understanding if and how biodiversity patterns will respond to environmental change (Fisher *et al.* 2010, Beck *et al.* 2012, Keith *et al.* 2012). Using a global-span dataset that I compiled from the literature, we found that the SAD and species richness were generally resilient under a suite of artificial and natural manipulations, whereas, species composition and total abundance responded readily. Our results suggest that the SAD and species richness are not strongly influenced by local scale interactions within communities and may be poor indicators of change.

These studies point out the important role that regional context and dispersal limitation play in regulating biodiversity and community structure in communities. Local processes are important determinants of species composition and abundance, and may set an upper limit to species richness in a particular location (Goheen *et al.* 2005, Magurran *et al.* 2011). Regional processes, including environmental heterogeneity and dispersal limitation, may be more important for a community’s ability to compensate for local scale changes and maintain biodiversity and community structure under environmental change scenarios (Magurran and Henderson 2010). Further, my studies suggest that species richness and macroecological diversity patterns may not, in fact, be good indicators for ecological change, although they are often used as such (Dornelas *et al.* 2011, Reich *et al.* 2012). If system-level properties are generally insensitive to ecological change, then for specific conservation questions, it may be important to understand how ecological change influences the occurrence, abundance and distribution key groups of species (*e.g.*, core-transient species, keystone species) in order to predict which biodiversity metrics will be altered. Other currencies for abundance (*i.e.*, biomass) may be more sensitive to environmental change and provide more important indicators for fundamental shifts occurring in a system (Jennings *et al.* 2001, Dornelas *et al.* 2011).

In conclusion, the results of my dissertation suggest that biodiversity and community structure result from the interplay of regional and local processes, and that these processes differentially influence species based on their life-history trade-offs. Disentangling the roles that these processes play in influencing community structure may aid in ecologists' ability to predict how communities will respond to ecological change. Species composition and abundance may be dominated by local processes (*i.e.*, species interactions, resource fluctuations), but my research suggests that other biodiversity metrics such as macroecological diversity patterns, evenness, species richness, are dominated by regional processes (*i.e.*, environmental heterogeneity, habitat connectivity) and are often invariant under changes applied to a local system. These results imply that ecologists must think carefully about the rationale behind choosing specific biodiversity metrics on which to base applied ecological decisions. My dissertation work shows that combining macroecology and experimental ecology is a powerful approach for investigating the processes underlying spatiotemporal diversity patterns and the response of biodiversity patterns to ecosystem changes.

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APPENDICES

Appendix A. Additional methodology on data restriction.

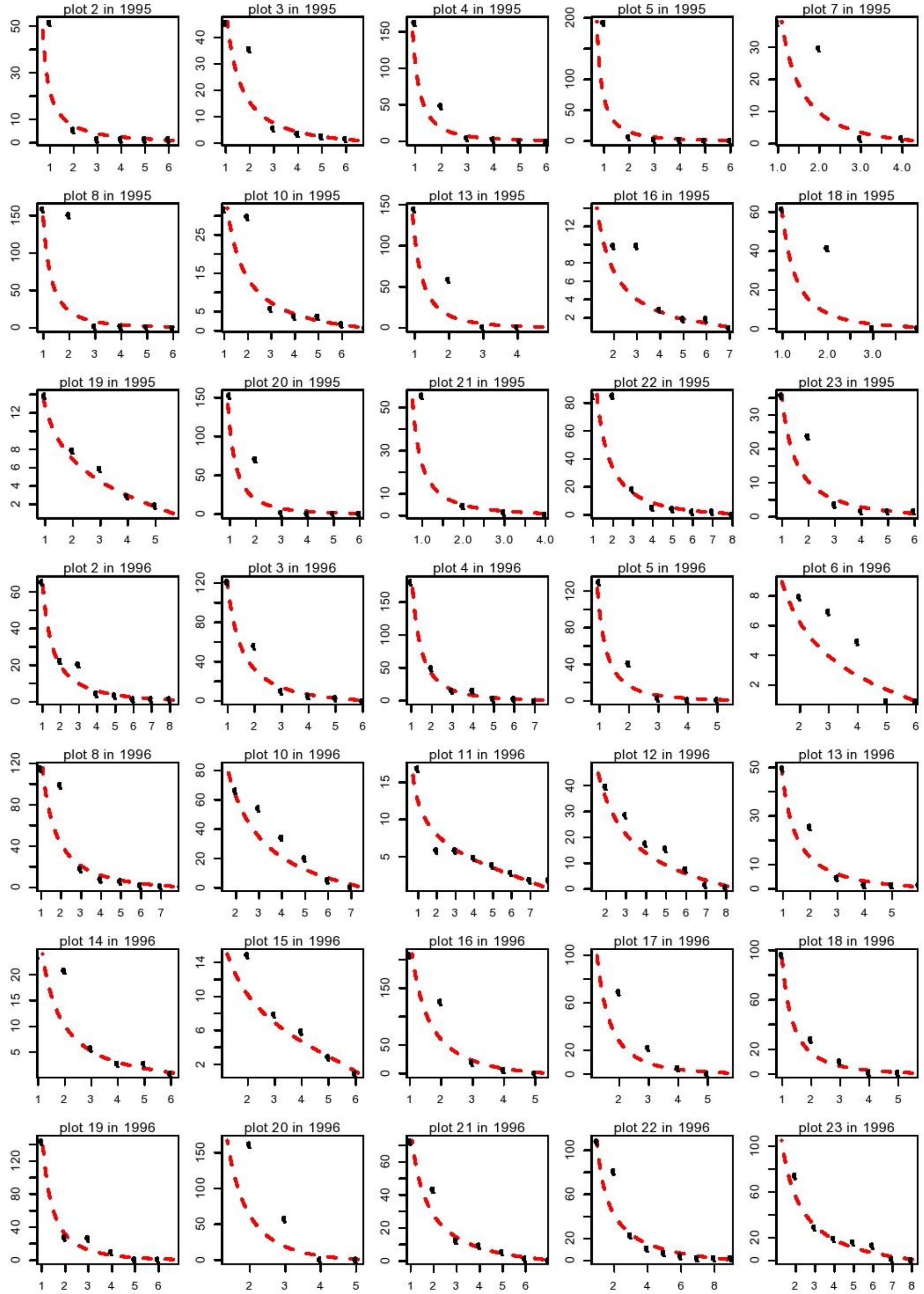
Due to changes in experimental design in 1988, we restricted our data to 1995-2009 to allow communities lag time to adjust. We excluded 3 plots (plots 1, 9 and 24) due to more recent plot changes. All other plot treatments remained constant throughout the study period (for additional details on study site and experimental design, 1; for raw data, 2). For the winter annual community we used all years (1995-2009) of data. For the summer annual community, years 1997-1998 were excluded due to high abundances (>10% total abundance) of unidentifiable dominant species (i.e., individuals were likely known species, but unidentifiable at time of census). We omitted individuals from the analyses that were unknown or only identified to genus level.

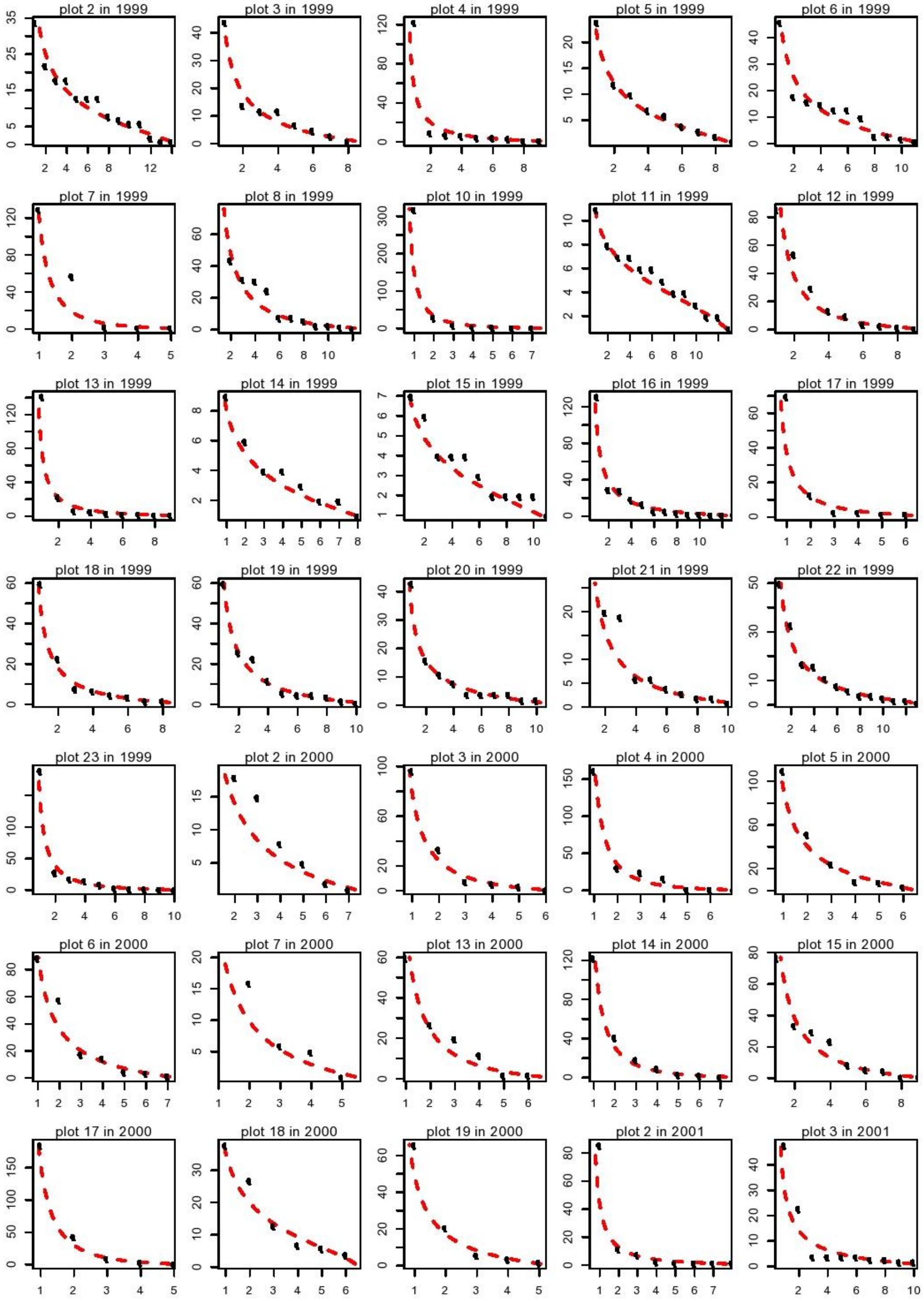
Appendix B. Figures for all the data and the functions used to characterize the macroecological pattern parameters.

Each pattern is labeled with the experimental plot identification number and year combination. Black points represent the plotted data and the red lines represent the function used to fit the data. SADs were characterized using the Poisson log-normal distribution and we plot the data as rank abundance distributions (RADs) for visual ease. The x-axis is rank and the y-axis is abundance. SADs and STRs were characterized using power-laws. For SARs, the x-axis is the area sampled (0.25, 0.5, 1, 2, 4) in square meters, and the y-axis is mean abundance at each spatial scale. For STRs, the x-axis is the timespan sampled in years (winter, 1-15; summer, 1-11), and the y-axis is mean abundance for each timespan. Experimental plot identification numbers refer to experimental treatment as follows: Controls (2, 4, 8, 11, 12, 14, 17, 22), Kangaroo rat removals (3, 6, 13, 15, 18, 19, 20, 21), and total rodent removals (5, 7, 10, 16, 23).

(Below) Panel B-1 Panel for all the data and functions used to characterize macroecological patterns

Summer rank abundance distributions

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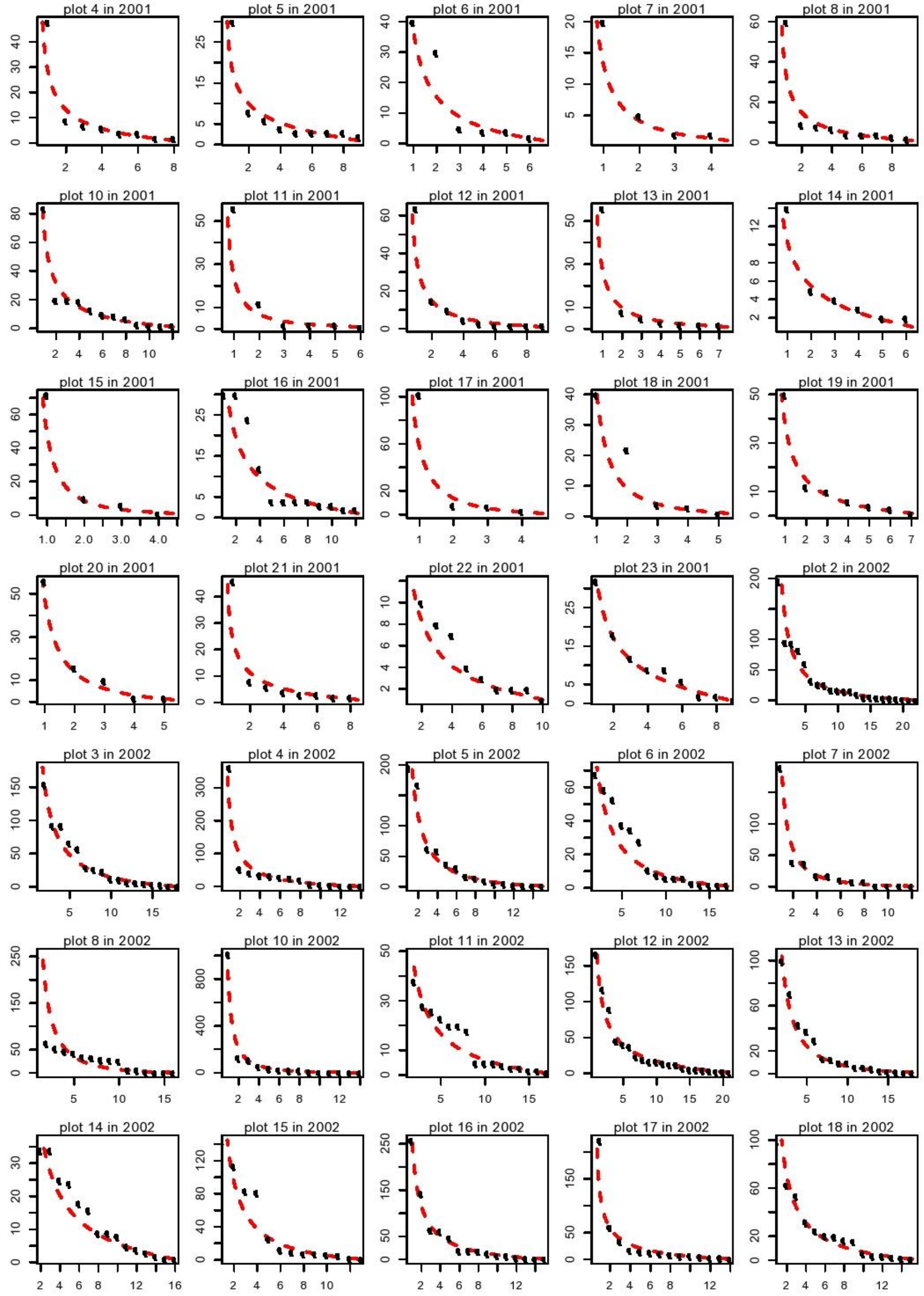
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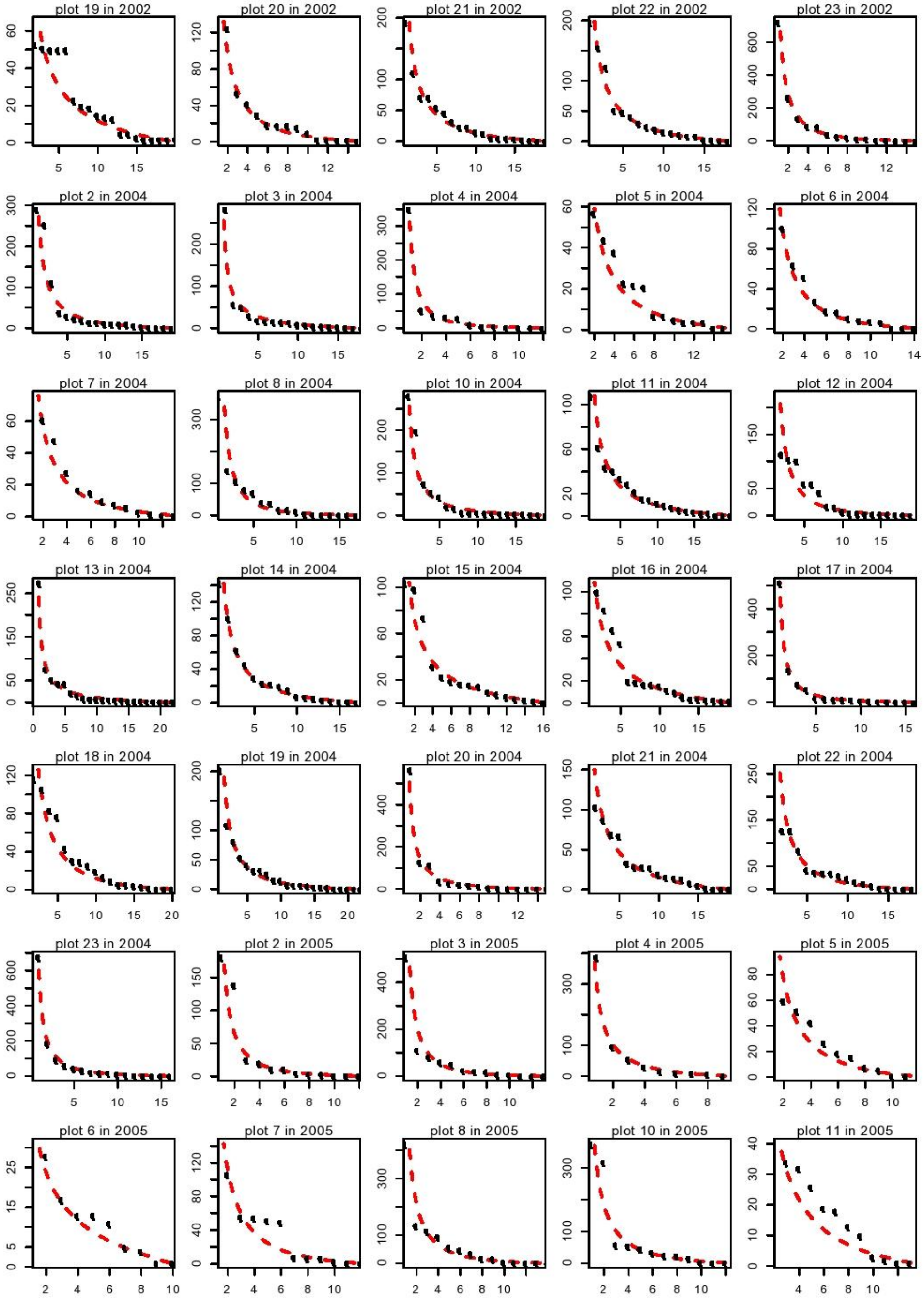
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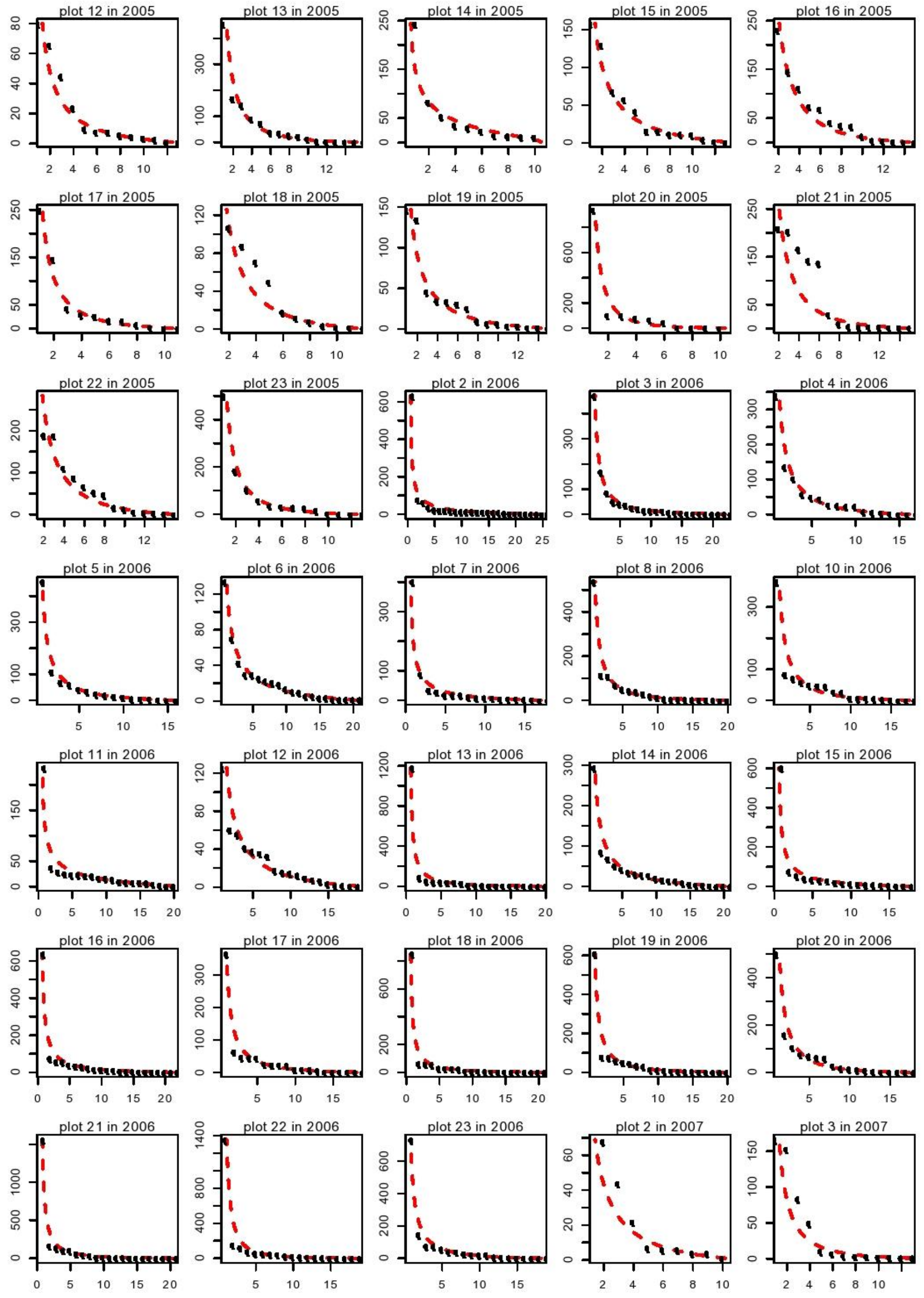
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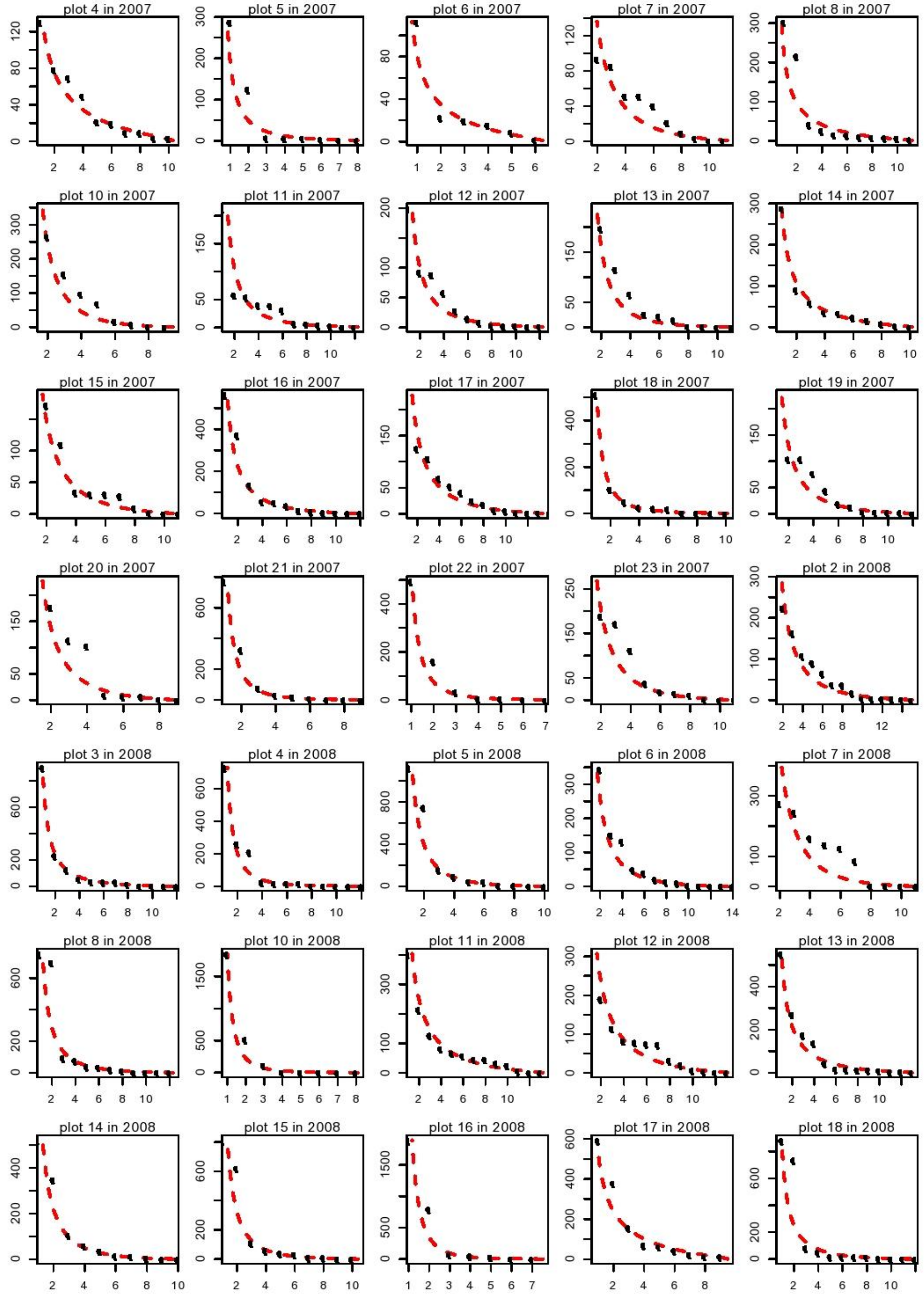
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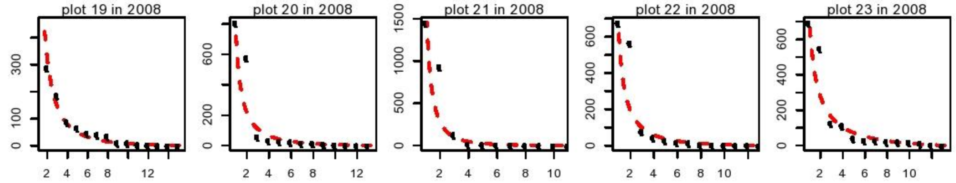
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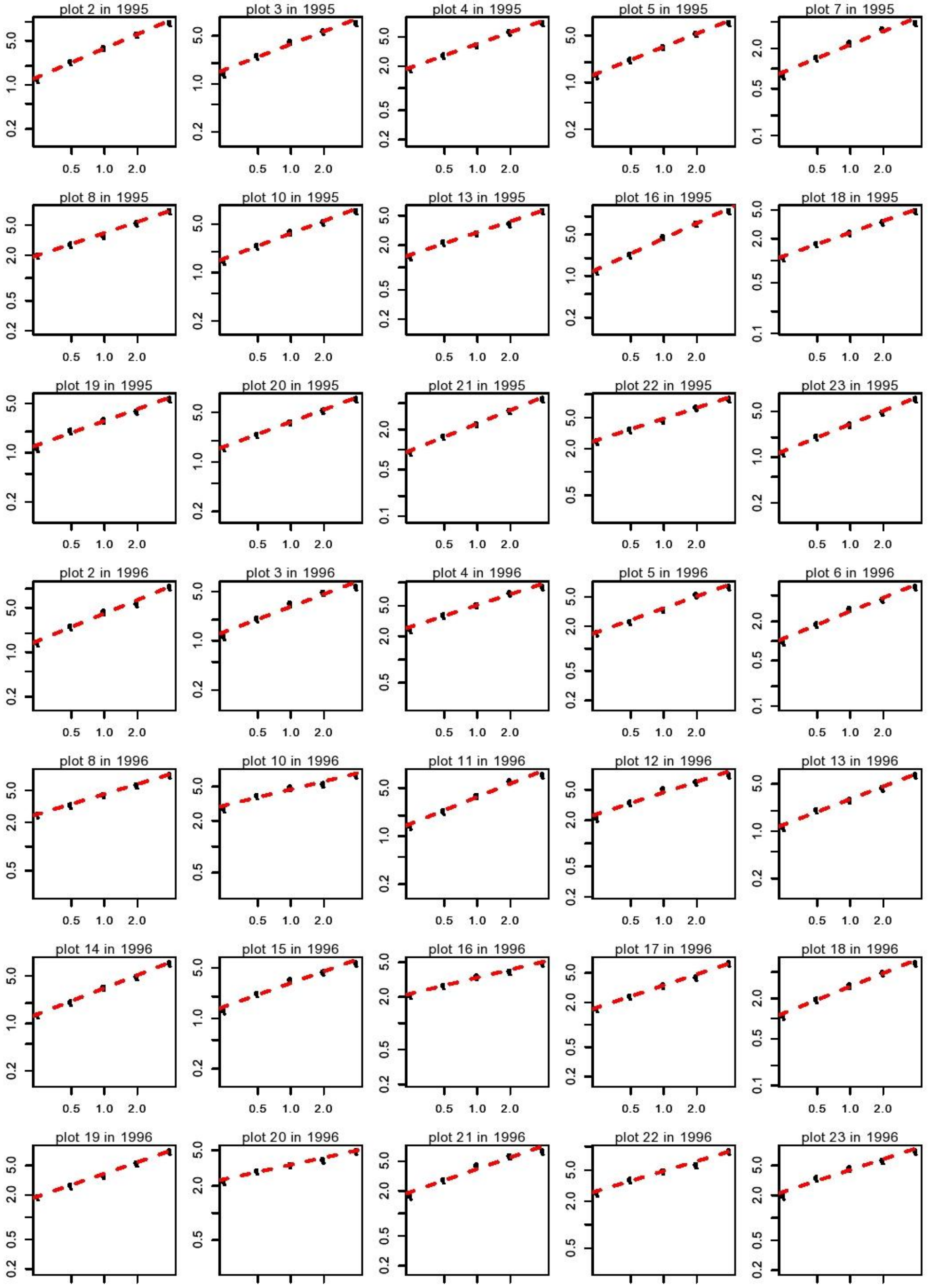

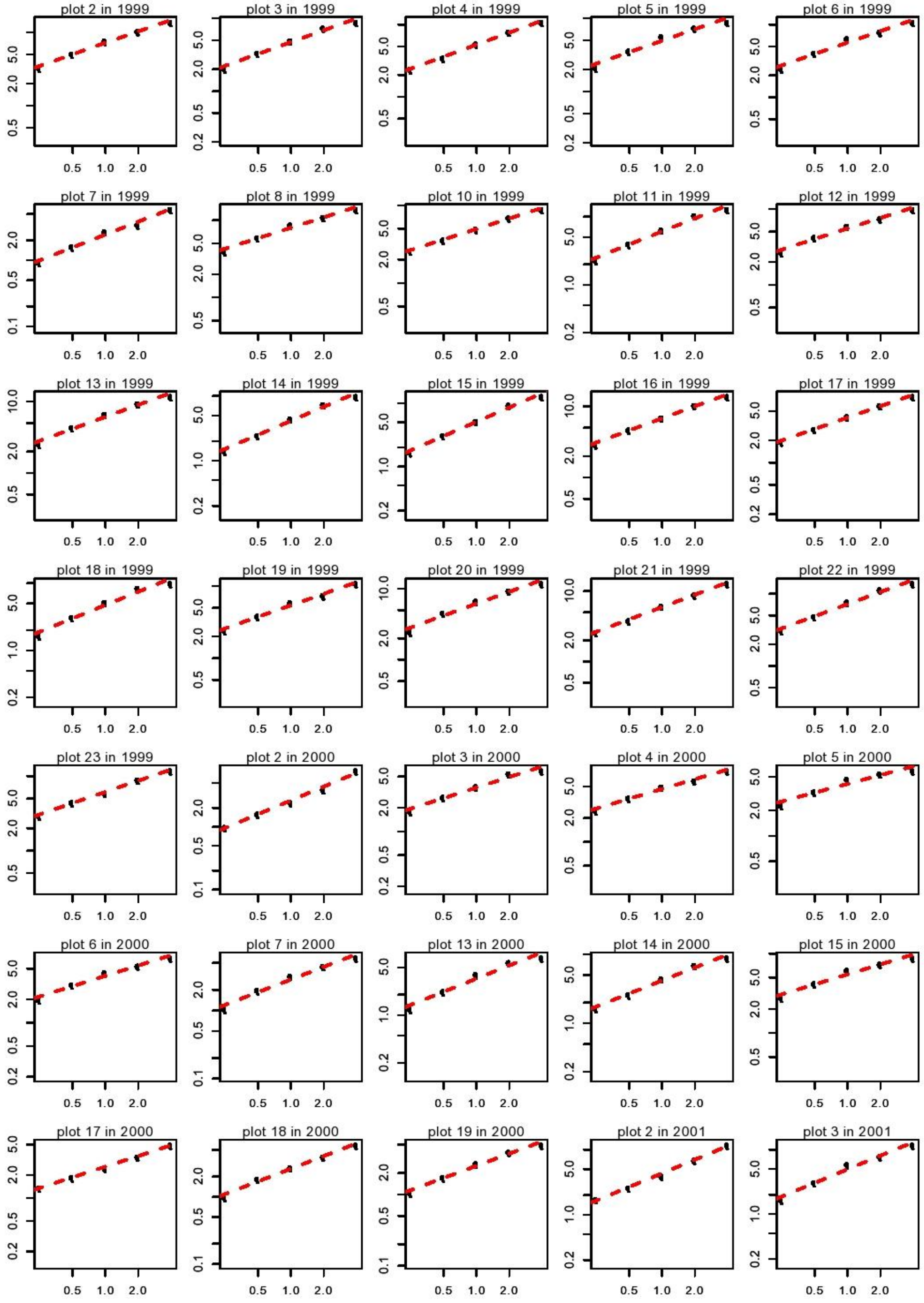
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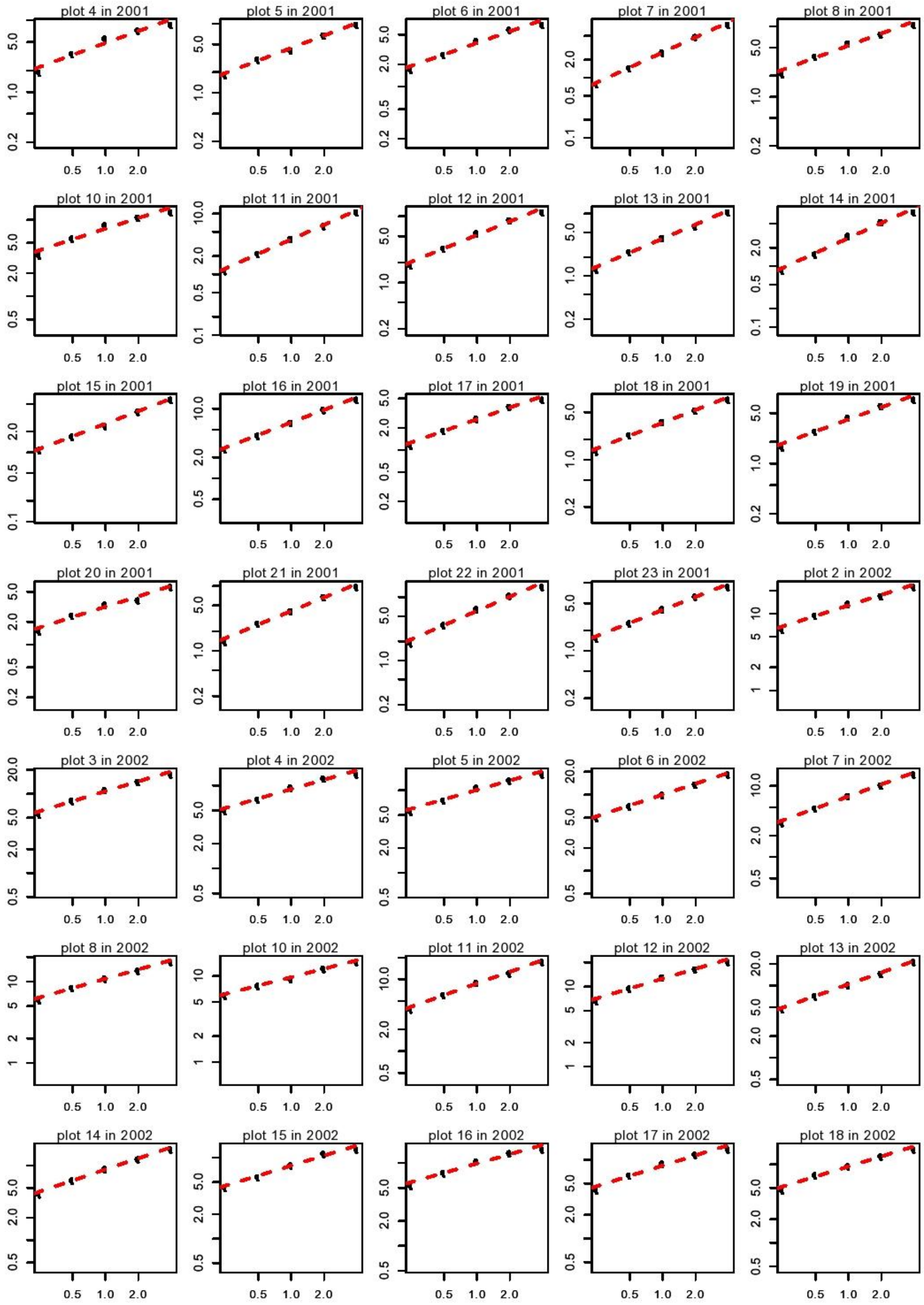
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plot 10 in 2002
1
2
5
10
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plot 11 in 2002
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1.0
2.0
plot 12 in 2002
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2
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10
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1.0
2.0
plot 13 in 2002
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plot 14 in 2002
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5.0
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2.0
plot 15 in 2002
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2.0
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1.0
2.0
plot 16 in 2002
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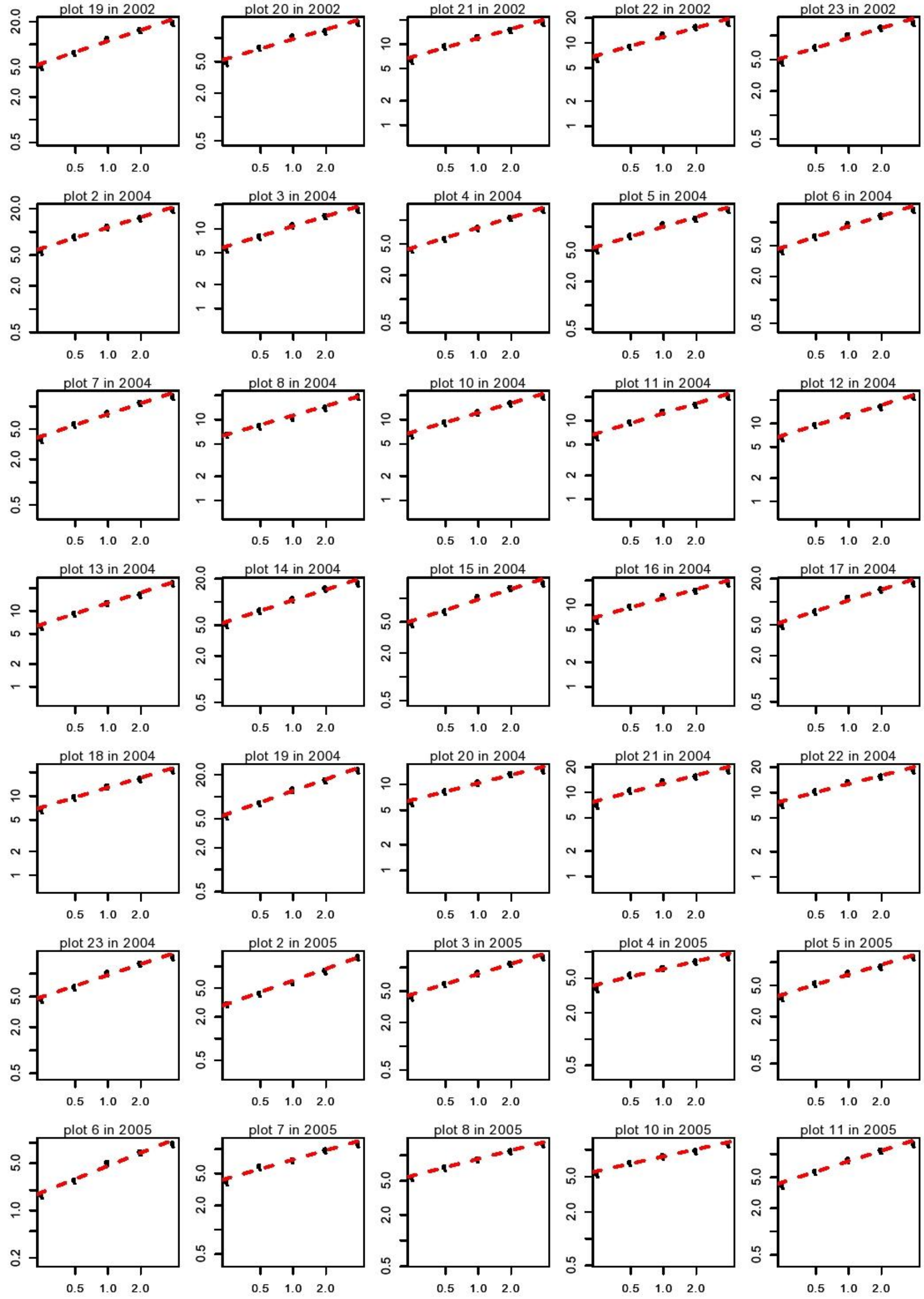
2.0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plot 23 in 2002
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plot 2 in 2004
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plot 3 in 2004
1 2 5 10
plot 4 in 2004
0.5 2.0 5.0
plot 5 in 2004
0.5 2.0 5.0
plot 6 in 2004
0.5 2.0 5.0
plot 7 in 2004
0.5 2.0 5.0
plot 8 in 2004
1 2 5 10
plot 10 in 2004
1 2 5 10
plot 11 in 2004
1 2 5 10
plot 12 in 2004
1 2 5 10
plot 13 in 2004
1 2 5 10
plot 14 in 2004
0.5 2.0 5.0 20.0
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0.5 2.0 5.0
plot 16 in 2004
1 2 5 10
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1 2 5 10
plot 19 in 2004
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plot 2 in 2005
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plot 4 in 2005
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plot 5 in 2005
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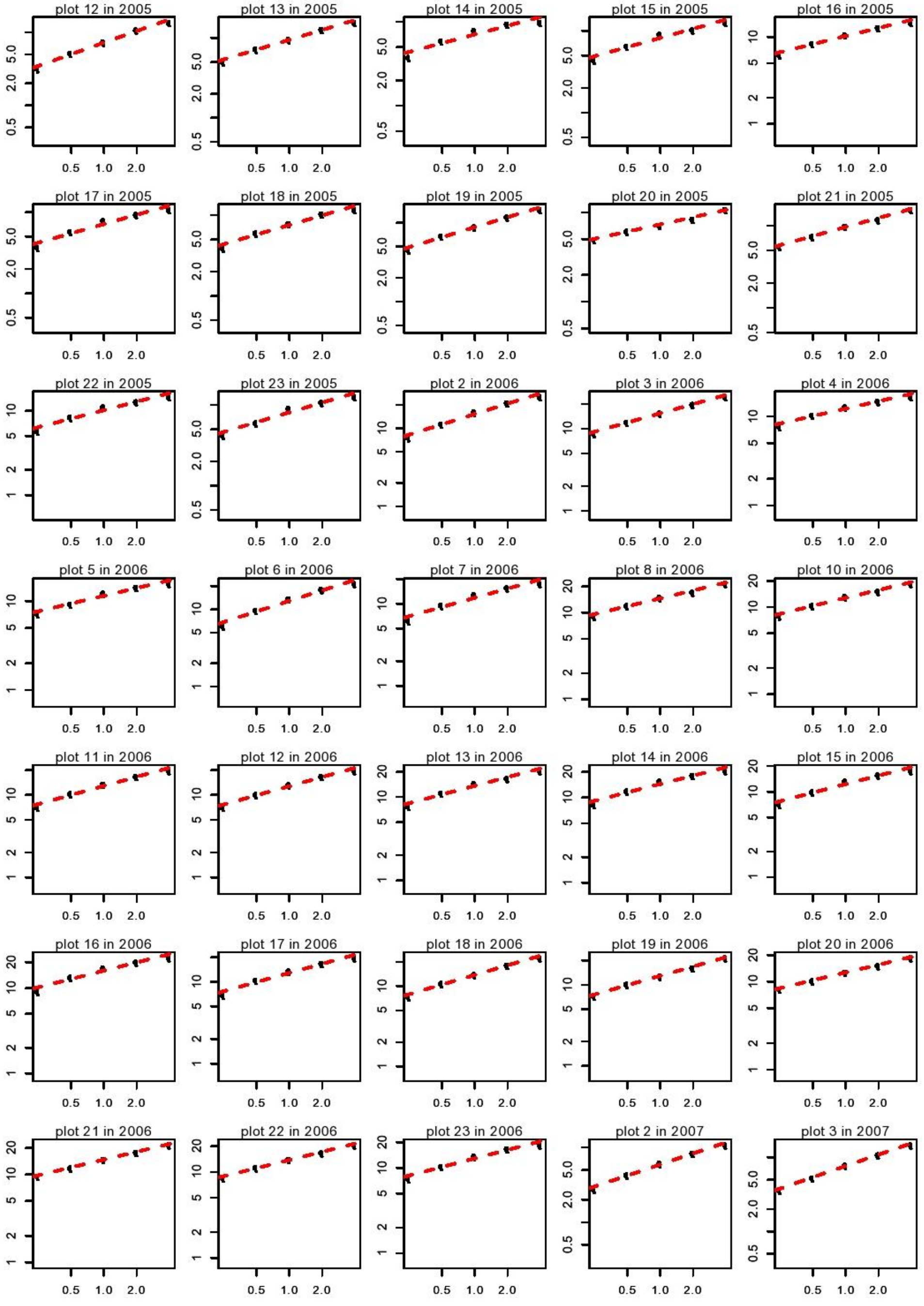
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plot 2 in 2006
plot 3 in 2006
plot 4 in 2006
plot 5 in 2006
plot 6 in 2006
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plot 8 in 2006
plot 10 in 2006
plot 11 in 2006
plot 12 in 2006
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plot 14 in 2006
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plot 19 in 2006
plot 20 in 2006
plot 21 in 2006
plot 22 in 2006
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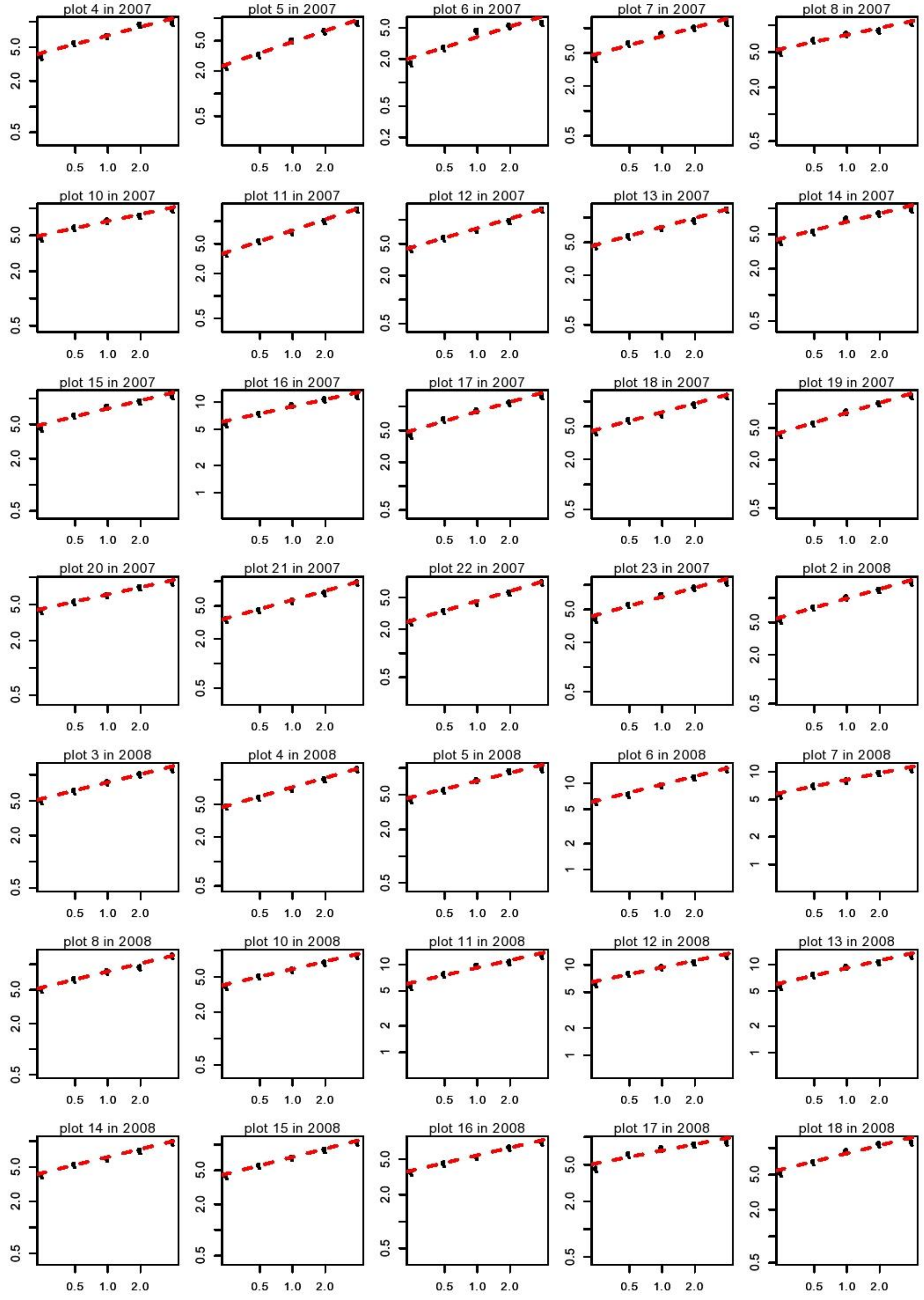
5
10
20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plot 19 in 2007
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plot 22 in 2007
plot 23 in 2007
plot 2 in 2008
plot 3 in 2008
plot 4 in 2008
plot 5 in 2008
plot 6 in 2008
plot 7 in 2008
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plot 12 in 2008
plot 13 in 2008
plot 14 in 2008
plot 15 in 2008
plot 16 in 2008
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5
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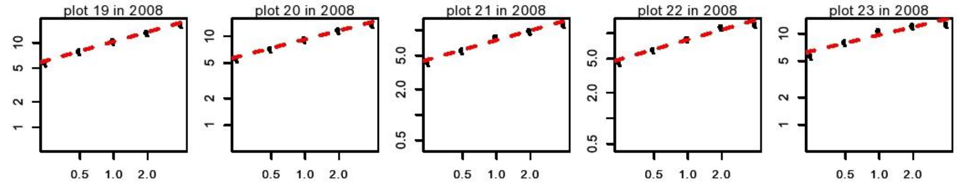
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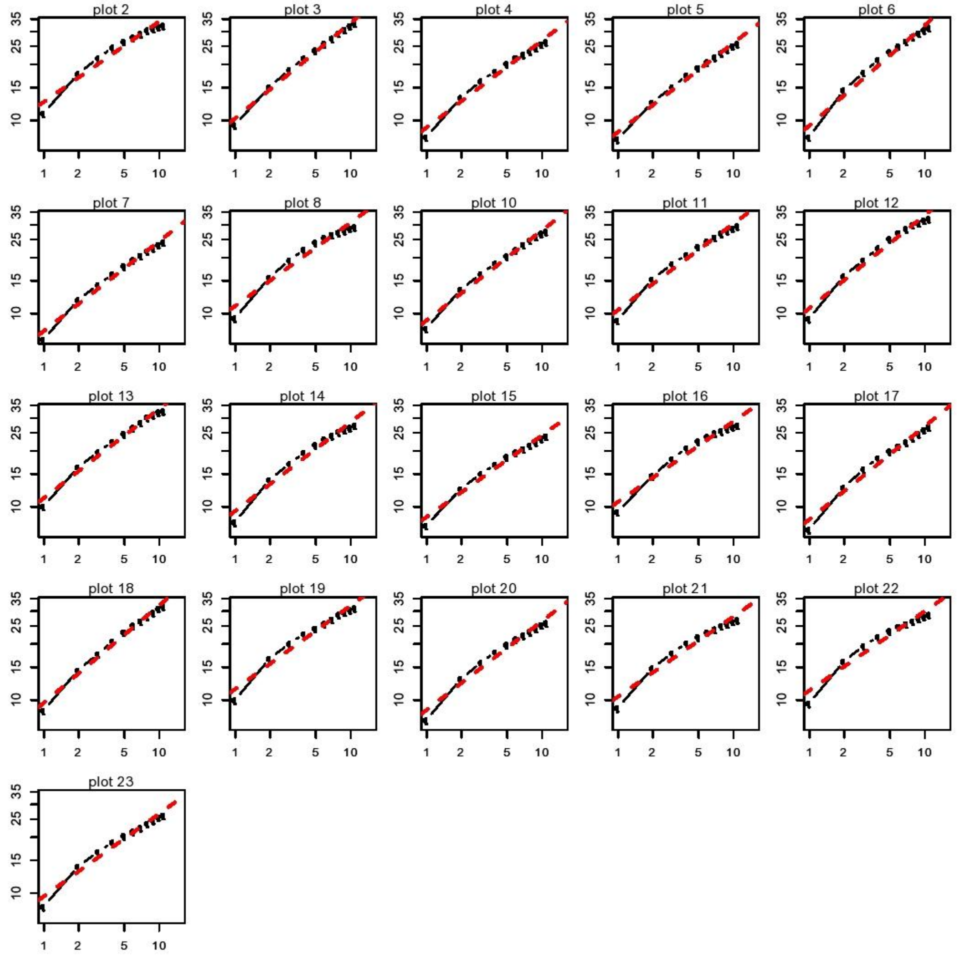
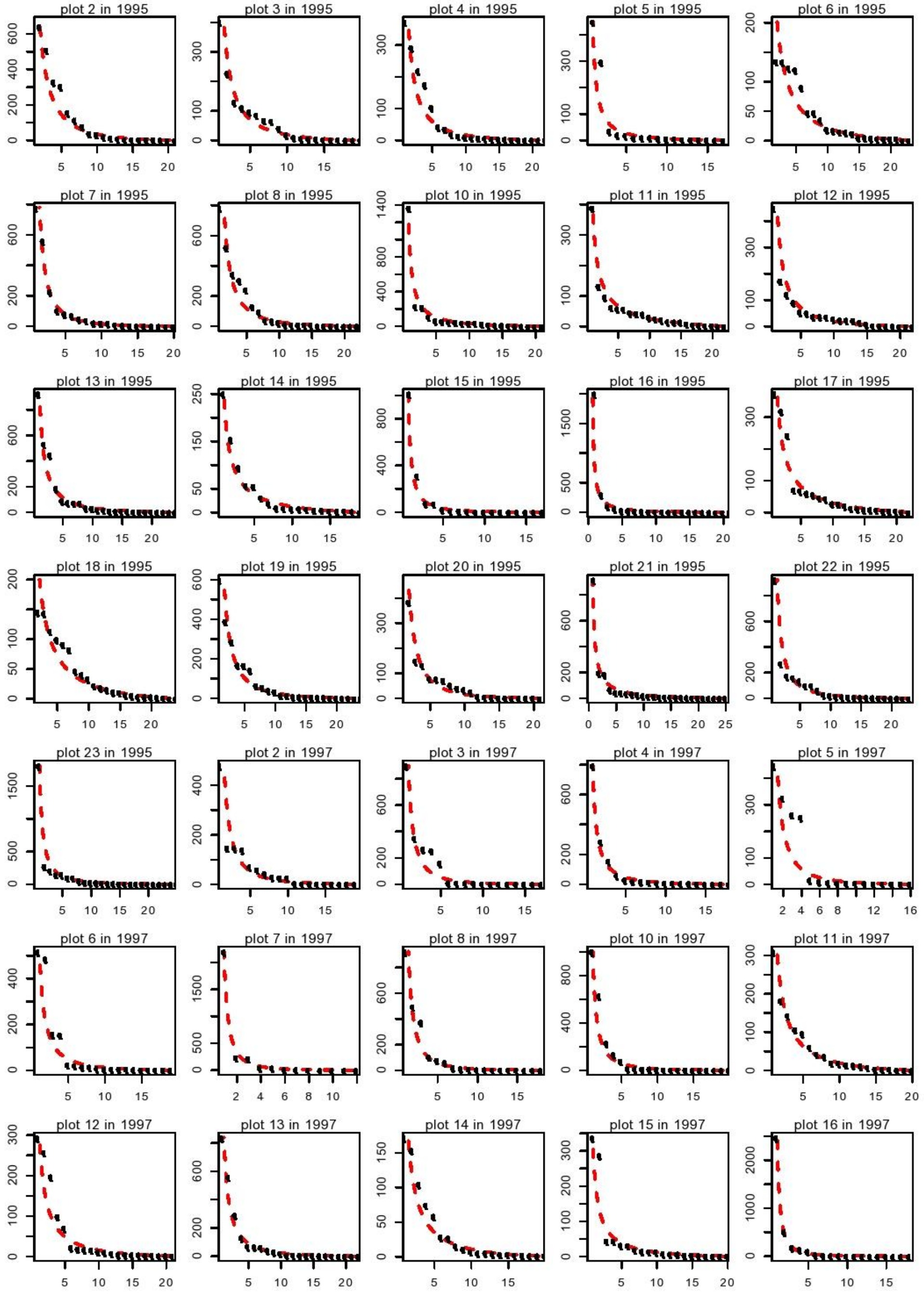
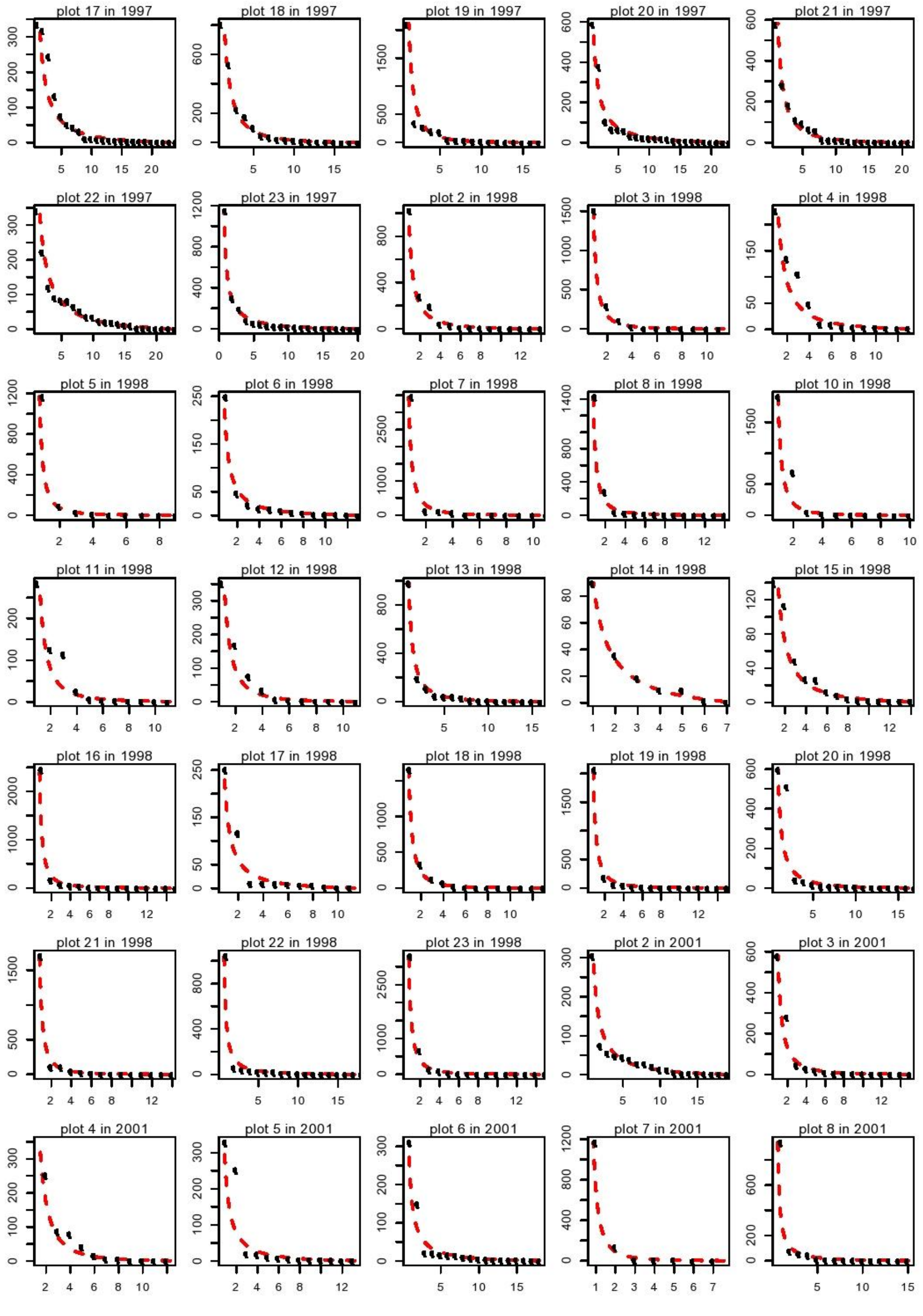
2.0

Summer species-time relationship



Winter rank abundance distribution

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plot 7 in 1998
plot 8 in 1998
plot 10 in 1998
plot 11 in 1998
plot 12 in 1998
plot 13 in 1998
plot 14 in 1998
plot 15 in 1998
plot 16 in 1998
plot 17 in 1998
plot 18 in 1998
plot 19 in 1998
plot 20 in 1998
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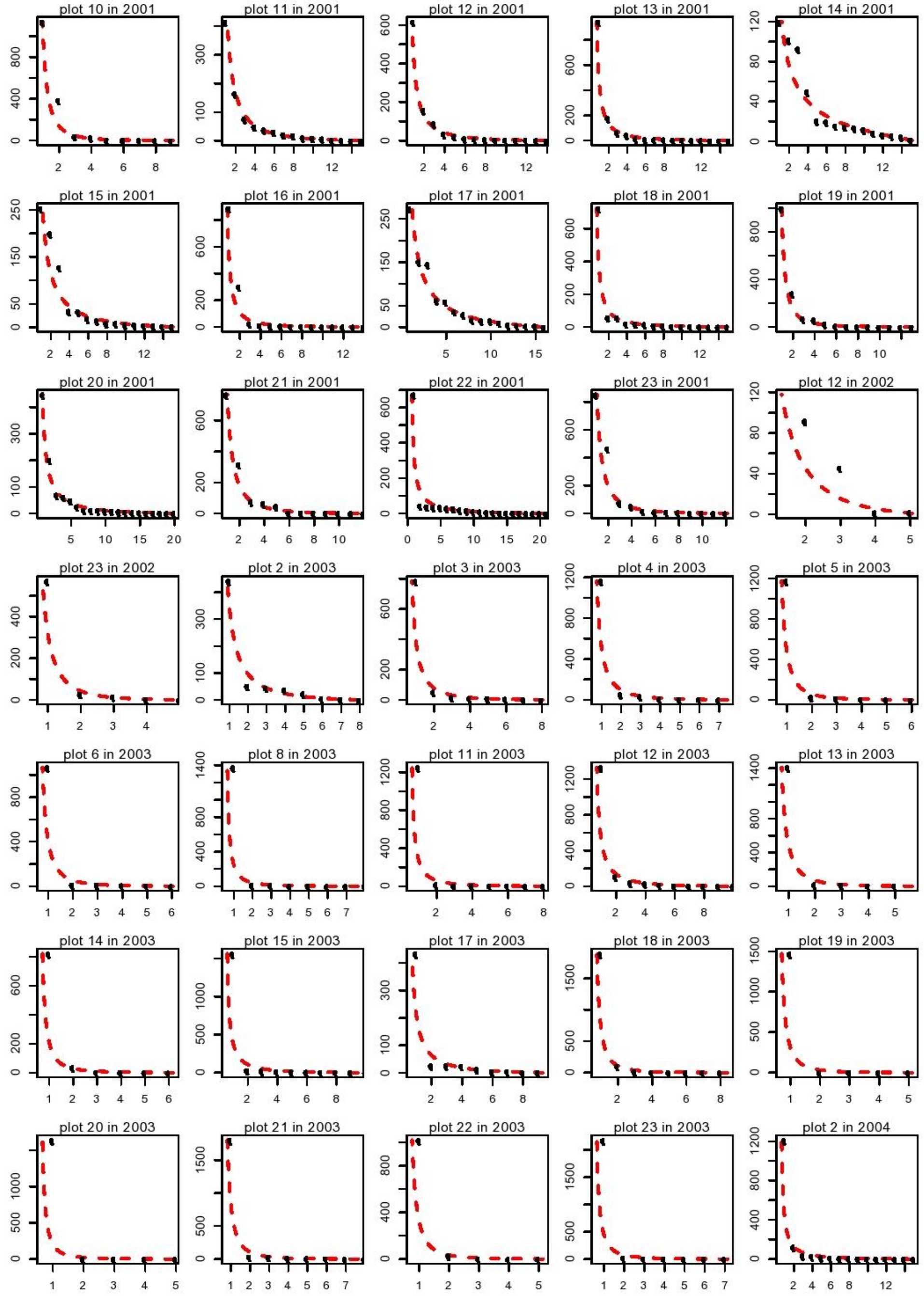
plot 8 in 2001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plot 19 in 2001
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plot 12 in 2002
plot 23 in 2002
plot 2 in 2003
plot 3 in 2003
plot 4 in 2003
plot 5 in 2003
plot 6 in 2003
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plot 11 in 2003
plot 12 in 2003
plot 13 in 2003
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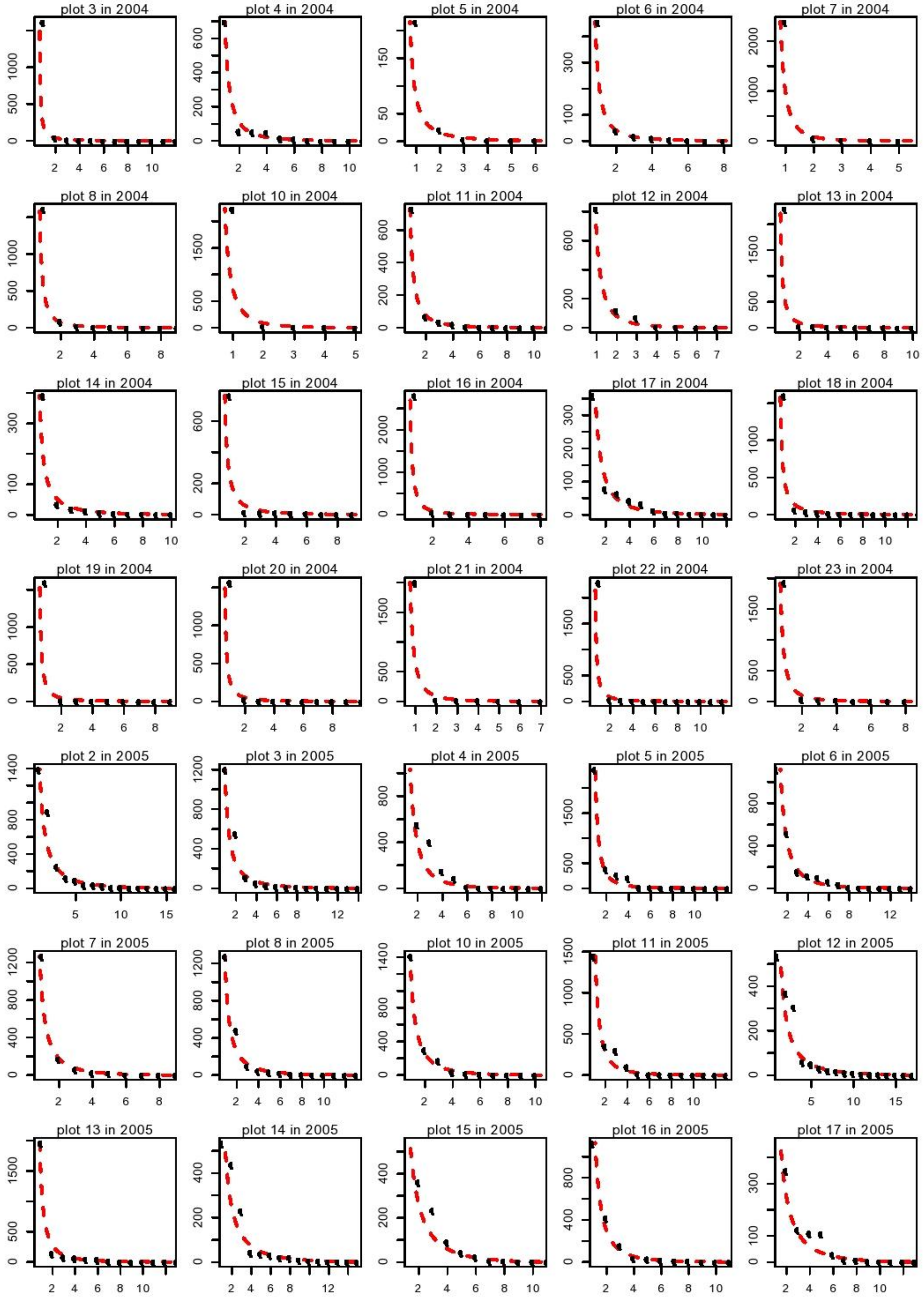
plot 2 in 2004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0 100 300
2 4 6 8
plot 7 in 2004
0 1000 2000
1 2 3 4 5
plot 8 in 2004
0 500 1000
2 4 6 8
plot 10 in 2004
0 500 1500
1 2 3 4 5
plot 11 in 2004
0 200 400 600
2 4 6 8 10
plot 12 in 2004
0 200 600
1 2 3 4 5 6 7
plot 13 in 2004
0 500 1500
2 4 6 8 10
plot 14 in 2004
0 100 300
2 4 6 8 10
plot 15 in 2004
0 200 600
2 4 6 8
plot 16 in 2004
0 1000 2000
2 4 6 8
plot 17 in 2004
0 100 200 300
2 4 6 8 10
plot 18 in 2004
0 500 1000
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plot 19 in 2004
0 500 1000
2 4 6 8
plot 20 in 2004
0 500 1000
2 4 6 8
plot 21 in 2004
0 500 1500
1 2 3 4 5 6 7
plot 22 in 2004
0 500 1500
2 4 6 8 10
plot 23 in 2004
0 500 1500
2 4 6 8
plot 2 in 2005
0 400 800 1400
5 10 15
plot 3 in 2005
0 400 800 1200
2 4 6 8 12
plot 4 in 2005
0 400 800
2 4 6 8 10
plot 5 in 2005
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0 400 800
2 4 6 8 12
plot 7 in 2005
0 400 800 1200
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plot 8 in 2005
0 400 800 1200
2 4 6 8 10
plot 10 in 2005
0 400 800 1400
2 4 6 8 10
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5 10 15
plot 13 in 2005
0 500 1500
2 4 6 8 10
plot 14 in 2005
0 200 400
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0 200 400
2 4 6 8 10
plot 16 in 2005
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2 4 6 8 10
plot 17 in 2005
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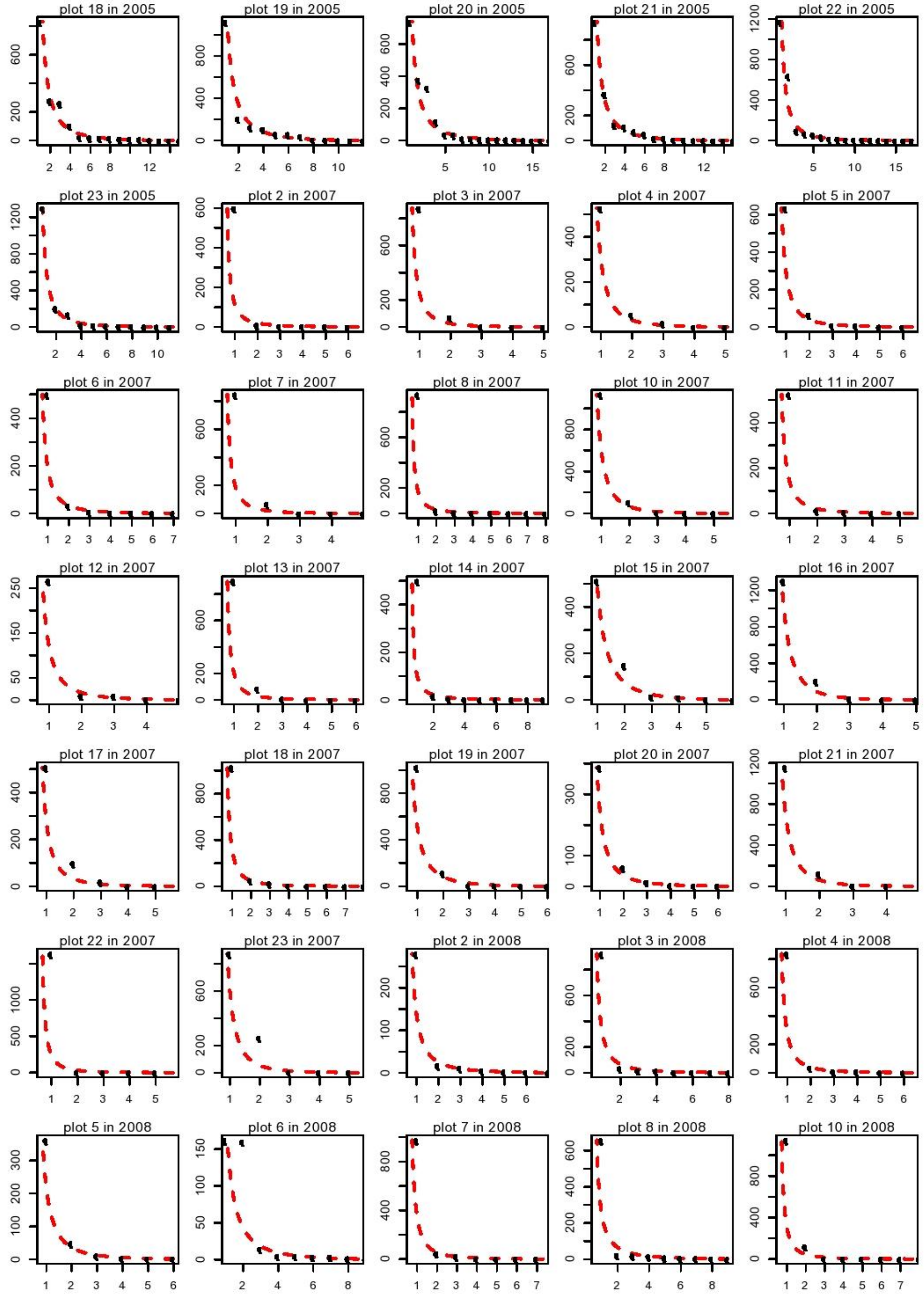
2 4 6 8 10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plot 5 in 2007
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plot 7 in 2007
plot 8 in 2007
plot 10 in 2007
plot 11 in 2007
plot 12 in 2007
plot 13 in 2007
plot 14 in 2007
plot 15 in 2007
plot 16 in 2007
plot 17 in 2007
plot 18 in 2007
plot 19 in 2007
plot 20 in 2007
plot 21 in 2007
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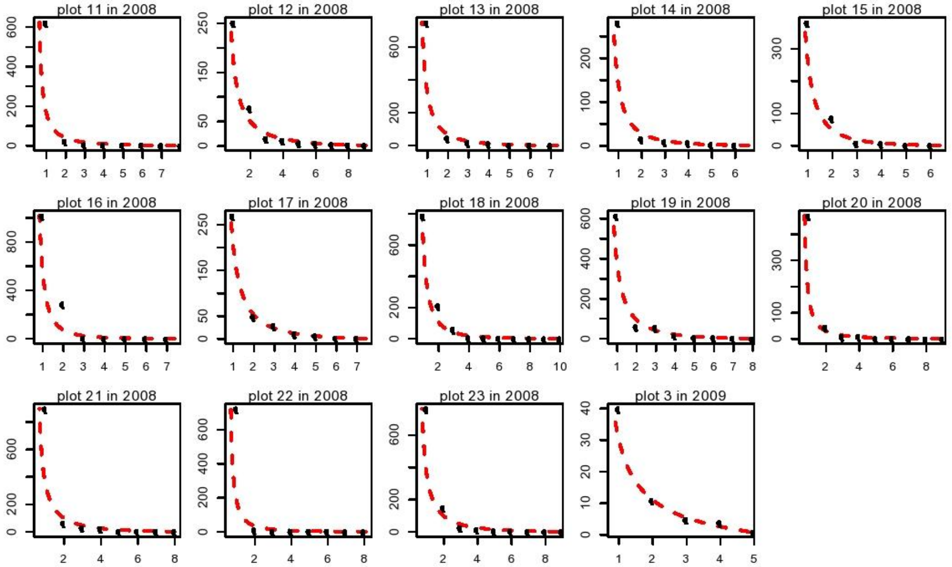
plot 2 in 2008
plot 3 in 2008
plot 4 in 2008
plot 5 in 2008
plot 6 in 2008
plot 7 in 2008
plot 8 in 2008
plot 10 in 2008


plot 11 in 2008
plot 12 in 2008
plot 13 in 2008
plot 14 in 2008
plot 15 in 2008
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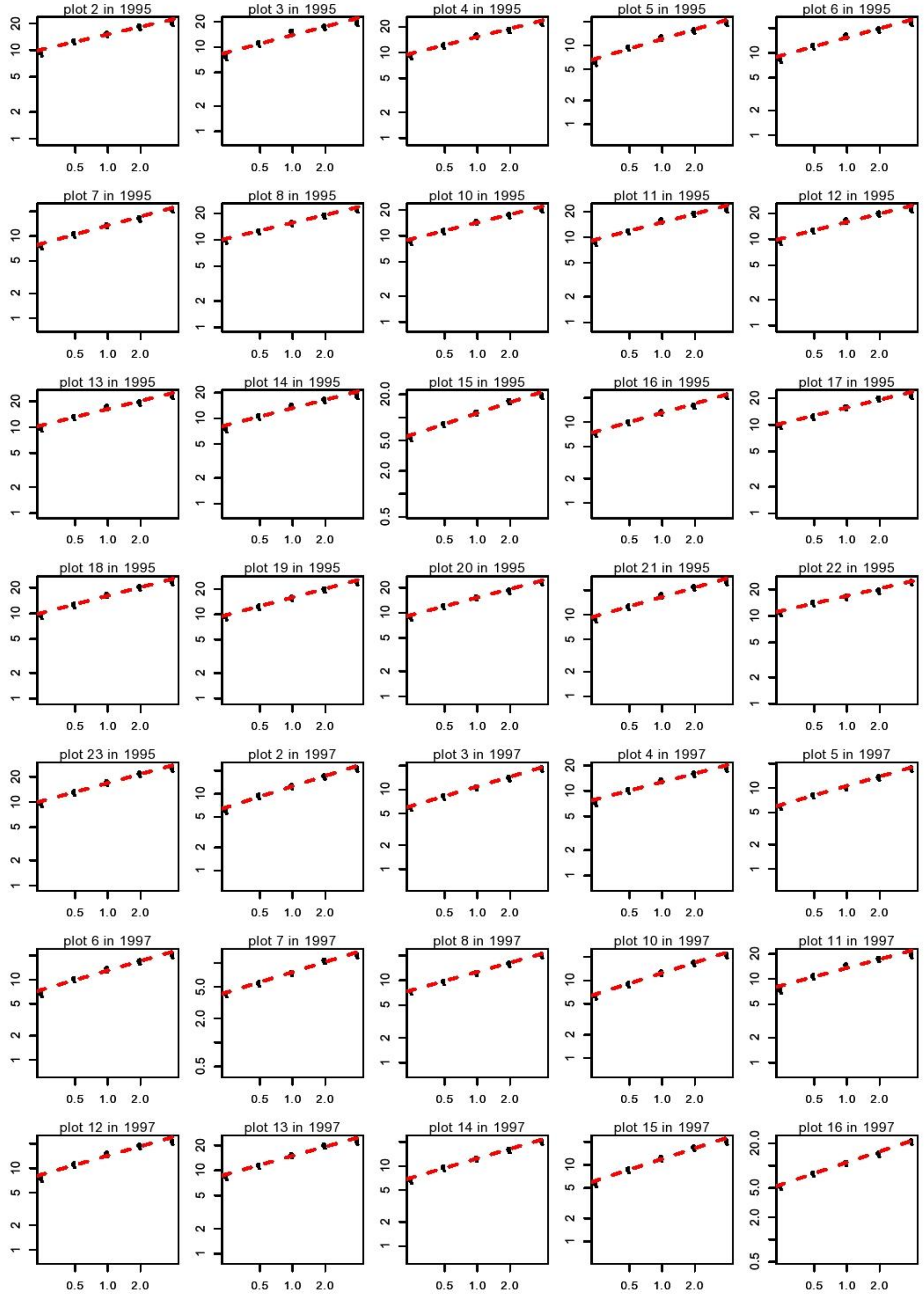
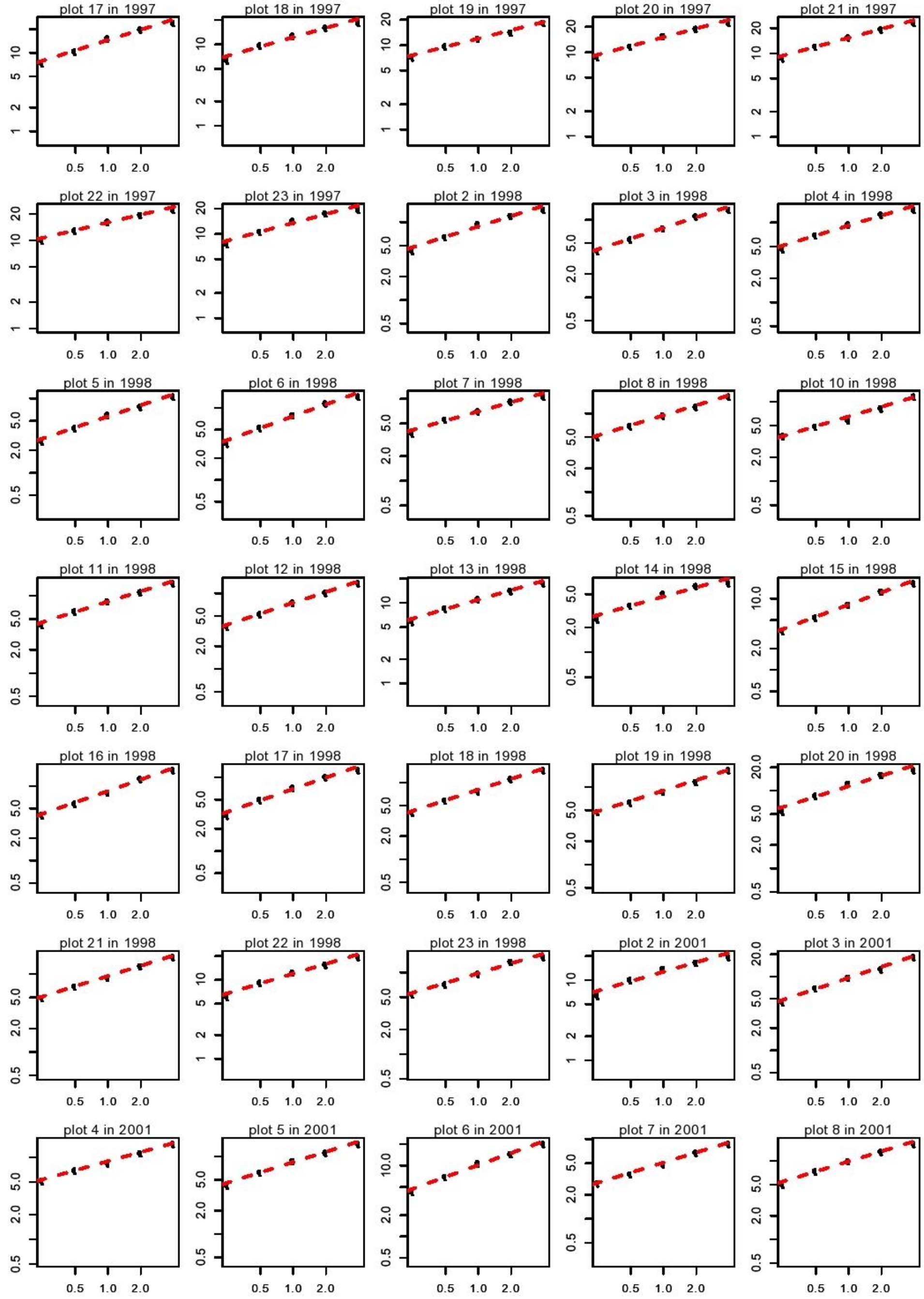
plot 18 in 2008
plot 19 in 2008
plot 20 in 2008
plot 21 in 2008
plot 22 in 2008
plot 23 in 2008
plot 3 in 2009

Winter species-area relationship

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plot 3 in 1998
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plot 11 in 1998
plot 12 in 1998
plot 13 in 1998
plot 14 in 1998
plot 15 in 1998
plot 16 in 1998
plot 17 in 1998
plot 18 in 1998
plot 19 in 1998
plot 20 in 1998
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plot 4 in 2001
plot 5 in 2001
plot 6 in 2001
plot 7 in 2001
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2.0
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2
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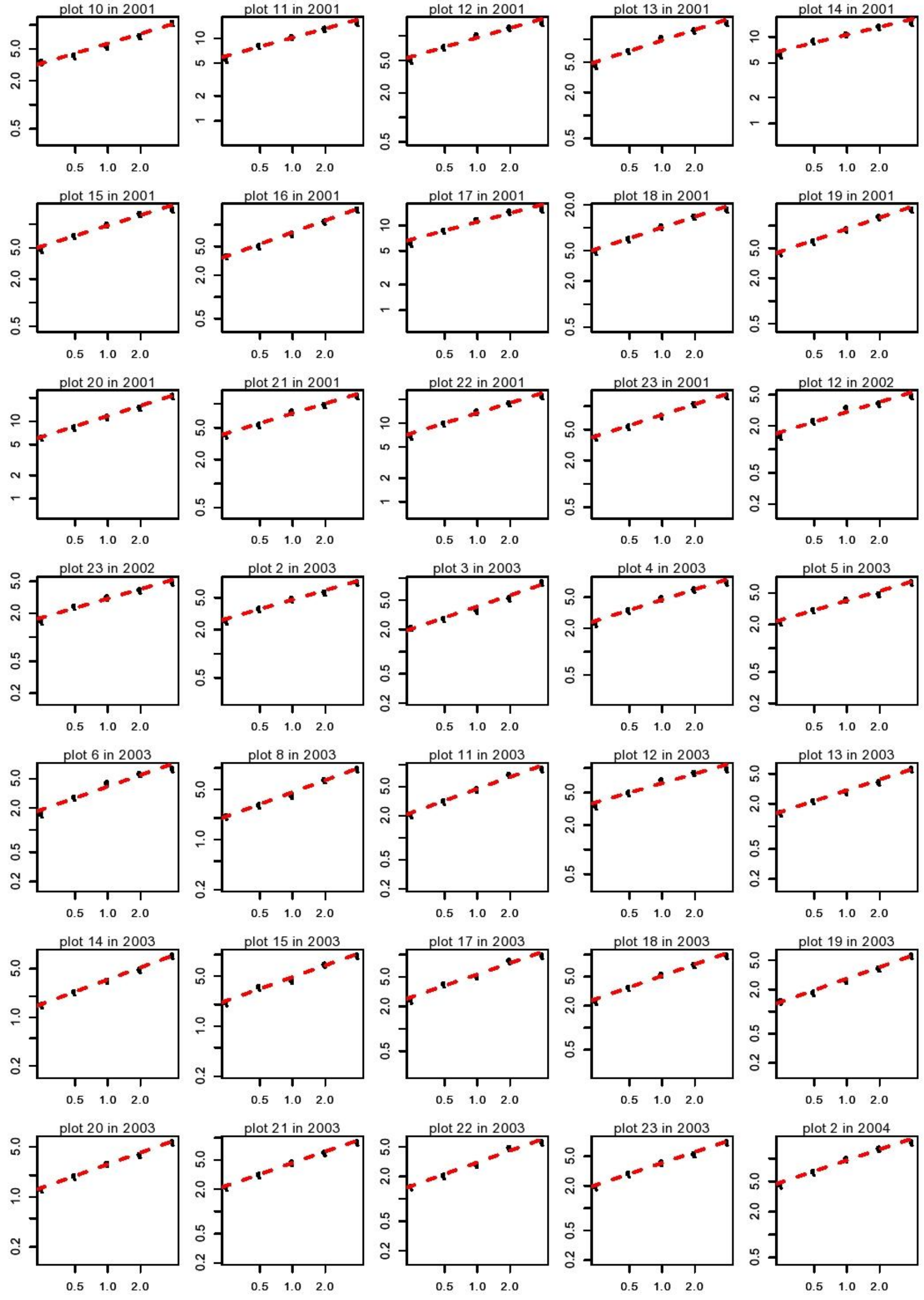
5.0
10.0
20.0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plot 23 in 2001
plot 12 in 2002
plot 23 in 2002
plot 2 in 2003
plot 3 in 2003
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plot 12 in 2003
plot 13 in 2003
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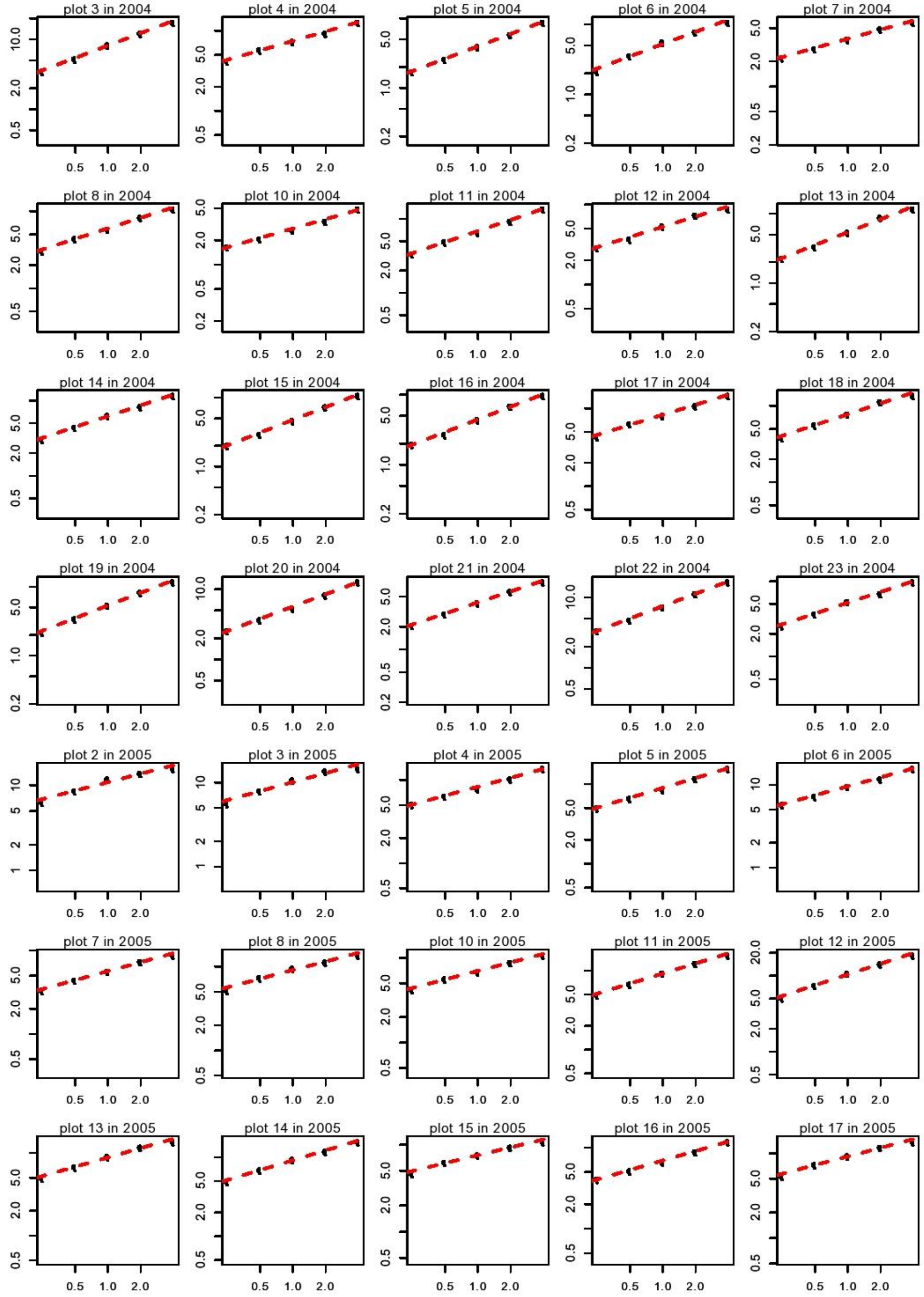
1.0
2.0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plot 5 in 2004
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plot 6 in 2004
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plot 7 in 2004
0.2 0.5 2.0 5.0
plot 8 in 2004
0.5 2.0 5.0
plot 10 in 2004
0.2 0.5 2.0 5.0
plot 11 in 2004
0.5 2.0 5.0
plot 12 in 2004
0.5 2.0 5.0
plot 13 in 2004
0.2 1.0 5.0
plot 14 in 2004
0.5 2.0 5.0
plot 15 in 2004
0.2 1.0 5.0
plot 16 in 2004
0.2 1.0 5.0
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plot 18 in 2004
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plot 19 in 2004
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plot 21 in 2004
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plot 3 in 2005
1 2 5 10
plot 4 in 2005
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plot 5 in 2005
0.5 2.0 5.0
plot 6 in 2005
1 2 5 10
plot 7 in 2005
0.5 2.0 5.0
plot 8 in 2005
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0.5 2.0 5.0
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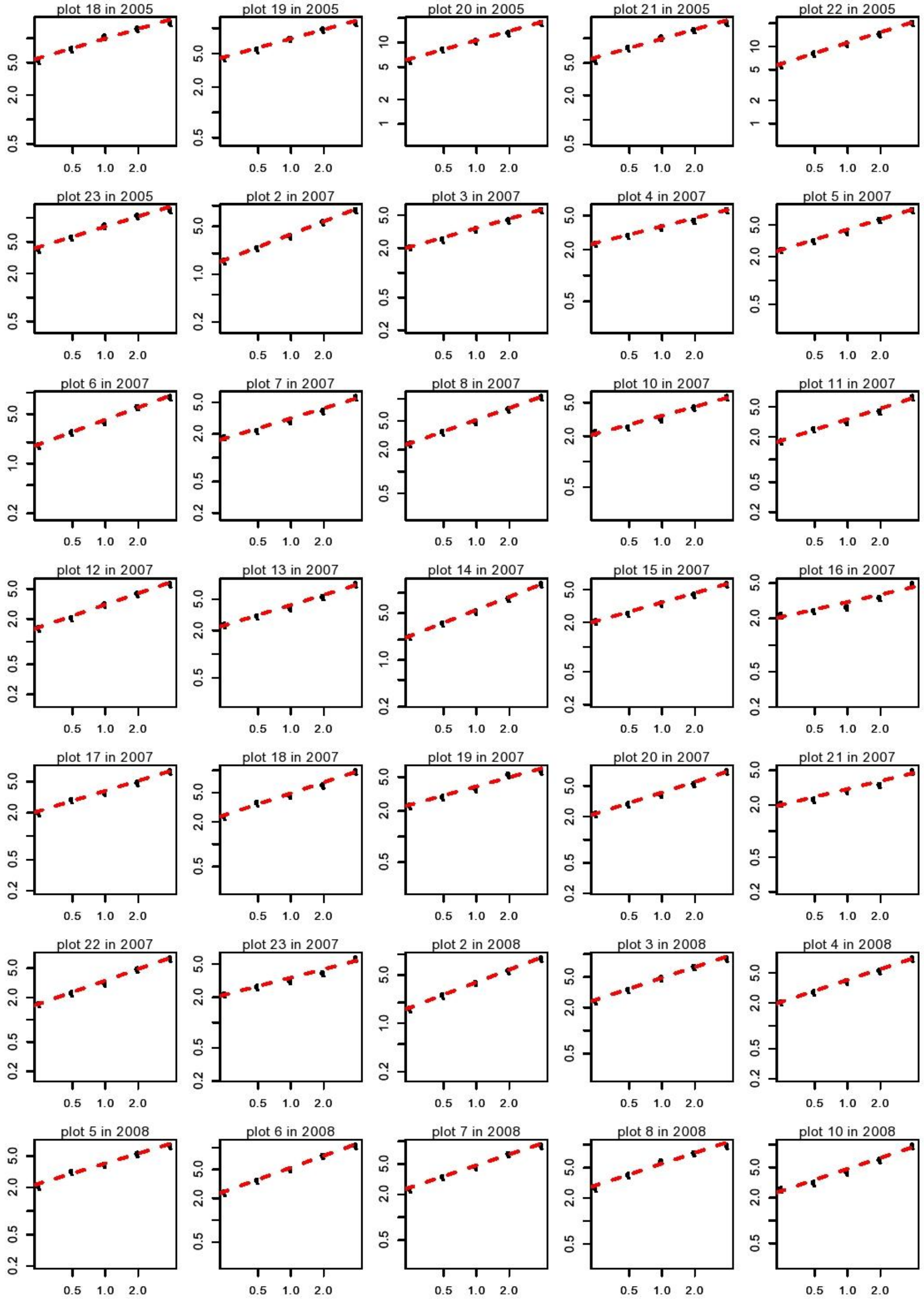
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plot 15 in 2007
plot 16 in 2007
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plot 19 in 2007
plot 20 in 2007
plot 21 in 2007
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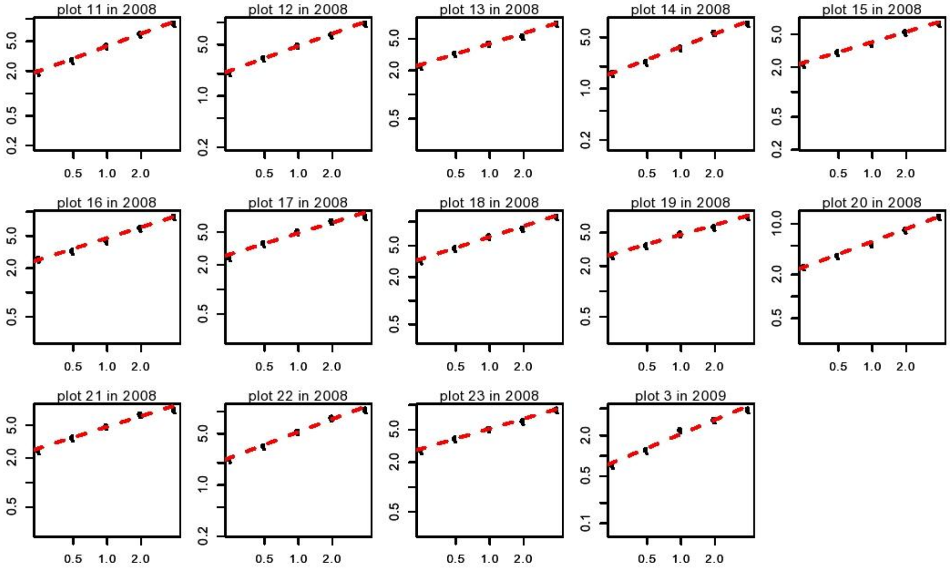
2.0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5.0
plot 14 in 2008
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1.0
5.0
plot 15 in 2008
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0.5
2.0
5.0
plot 16 in 2008
0.5
2.0
5.0
plot 17 in 2008
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2.0
5.0
plot 18 in 2008
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plot 19 in 2008
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2.0
5.0
plot 20 in 2008
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2.0
10.0
plot 21 in 2008
0.5
2.0
5.0
plot 22 in 2008
0.2
1.0
5.0
plot 23 in 2008
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5.0
plot 3 in 2009
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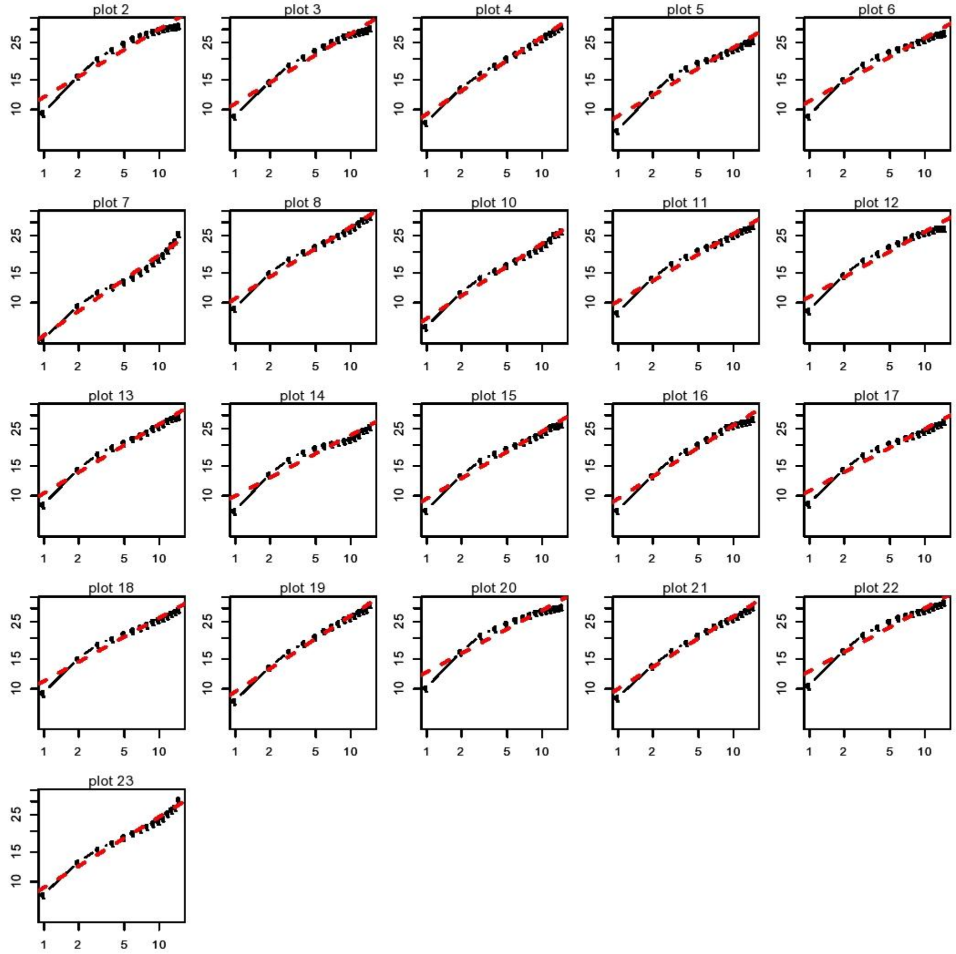
0.5
1.0
2.0

Winter species-time relationship



Appendix C. Details on the methods and results of equivalence testing.

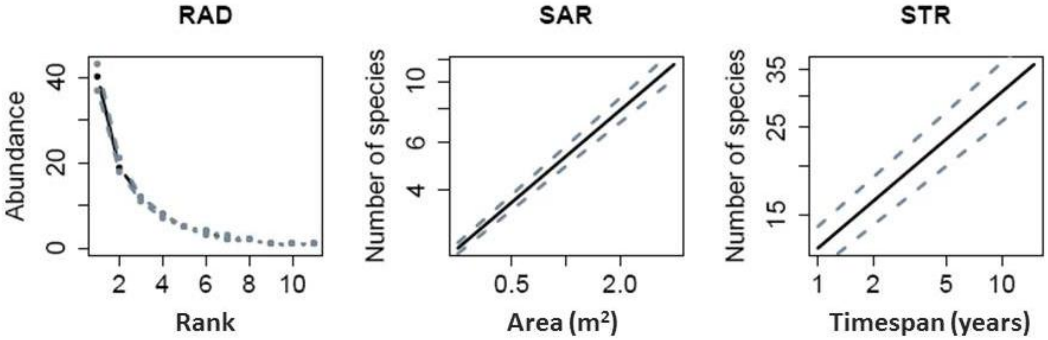
Unlike conventional tests that strive to reject the null hypothesis that two quantities are the same, equivalence tests use the null hypothesis that the difference between two quantities lies outside some pre-specified range. Therefore the rejection of the null implies that the quantities under study are meaningfully similar (Dixon and Pechmann 2005; Camp *et al.* 2008; Dixon and Pechmann 2008).

Equivalence tests are seldom used in ecological studies, and there is no conventional rule determining how the equivalence range should be specified. We made the *ad hoc* decision that the ranges within which the patterns were deemed equivalent were +/- 5% for all responsive variables. In cases where the variables were transformed to fulfill statistical assumptions, the ranges were defined with respect to the untransformed variables (i.e., exp(μ), σ, slopes, and intercepts) for consistency. These ranges translate roughly into 20% deviations in S across scales for SARs and STRs, and 25% deviations in the abundance of the most abundant species for SADs, which we felt represented reasonable fluctuation for claiming equivalence (Fig. B1).

We examined the probability that the difference of the five parameters (SAD exp(μ) and σ, SAR slope and intercept, STR slope) between treatments fell within the specified equivalence range using liner mixed effects models (Bates *et al.* 2011) for SADs and SARs and ANOVAs for STRs. For linear mixed models, this is achieved by generating 10 000 samples from the posterior distribution of the estimated parameters of the fitted model using “pvals.fnc” (languageR; Baayen 2010) and calculating the proportion of the samples where the difference of parameter estimates falls within the equivalence range. For ANOVAs, this is achieved by directly calculating the probability of the difference falling within the equivalence range using the *t*-distribution.

We based our definition of similarity on our knowledge of this system (+/- 5% of a given response variable). However, tests of how sensitive our results were to our *ad hoc* definition of similarity showed that some equivalence tests were sensitive to relatively small changes in this value. For both the STR and the SAR, an increase in the definition of similarity to +/- 12% resulted in most patterns being statistically similar across treatments when species richness and total abundance do not change. In contrast, the results for the SAD were robust up to a +/- 40% definition of similarity.

Figure C-1. Visual depiction of equivalence test ranges. We deemed ranges within patterns equivalent +/- 5% for all response variables. These ranges translate to roughly 25% deviation in the abundance of the most abundant species for SADs (left) and a 20% deviation in species richness for SARs and STRs at all scales (middle, right), which we felt represented reasonable fluctuation for claiming equivalence.



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Camp, R. J., N. E. Seavy, P. M. Gorresen, and M. H. Reynolds. 2008. A statistical test to show negligible trend: Comment. Ecology 89: 1469-1472.

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

Dixon, P. M. and J. H. K. Pechmann. 2008. A statistical test to show negligible trend: Reply. Ecology 89: 1473.

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.

Original Variable Summer	**Transformed Variable Summer**	**Original Variable Winter**	**Transformed Variable Winter**
Species richness (S)	S	Species richness (S)	$S^{0.75}$
Total abundance (N)	$N^{1/3}$	Total abundance (N)	$N^{1/3}$
SAD geometric mean exp(μ)	$\exp(\mu)^{0.5}$	SAD geometric mean exp(μ)	$\exp(\mu)^{0.3}$
SAD standard deviation σ	$\sigma^{0.3}$	SAD standard deviation σ	$\sigma^{0.1}$
SAR slope	slope	SAR slope	slope
SAR intercept	$(\text{intercept})^{2.5}$	SAR intercept	$(\text{intercept})^{2}$
STR slope	slope	STR slope	slope

TABLE D-1. Transformation applied to each variable to ensure the normality and homoscedasticity of the residuals in regression analyses.

Parameters	**Control – kangaroo rat removals**	**Control –total rodent removals**	**Kangaroo rat removals – total rodent removals**
Species richness	0.981	**0.0012**	**0.0013**
Total abundance	0.2541	**0.0138**	0.152
SAD exp(μ)	0.7826	0.1645	0.2475
SAD σ	0.1804	**0.0004**	**0.0094**
SAR slope	0.437	0.9083	0.3999
SAR intercept	0.4094	**0.0002**	**0.0024**
STR slope	0.6869	**0.0294***	0.0601

TABLE D-2. Paired comparisons among treatments in the winter annual community. Bold indicates significance at α=0.05, * indicates the value was no longer significant after controlling for false discovery rate within the seasonal community.

Parameters	**Control – kangaroo rat removals**	**Control –total rodent removals**	**Kangaroo rat removals – total rodent removals**
Species richness	0.7532	0.1653	0.2675
Total abundance	0.734	0.3095	0.4745
SAD exp(μ)	0.7243	0.2006	0.1091
SAD σ	0.6853	0.4862	0.7298
SAR slope	0.9324	0.4385	0.3949
SAR intercept	0.4102	0.3374	0.811
STR slope	0.6006	0.5929	0.3251

TABLE D-3. Paired comparisons among treatments in the summer annual community. No comparison was statistically significant ($\alpha>0.05$ in all cases).

Parameters	**Control – kangaroo rat removals**	**Control –total rodent removals**	**Kangaroo rat removals – total rodent removals**
SAD exp(μ)	0.1771	0.0661	0.0861
SAD σ	0.7587	0.021	0.2483
SAR slope	0.6025	0.7571	0.5471
SAR intercept	0.8964	0.0124	0.0828
STR slope	0.7819	0.1302	0.2155

TABLE D-4. Paired equivalence testing results comparing treatments in the winter annual community. No test was statistically significant (α>0.05 in all cases).

Parameters	**Control – kangaroo rat removals**	**Control –total rodent removals**	**Kangaroo rat removals – total rodent removals**
SAD exp(μ)	0.2751	0.1356	0.0943
SAD σ	0.8536	0.7149	0.8068
SAR slope	0.6985	0.4706	0.4426
SAR intercept	0.8819	0.7871	**0.9377***
STR slope	0.6722	0.6065	0.4690

TABLE D-5. Paired equivalence testing results comparing treatments in the summer annual community. Bold indicates significance at α=0.05, * indicates the value was no longer significant after controlling for false discovery rate within the seasonal community.

Appendix E: Supplemental material on the data and code used

Sarah R. Supp, Xiao Xiao, S. K. Morgan Ernest, and Ethan P. White. 2012. An experimental test of the response of macroecological patterns to altered species interactions. doi:10.1890/12-0370.1

Supplement

The R source code to conduct the analyses and produce the figures within the paper, including the raw data.

Authors

Sarah R. Supp
Department of Biology and the Ecology Center
Utah State University
5305 Old Main Hill
Logan, UT 84322 USA
Email: sarah.supp@usu.edu

Xiao Xiao
Department of Biology and the Ecology Center
Utah State University
5305 Old Main Hill
Logan, UT 84322 USA
Email: xiao.xiao@usu.edu

S. K. Morgan Ernest
Department of Biology and the Ecology Center
Utah State University
5305 Old Main Hill
Logan, UT 84322 USA
Email: morgan.ernest@usu.edu

Ethan P. White
Department of Biology and the Ecology Center
Utah State University
5305 Old Main Hill
Logan, UT 84322 USA
Email: ethan@weecology.org

File list

`PortalPlants_ms12-0370R2.R`

R script that cleans the data of errors, constructs the macroecological patterns, pulls out descriptive parameters of these patterns, runs the statistical analyses, and outputs figures.

`PortalPlants_fxns.R`
R script that holds the relevant functions for executing the PortalPlants_ms12-0370R2.R script.

`PortalSummerAnnuals_1995_2009.csv`
Data file containing raw summer annual plant community abundance data for years 1995-2009.

`PortalWinterAnnuals_1995_2009.csv`
Data file containing raw winter annual plant community abundance data for years 1995-2009.

Description
The code and data in this supplement allow for the analyses and figures in the paper to be fully replicated using a subset of the published Portal dataset which includes annual plant data from 1995-2009.

Requirements: R 2.x and the following packages: Biodiversity R, car, CCA, equivalence, gplots, graphics, languageR, lme4, nlme, plotrix, poilog, vegan, VGAM and the file containing functions specific to this code, PortalPlants_fxns.R.

The analyses can then be replicated by changing the working directory at the top of the file `PortalPlants_ms12-0370R2.R` to the location on your computer where you have stored the `.R` and `.csv` files and running the code.

Please note that the pvalues generated for Appendix D in the published paper were generated using R 2.12.2. Because of approximations, the values for SAD sigma and mu may differ slightly (around the 10th decimal place) from Appendix D, Tables S2 and S3. Because the equivalence testing also uses approximations, there may be very small differences in the exact values generated compared to Appendix D, tables S4 and S5.

It should take approximately 30 minutes to run all the code from start to finish. Figures should output as pdfs in your working directory.

Version Control Repository: The full version control repository for this project (including post-publication improvements) is publicly available at https://github.com/weecology/portal-experimental-macroeco. If you would like to use the code in this Supplement for your own analyses it is strongly suggested that you use the equivalent code in the repositories as this is the code that is being actively maintained.

Data use: Data is provided in this supplement for the purposes of replication. If you wish to use the data for additional research, they should be obtained from the published source (Ecological Archives E090-118-D1; S. K. Morgan Ernest, Thomas J. Valone, and James H. Brown. 2009. Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. Ecology 90:1708. doi:10.1890/08-1222.1)

Software License:
This code is available under a BSD 2-Clause License.

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Appendix F: Metadata and data for the communities included in the analysis.

CLASS I. DATA SET DESCRIPTORS

A. **Dataset identity:** Species composition and abundance of manipulated animal communities compiled from published literature.

B. **Dataset identification code:**

Suggested Data Set Identify Code: Manipulated Animal Community Database (MACD)

C. **Dataset description:**

6,698 records indicated the presence and abundance of animal species, including representatives across trophic groups and size classes documented at 254 sites throughout the world, encompassing a variety of habitats.

D. **Keywords:** abundance, community, community structure, composition, experiment, manipulation, environmental change

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. **Overall project description**

Identity: Species composition and abundance of manipulated animal communities compiled from published sources.

Originators: Sarah R. Supp and S. K. Morgan Ernest

Period of Study: Data compiled in this project were published from 1982 – 2010. The authors intend to continue adding to the database, and encourage others to contribute their data and/or recommendations for additional sources to this effort.

Objectives: To provide data for macroecological analyses of experimental/manipulated community assembly and structure

Taxonomy: Taxonomy follows that reported in each published paper.

Sources of Funding: Utah State Ecology Center Fellowship and Utah State School of Graduate Studies Fellowship

CLASS III. DATA SET STATUS AND ACCESSBILITY

A. **Status**

Latest update: 29 January 2013 for the final format of all files

Latest Archive date: January 2013

Metadata status: The metadata are complete and up to date.

Data verification: Data quality has been carefully checked as described in class V, section B, below.

B. **Accessibility**

Storage location and medium: Copies of the latest version of the data file are being stored on the principal investigator's personal computer, Dropbox, and on GitHub (https://github.com/weecology/experimental-rads.git) in Microsoft Excel, Text, and CSV formats

Contact person: Sarah R. Supp, Department of Biology and the Ecology Center, Utah State University, Logan, UT, 84322-5305; sarah@weecology.org
Copyright restrictions: None.
Proprietary restrictions: None.
Costs: None.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

REFERENCE DATA

A. Data Set File

Identity: ref_data_analysis.csv
Size: 47 records, not including header row, 12,774 bytes.
Format and storage mode: ASCII text, comma delimited
Header information: The first row of the file contains the variable names. See section B below for detailed descriptions of the column contents
Alphanumeric attributes: Mixed.
Special characters/fields: If no information is available for a given record, this is indicated by NULL.
Authentication procedures:

A. Variable information

Variable name	Variable definition	Storage type	Missing value codes
referenceID	Unique identifier for each reference; links to sites and references tables	Character	N/A
reference_source	Search engine and keywords used to locate the reference	Character	NULL
authors	Names of authors, in the order given	Character	N/A
year	Year of publication, if published, otherwise null	Integer	NULL
title	Title of publication, if published, otherwise “unpublished”	Character	N/A
source	Journal, government agency, book, or university that published the reference, if published	Character	NULL

vol	Volume number of source, if applicable	Integer	NULL
first_page	First page number	Integer	NULL
last_page	Last page number	Integer	NULL
num_sites	Total number of sites in reference for which data are included	Integer	N/A
num_manips	Total number of unique experiments/manipulations in the reference for which data are included	Integer	N/A

SITES DATA

B. Data Set File

Identity: sites_data_analysis.csv
Size: 253 records, not including header row, 42,011 bytes.
Format and storage mode: ASCII text, comma delimited
Header information: The first row of the file contains the variable names. See section B below for detailed descriptions of the column contents
Alphanumeric attributes: Mixed.
Special characters/fields: If no information is available for a given record, this is indicated by NULL.
Authentication procedures:

C. Variable information

Variable name	Variable definition	Units	Storage type	Variable codes and definitions	Missing value codes
referenceID	Unique identifier for each reference; links to sites and references tables	N/A	Character	N/A	N/A
siteID	Unique numeric	N/A	Integer	N/A	N/A

	code for each site; links to sites and experiments tables				
country	Country in which site is located	N/A	Character	Full names used except for the United States (USA)	NULL
state	State/province where the site is located	N/A	Character	Full names used except for the United States (USA), for which standard state abbreviations are used	NULL
location_details	Details of site location and names given in the original paper	N/A	Character	N/A	N/A
latitude	Latitude where the site is	Decimal degrees,	Fixed point	N/A	NULL

	located	WGS84			
longitude	Longitude where the site is located	Decimal degrees, WGS84	Fixed point	N/A	NULL
uncertainty_radius	The approximate radius of uncertainty for the given coordinates	kilometers	Integer	N/A	NULL
elevation_min	The minimum, or estimated minimum, elevation of the study area	meters	Integer	N/A	NULL
elevation_max	The maximum, or estimated maximum, elevation of the study area	meters	Integer	N/A	NULL
spatial_extent	Approximate spatial extent of the trapping grids/transects/w	square meters	Integer	N/A	NULL

	ebs				
first_year	The first year of data collection	N/A	Integer	N/A	NULL
end_year	The final year of data collection	N/A	Integer	N/A	NULL
notes	Miscellaneous notes about the site data	N/A	Character	N/A	NULL

EXPERIMENTS DATA

A. Data Set File

Identity: experiments_data_analysis.csv
Size: 253 records, not including header row, 30,057 bytes.
Format and storage mode: ASCII text, comma delimited
Header information: The first row of the file contains the variable names. See section B below for detailed descriptions of the column contents
Alphanumeric attributes: Mixed.
Special characters/fields: If no information is available for a given record, this is indicated by NULL.
Authentication procedures:

B. Variable information

Variable name	Variable definition	Units	Storage type	Variable codes and definitions	Missing value codes
referenceID	Unique identifier for each reference; links to sites and references tables	N/A	Character	N/A	N/A
siteID	Unique numeric	N/A	Integer	N/A	N/A

	code for each site; links to sites and experiments tables				
experiment	Indicates the type of treatment the data represents	N/A	Integer	0 = control/unmanipulated; 1 = artificial manipulation; 2 = ‘natural’ or human-mediated manipulation	N/A
experiment_type	Indicates the category of manipulation	N/A	Character	N/A	N/A
experiment_description	Brief description of the experiment or manipulation on the community	N/A	Character	N/A	N/A
replicates	Indicates the	N/A	Integer	N/A	NULL

	number of replicates aggregated or averaged over in the abundance data for the community table				
taxa	Indicates the taxonomic group represented by the data	N/A	Character	N/A	N/A
biome	Indicates if the study is terrestrial or aquatic	N/A	Integer	0 = aquatic; 1 = terrestrial	N/A
habitat	Brief description of general habitat category	N/A	Character	N/A	N/A
raw_abundance	Indicates data type	N/A	Integer	0 = not raw abundance, 1 = raw abundance given	N/A
mean_abundance	Indicates data type	N/A	Integer	0 = not mean	N/A

				abundance, 1 = meaned abundance given	

COMMUNITY DATA

A. Data Set File

Identity: community_data_analysis.csv
Size: 5,990 records, not including header row, 325,430 bytes.
Format and storage mode: ASCII text, comma delimited
Header information: The first row of the file contains the variable names. See section B below for detailed descriptions of the column contents
Alphanumeric attributes: Mixed.
Special characters/fields: If no information is available for a given record, this is indicated by NULL.
Authentication procedures:

B. Variable information

Variable name	Variable definition	Units	Storage type	Variable codes and definitions	Missing value codes
referenceID	Unique identifier for each reference; links to sites and references tables	N/A	Character	N/A	N/A
siteID	Unique numeric code for each site; links to sites and experiments tables	N/A	Integer	N/A	N/A
initial_year	Initial year of sampling for the	N/A	Integer	N/A	NULL

	associated data; some sites may have several years of data presented in aggregate				
family	Family to which the species listed belongs	N/A	Character	N/A	NULL
genus	Genus to which the species listed belongs	N/A	Character	N/A	N/A
species	Specific epithet	N/A	Character	N/A	N/A
id2species	Indicates whether the taxon has been identified to the species level	N/A	Integer	0 = not identified to species; 1 = identified to species; 2 = identified to species pair or morphospecies (i.e., either of two possible species, or c.f.)	N/A
abundance	Abundance data	N/A	Fixed point	N/A	NULL

COMPARISON DATA

A. **Data Set File**

Identity: comparison_analysis_data.csv
Size: 155 records, not including header row, 3,143 bytes.
Format and storage mode: ASCII text, comma delimited
Header information: The first row of the file contains the variable names. See section B below for detailed descriptions of the column contents
Alphanumeric attributes: Mixed.
Special characters/fields: If no information is available for a given record, this is indicated by NULL.
Authentication procedures:

B. **Variable information**

Variable name	Variable definition	Storage type	Missing value codes
reference	Unique identifier for each reference; links to sites and references tables	Character	N/A
control_site	Unique numeric code for site; represents the control or unmanipulated community; links to community table	Integer	N/A
comparison_site	Unique numeric code for site; represents an experimental or manipulated site to be compared to the control site; links to community table	Integer	N/A

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data Acquisition

The published literature was searched using the databases and keywords listed in the following table:

Database	Keywords	Access
Google Scholar	spider, community, experiment	Online; accessed 12/2011 – 3/2012
Google Scholar	butterfly, community data, experiment	Online; accessed 12/2011 – 3/2012
Google Scholar	butterfly, burn*, community	Online; accessed 12/2011 – 3/2012
Google Scholar	carabid*, community, experiment	Online; accessed 12/2011 – 3/2012

Google Scholar	grasshopper, community, experiment	Online; accessed 12/2011 – 3/2012
Google Scholar	lizard, experiment, community	Online; accessed 12/2011 – 3/2012
Google Scholar	lizard, burn, community	Online; accessed 12/2011 – 3/2012
Google Scholar	bird, experiment, communit*	Online; accessed 12/2011 – 3/2012
Google Scholar	mammal, experiment*, communit*	Online; accessed 12/2011 – 3/2012

B. Quality assurance/quality control procedures:
Each record was entered by the author, and then carefully double-checked against the original reference at a later date.

C. Related material: N/A

D. Computer programs and data processing algorithms: N/A

E. Archiving: Data files and metadata have been archived and are under version control on GitHub (https://github.com/weecology/experimental-rads.git)

F. Literature Cited: Contained in the references table

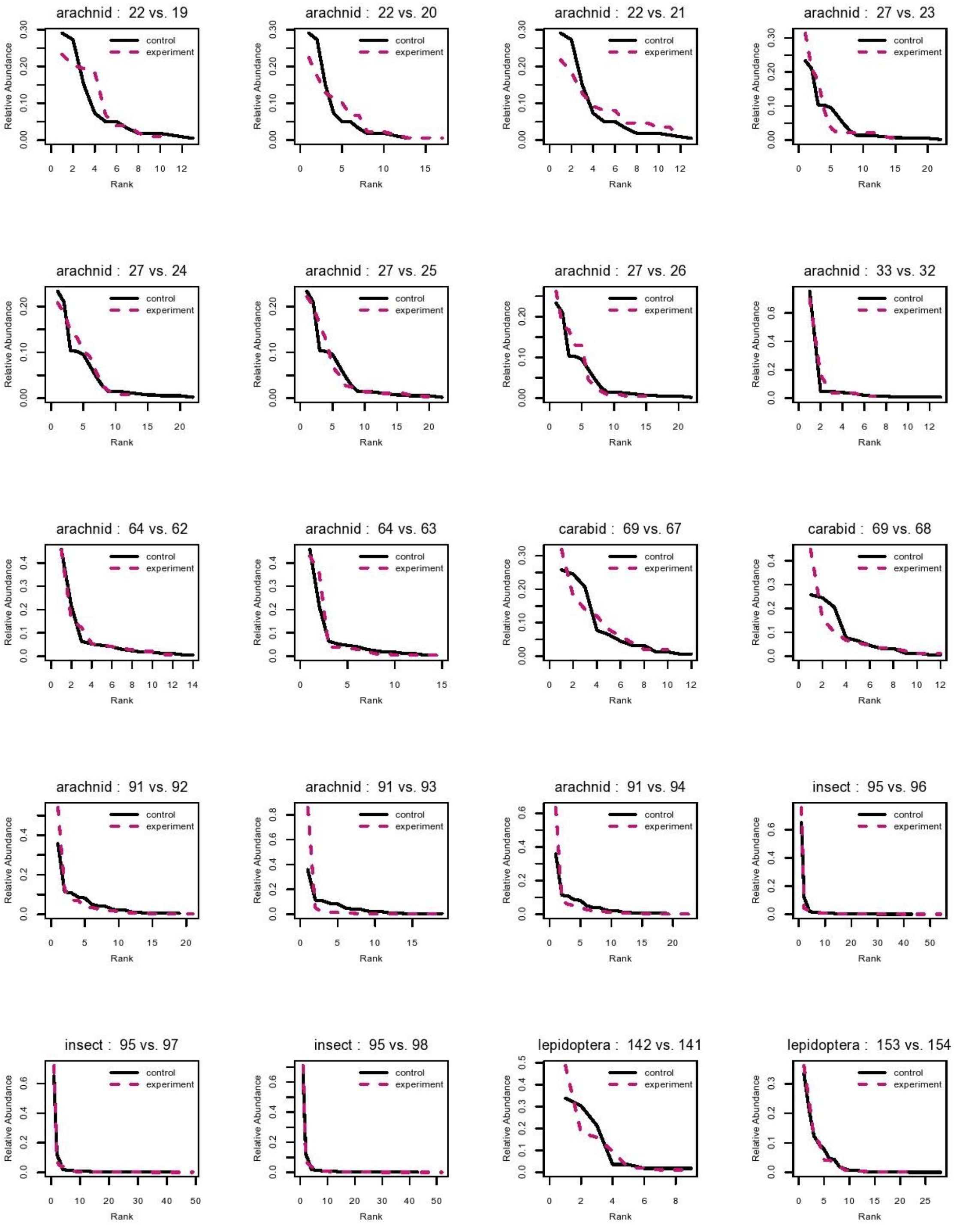
G. History of data set usage:
Data set update history: N/A
Review history: N/A
Questions and comments from secondary users: N/A

ACKNOWLEDGEMENTS

We thank all of the investigators who collected and published these data. Sarah Supp was supported by the Utah State University Graduate Studies Dissertation Fellowship and by the Utah State Ecology Center Fellowship.

Appendix G. Figures for all the paired community data represented as species abundance distributions.

Each plot is labeled with the taxonomic group, control and experimental site identification number (in that order). Black solid lines represent the control/unmanipulated site and pink dashed lines represent the experimental/manipulated site. SADs are plotted as rank-abundance distributions (RADs) for visual ease. The x-axis is rank and the y-axis is relative abundance. (Below) Panel G-1 Panel of paired community data represented as rank abundance distributions.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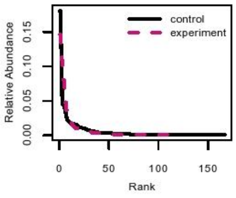
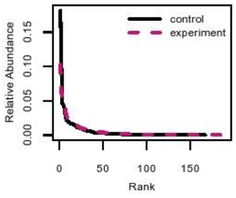
arachnid : 22 vs. 20
arachnid : 22 vs. 21
arachnid : 27 vs. 23
arachnid : 27 vs. 24
arachnid : 27 vs. 25
arachnid : 27 vs. 26
arachnid : 33 vs. 32
arachnid : 64 vs. 62
arachnid : 64 vs. 63
carabid : 69 vs. 67
carabid : 69 vs. 68
arachnid : 91 vs. 92
arachnid : 91 vs. 93
arachnid : 91 vs. 94
insect : 95 vs. 96
insect : 95 vs. 97
insect : 95 vs. 98
lepidoptera : 142 vs. 141
lepidoptera : 153 vs. 154
control
experiment
Relative Abundance
Rank

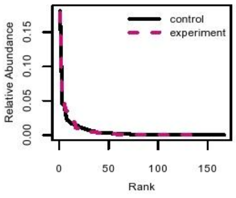
lepidoptera : 164 vs. 165



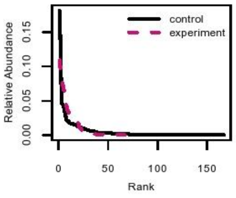
lepidoptera : 164 vs. 166



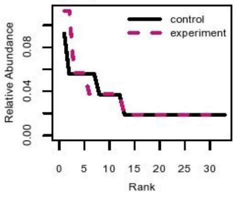
lepidoptera : 164 vs. 167



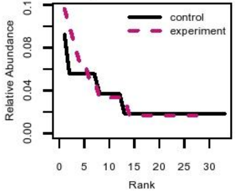
lepidoptera : 164 vs. 169



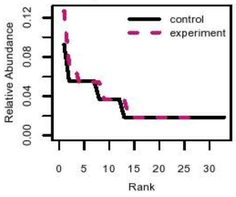
lepidoptera : 178 vs. 179



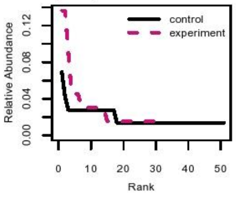
lepidoptera : 178 vs. 177



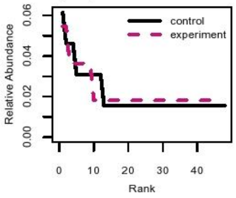
lepidoptera : 178 vs. 180



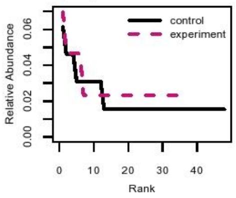
lepidoptera : 182 vs. 181



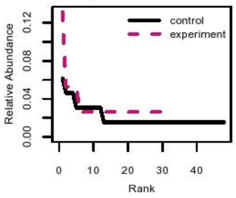
lepidoptera : 185 vs. 184



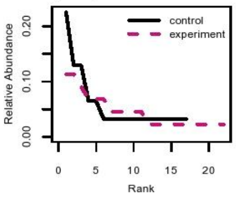
lepidoptera : 185 vs. 186



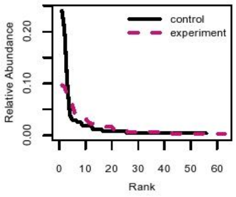
lepidoptera : 185 vs. 187



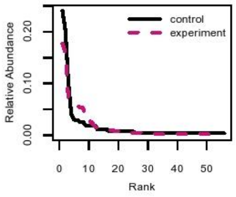
lepidoptera : 189 vs. 188



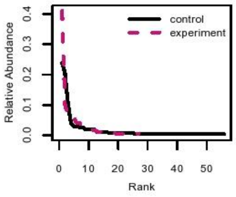
lepidoptera : 190 vs. 191



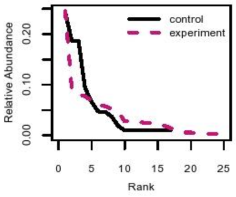
lepidoptera : 190 vs. 192



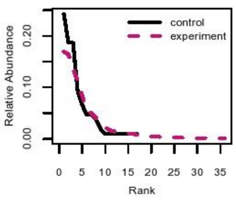
lepidoptera : 190 vs. 193



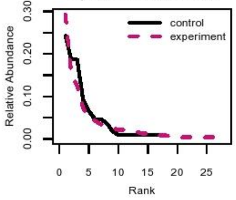
reptile : 225 vs. 226



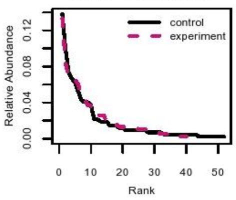
reptile : 225 vs. 227



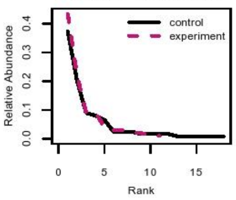
reptile : 225 vs. 230

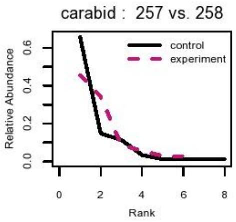


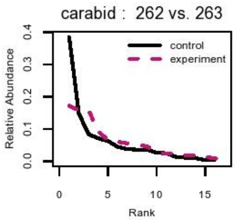
bird : 236 vs. 235



carabid : 252 vs. 253




carabid : 257 vs. 258
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
2
4
6
8
Rank


carabid : 262 vs. 263
control
experiment
Relative Abundance
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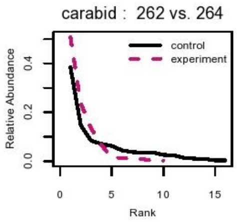
0.2
0.3
0.4
0
5
10
15
Rank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control
experiment
Relative Abundance
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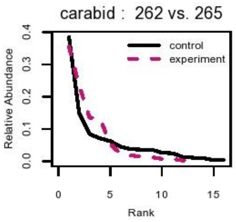
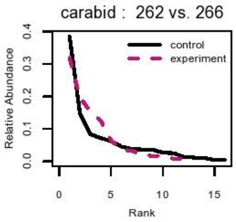
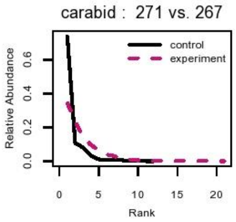
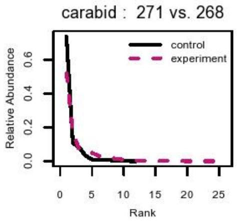
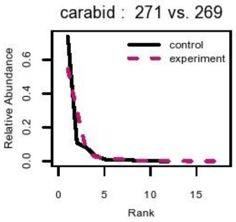
0.2
0.4
0
5
10
15
Rank

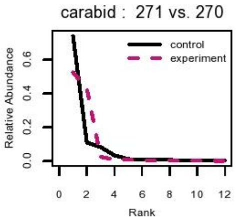

carabid : 262 vs. 265
control
experiment
Relative Abundance
0.0
0.1
0.2
0.3
0.4
0
5
10
15
Rank

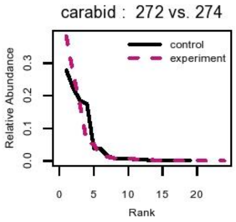

carabid : 262 vs. 266
control
experiment
Relative Abundance
0.0
0.1
0.2
0.3
0.4
0
5
10
15
Rank

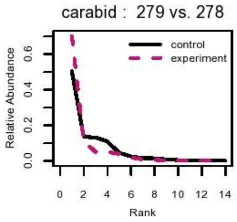

carabid : 271 vs. 267
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
5
10
15
20
Rank

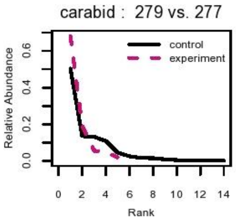

carabid : 271 vs. 268
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
5
10
15
20
25
Rank

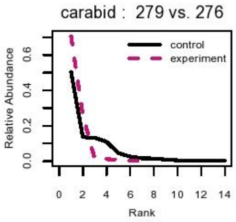

carabid : 271 vs. 269
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
5
10
15
Rank

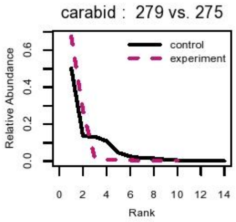

carabid : 271 vs. 270
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
2
4
6
8
10
12
Rank

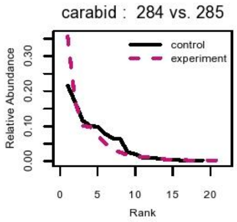

carabid : 272 vs. 274
control
experiment
Relative Abundance
0.0
0.1
0.2
0.3
0
5
10
15
20
Rank

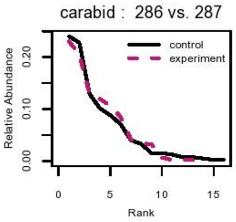

carabid : 279 vs. 278
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
2
4
6
8
10
12
14
Rank

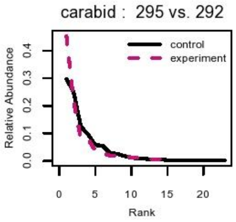

carabid : 279 vs. 277
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
2
4
6
8
10
12
14
Rank

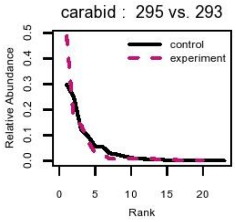

carabid : 279 vs. 276
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
2
4
6
8
10
12
14
Rank

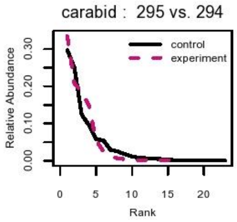

carabid : 279 vs. 275
control
experiment
Relative Abundance
0.0
0.2
0.4
0.6
0
2
4
6
8
10
12
14
Rank

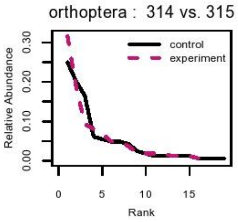

carabid : 284 vs. 285
control
experiment
Relative Abundance
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0
5
10
15
20
Rank


carabid : 286 vs. 287
control
experiment
Relative Abundance
0.00
0.10
0.20
0
5
10
15
Rank

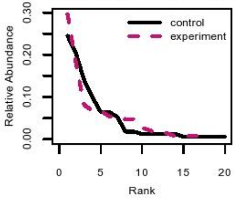

carabid : 295 vs. 292
control
experiment
Relative Abundance
0.0
0.1
0.2
0.3
0.4
0
5
10
15
20
Rank


carabid : 295 vs. 293
control
experiment
Relative Abundance
0.0
0.1
0.2
0.3
0.4
0.5
0
5
10
15
20
Rank

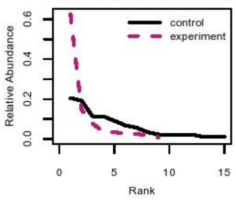

carabid : 295 vs. 294
control
experiment
Relative Abundance
0.00
0.10
0.20
0.30
0
5
10
15
20
Rank


orthoptera : 314 vs. 315
control
experiment
Relative Abundance
0.00
0.10
0.20
0.30
0
5
10
15
Rank

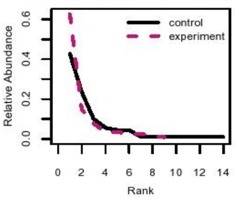
orthoptera : 316 vs. 317



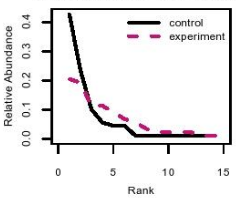
herpetofauna : 363 vs. 364



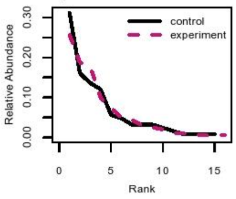
herpetofauna : 365 vs. 364



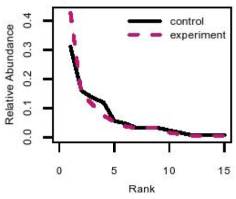
herpetofauna : 365 vs. 363



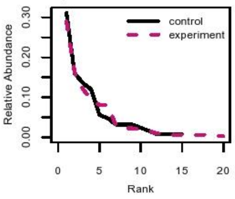
herpetofauna : 401 vs. 398



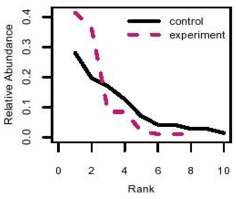
herpetofauna : 401 vs. 399



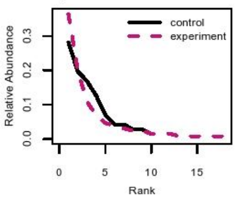
herpetofauna : 401 vs. 400



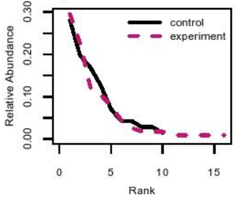
herpetofauna : 405 vs. 402



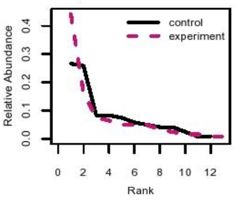
herpetofauna : 405 vs. 403



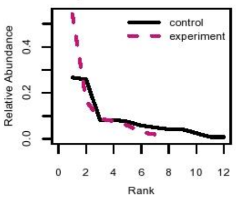
herpetofauna : 405 vs. 404



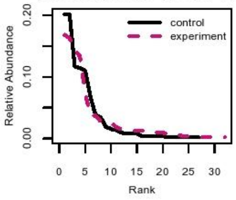
reptile : 411 vs. 410



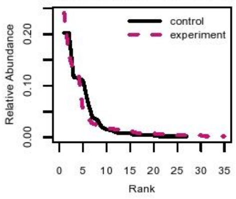
reptile : 411 vs. 412



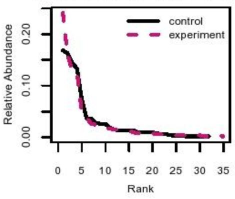
herpetofauna : 413 vs. 414



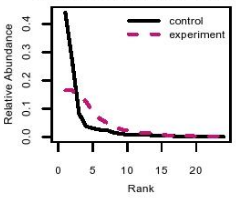
herpetofauna : 413 vs. 415



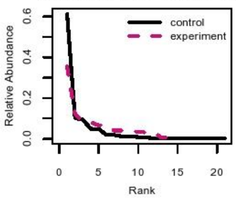
herpetofauna : 414 vs. 415



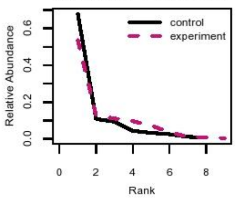
herpetofauna : 421 vs. 422



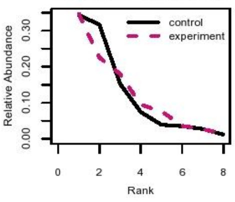
herpetofauna : 423 vs. 424



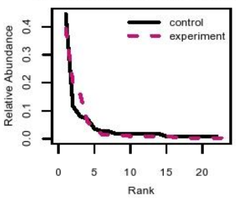
mammal : 425 vs. 426



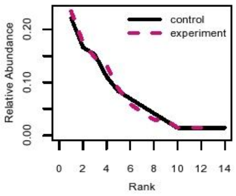
mammal : 427 vs. 428



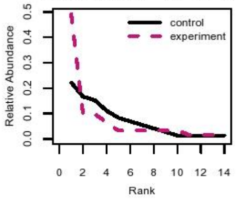
herpetofauna : 430 vs. 429



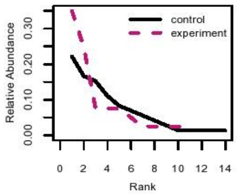
herpetofauna : 441 vs. 442



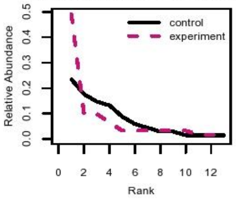
herpetofauna : 441 vs. 443



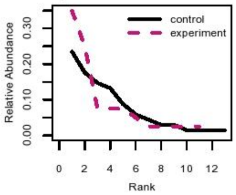
herpetofauna : 441 vs. 444



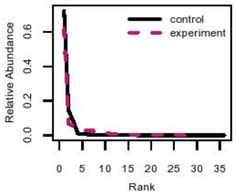
herpetofauna : 442 vs. 443



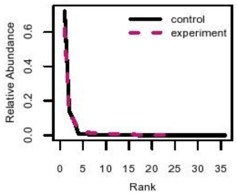
herpetofauna : 442 vs. 444



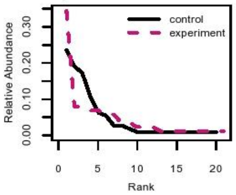
herpetofauna : 447 vs. 445



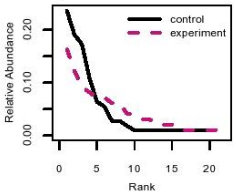
herpetofauna : 447 vs. 446



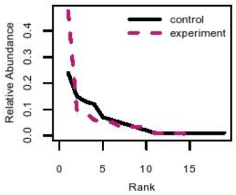
herpetofauna : 450 vs. 448



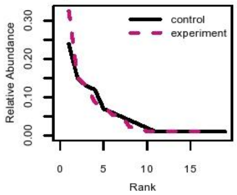
herpetofauna : 450 vs. 449



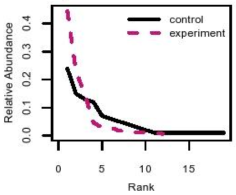
herpetofauna : 456 vs. 455



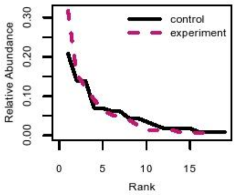
herpetofauna : 456 vs. 457



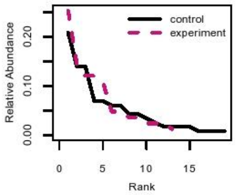
herpetofauna : 456 vs. 458



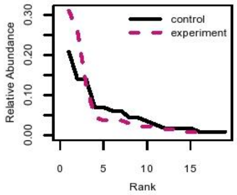
herpetofauna : 460 vs. 459



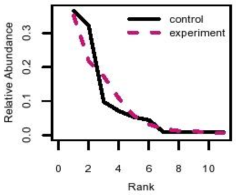
herpetofauna : 460 vs. 461



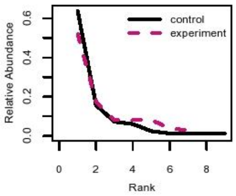
herpetofauna : 460 vs. 462



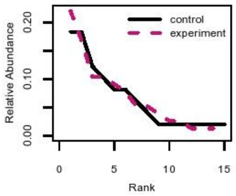
reptile : 463 vs. 464



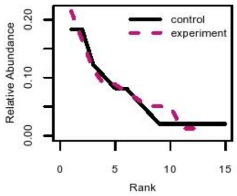
reptile : 465 vs. 466



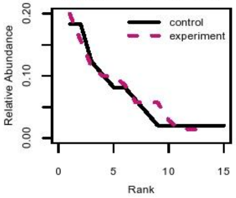
reptile : 467 vs. 468

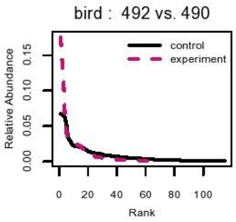


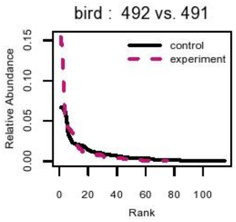
reptile : 467 vs. 469

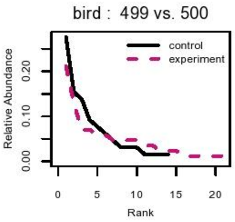


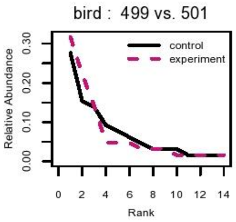
reptile : 467 vs. 470

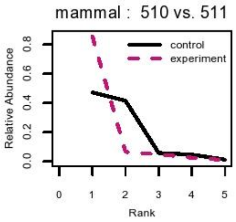



bird : 492 vs. 490
control
experiment
Relative Abundance
0.00
0.05
0.10
0.15
0
20
40
60
80
100
Rank


bird : 492 vs. 491
control
experiment
Relative Abundance
0.00
0.05
0.10
0.15
0
20
40
60
80
100
Rank


bird : 499 vs. 500
control
experiment
Relative Abundance
0.00
0.10
0.20
0
5
10
15
20
Rank


bird : 499 vs. 501
control
experiment
Relative Abundance
0.00
0.10
0.20
0.30
0
2
4
6
8
10
12
14
Rank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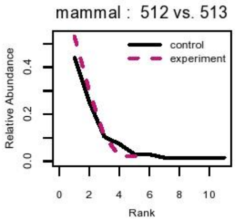
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experiment
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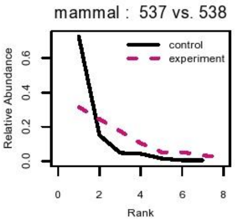
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experiment
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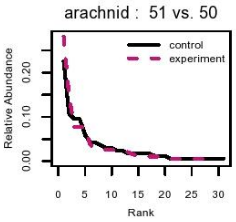
Rank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0
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10
15
20
25
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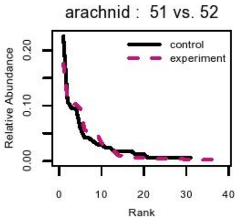
Rank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experiment
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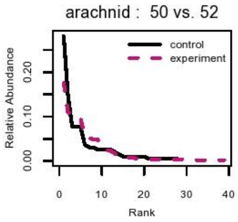
Rank


arachnid : 50 vs. 52
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experiment
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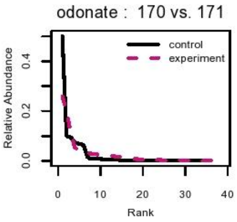
Rank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experiment
Relative Abundance
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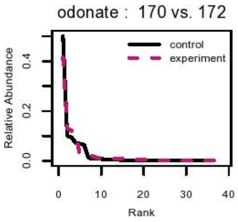
Rank


odonate : 170 vs. 172
control
experiment
Relative Abundance
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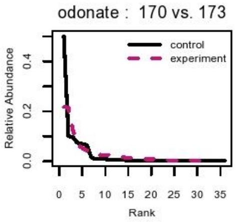
Rank


odonate : 170 vs. 173
control
experiment
Relative Abundance
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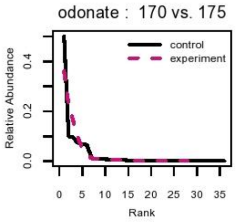
35
Rank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control
experiment
Relative Abundance
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15
20
25
30
35
Rank

Appendix H. Additional methodology and results on variance partitioning.

Communities that are incompletely sampled may display different characteristics in the form of the species abundance distribution (Ulrich *et al.* 2010, McGill *et al.* 2007). To avoid bias in our results by including communities which were more likely to be undersampled (total abundance < 300; McGill *et al.* 2007), we performed a variance partitioning analysis on the standardized variables (Legendre and Legendre 2012) using only communities with total abundance ≥ 300 (n = 53, paired comparisons = 37). Data representing large communities included 25 insect, 6 herpetofaunal, and 6 bird communities. Species richness ranged from 7 to 189 and total abundance ranged from 343 to 6,483. The results were qualitatively similar to the analysis using all the data (Table H-1).

In addition to determining the explanatory influence of species composition and community-level variables (species richness and total abundance) on observed variation in the form of the rank abundance distribution, we also evaluated the explanatory influence of taxonomic group and experimental type on the form of the rank abundance distribution using all the data in the variance partitioning framework. Adding these variables did little to increase total explanatory power, and the factors of taxonomic group and experiment type explained little observed variation in the rank abundance distribution (Table H-2).

Table H-1. Results from variance partitioning analysis using data for communities where total abundance ≥ 300.

Model	R^2	R^2 composition	R^2 state vars	Comp var explained	SandN var explained
composition + N + S + N*S	0.3514	0.1741	0.3246	0.0268	0.1772
composition + %N + %S + %N*%S	0.2842	0.1741	0.1862	0.098	0.1101

Table H-2. Results from variance partitioning analysis including taxonomic group and experiment type as factors.

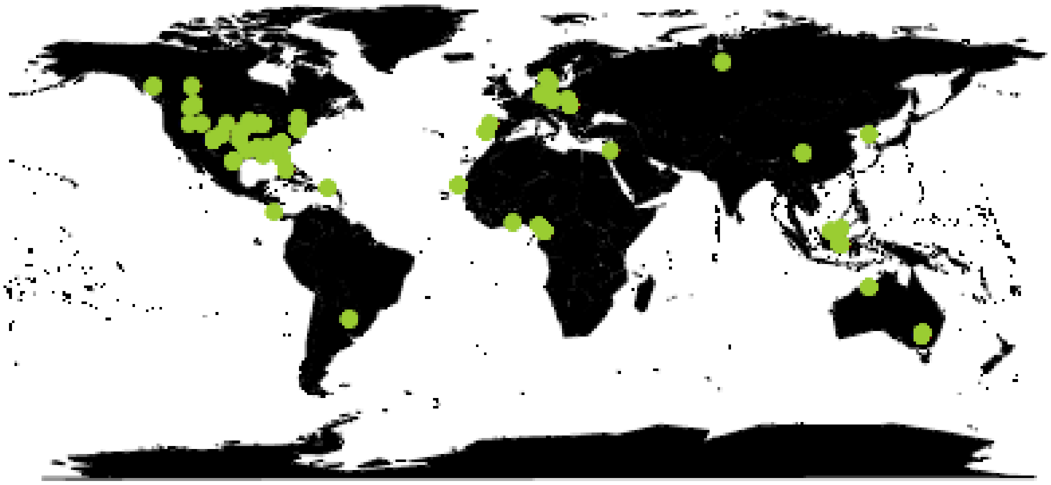
Model	R^2	R^2 composition and state vars	R^2 factor	community var explained	factor var explained
composition + N + S + N*S + taxa	0.2953	0.2838	0.0047	0.2906	0.0115
composition + %N + %S + %N*%S + taxa	0.3129	0.2987	0.0047	0.3082	0.0142
composition + N + S + N*S + experiment type	0.4062	0.2838	0.1241	0.2821	0.1224
composition + %N + %S + %N*%S + experiment type	0.3881	0.2987	0.1241	0.2640	0.0895

References

1. Legendre, P. and L. Legendre. 2012. Numerical Ecology, 3rd English Edition. Elsevier.
2. McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas,B. J. Enquist, J. L. Green, F. He, A. H. Hurlbert, A. E. Magurran, P. A. Marquet, B. A. Maurer, Ostling, C. U. Soykan, K. I. Ugland, and E. P. White. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10: 995-1015.
3. Ulrich, W., M. Ollik, and K. I. Ugland. 2010. A meta-analysis of species-abundance distributions. Oikos 119:1149–1155.

Appendix I. Location of manipulated communities.

Figure I-1. Study sites for the communities used in the study represent a wide geographic distribution including all continents except Antarctica. More details on the specific sites can be found in the sites table (Appendix F).



Appendix J. Supplement for the data and code used

Sarah R. Supp and S. K. Morgan Ernest. XXXX. Do system-level properties respond to environmental change? Biodiversity and the species-abundance distribution. doi: XXXXXXX

Supplement

The R source code and raw data to conduct the analyses and produce the figures within the paper.

Authors

Sarah R. Supp
Department of Biology and the Ecology Center
Utah State University
5305 Old Main Hill
Logan, UT 84322 USA
Email: sarah.supp@usu.edu

S. K. Morgan Ernest
Department of Biology and the Ecology Center
Utah State University
5305 Old Main Hill
Logan, UT 84322 USA
Email: morgan.ernest@usu.edu

File list

`expRAD_ms_script.R`
R script that cleans up the data, runs the statistical analyses, and outputs figures.

`ExpRADsFunctions.R`
R script that holds the relevant functions for executing the `expRAD_ms_script.R` script.

`ref_analysis_data.csv`
Data file containing the relevant information for the references included in the analysis

`sites_analysis_data.csv`
Data file containing the site specific details for each community in the analysis.

`experiments_analysis_data.csv`
Data file containing the site specific experimental details for each community in the analysis.

`community_analysis_data.cav`
Data file containing the raw abundance for each species in each community in the analysis.

`comparison_analysis_data.csv`
Data file containing the appropriate control-manipulation comparisons to be made among each of the sites in the analysis.

Description
The code and data in this supplement allow for the analyses and figures in the paper to be fully replicated using a dataset compiled by Sarah R. Supp from the published literature. Collaborators on this project include Sarah R. Supp and S. K. Morgan Ernest. Code was written by Sarah R. Supp.

Requirements: R 2.x, R packages vegan, BiodiversityR, plotrix, graphics, CCA, VGAM, nlme, lme4, languageR, poilog, scatterplot3d, hydroGOF, and VennDiagram, and the file containing functions specific to this code, `expRADsFunctions.R`.

The analyses can be replicated by changing the working directory at the top of the file `expRAD_ms_script.R` to the location on your computer where you have stored the .R and .csv files.

Code should take approximately 15 minutes to run start to finish. Figures should output as pdfs to your working directory.

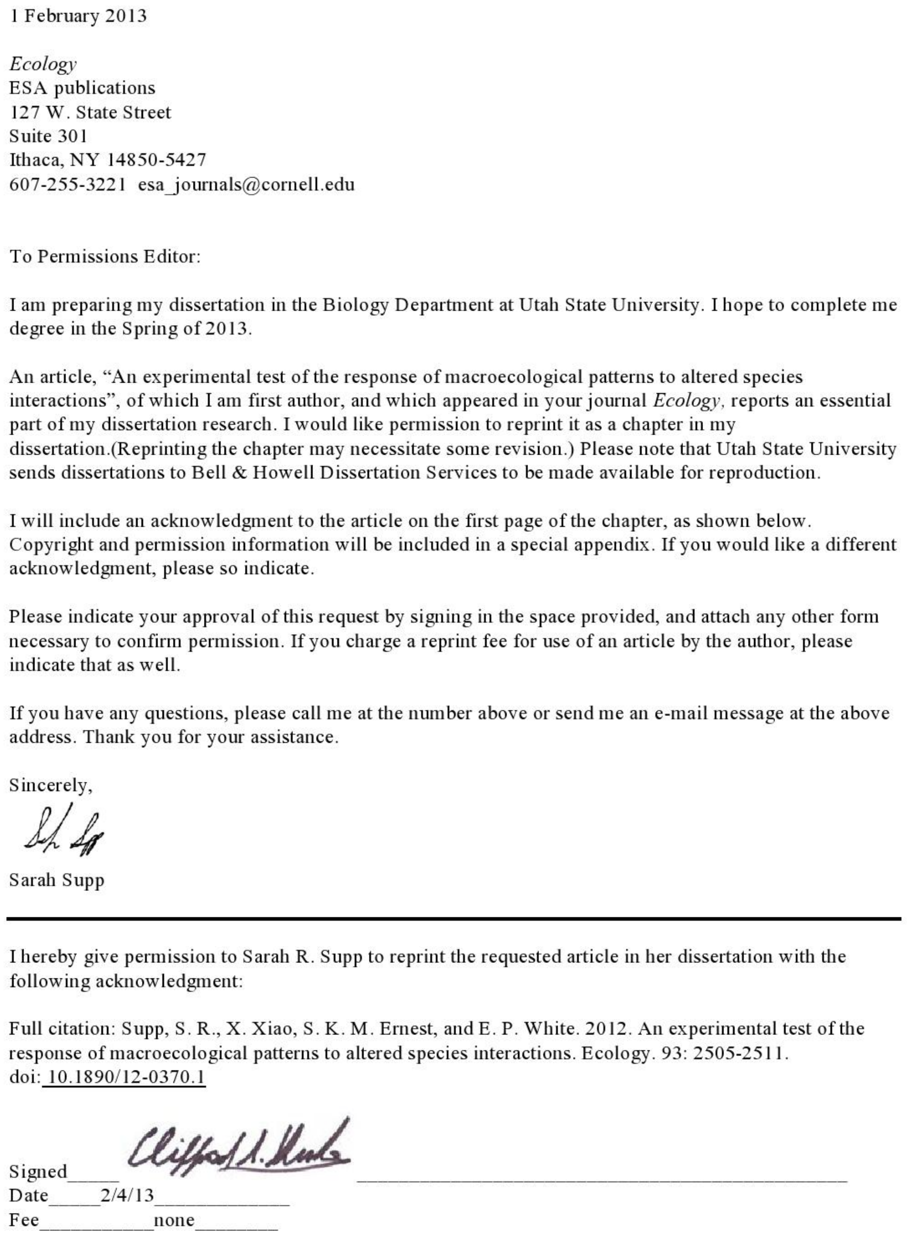
Version Control Repository: The full version control repository for this project (including post-publication improvements) is publicly available at https://github.com/weecology/experimental-rads/. If you would like to use the code in this Supplement for your own analyses it is strongly suggested that you use the equivalent code in the repositories as this is the code that is being actively maintained.

Data use: Data is provided in this supplement for the purposes of replication. If you wish to use the data for additional research, the most current version should be obtained from Sarah R. Supp (sarah@weecology.org) or from the GitHub repository.

Redistributions of source code must retain the above copyright notice, this list of conditions and the following disclaimer. Redistributions in binary form must reproduce the above copyright notice, this list of conditions and the following disclaimer in the documentation and/or other materials provided with the distribution.

THIS SOFTWARE IS PROVIDED BY THE COPYRIGHT HOLDERS AND CONTRIBUTORS "AS IS" AND ANY EXPRESS OR IMPLIED WARRANTIES, INCLUDING, BUT NOT LIMITED TO, THE IMPLIED WARRANTIES OF MERCHANTABILITY AND FITNESS FOR A PARTICULAR PURPOSE ARE DISCLAIMED. IN NO EVENT SHALL THE COPYRIGHT HOLDER OR CONTRIBUTORS BE LIABLE FOR ANY DIRECT, INDIRECT, INCIDENTAL, SPECIAL, EXEMPLARY, OR CONSEQUENTIAL DAMAGES (INCLUDING, BUT NOT LIMITED TO, PROCUREMENT OF SUBSTITUTE GOODS OR SERVICES; LOSS OF USE, DATA, OR PROFITS; OR BUSINESS INTERRUPTION) HOWEVER CAUSED AND ON ANY THEORY OF LIABILITY, WHETHER IN CONTRACT, STRICT LIABILITY, OR TORT (INCLUDING NEGLIGENCE OR OTHERWISE) ARISING IN ANY WAY OUT OF THE USE OF THIS SOFTWARE, EVEN IF ADVISED OF THE POSSIBILITY OF SUCH DAMAGE.

Appendix K. Permission to reprint Chapter 3



1 February 2013

Ecology
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607-255-3221 esa_journals@cornell.edu

To Permissions Editor:

I am preparing my dissertation in the Biology Department at Utah State University. I hope to complete me degree in the Spring of 2013.

An article, "An experimental test of the response of macroecological patterns to altered species interactions", of which I am first author, and which appeared in your journal *Ecology,* reports an essential part of my dissertation research. I would like permission to reprint it as a chapter in my dissertation.(Reprinting the chapter may necessitate some revision.) Please note that Utah State University sends dissertations to Bell & Howell Dissertation Services to be made available for reproduction.

I will include an acknowledgment to the article on the first page of the chapter, as shown below. Copyright and permission information will be included in a special appendix. If you would like a different acknowledgment, please so indicate.

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If you have any questions, please call me at the number above or send me an e-mail message at the above address. Thank you for your assistance.

Sincerely,

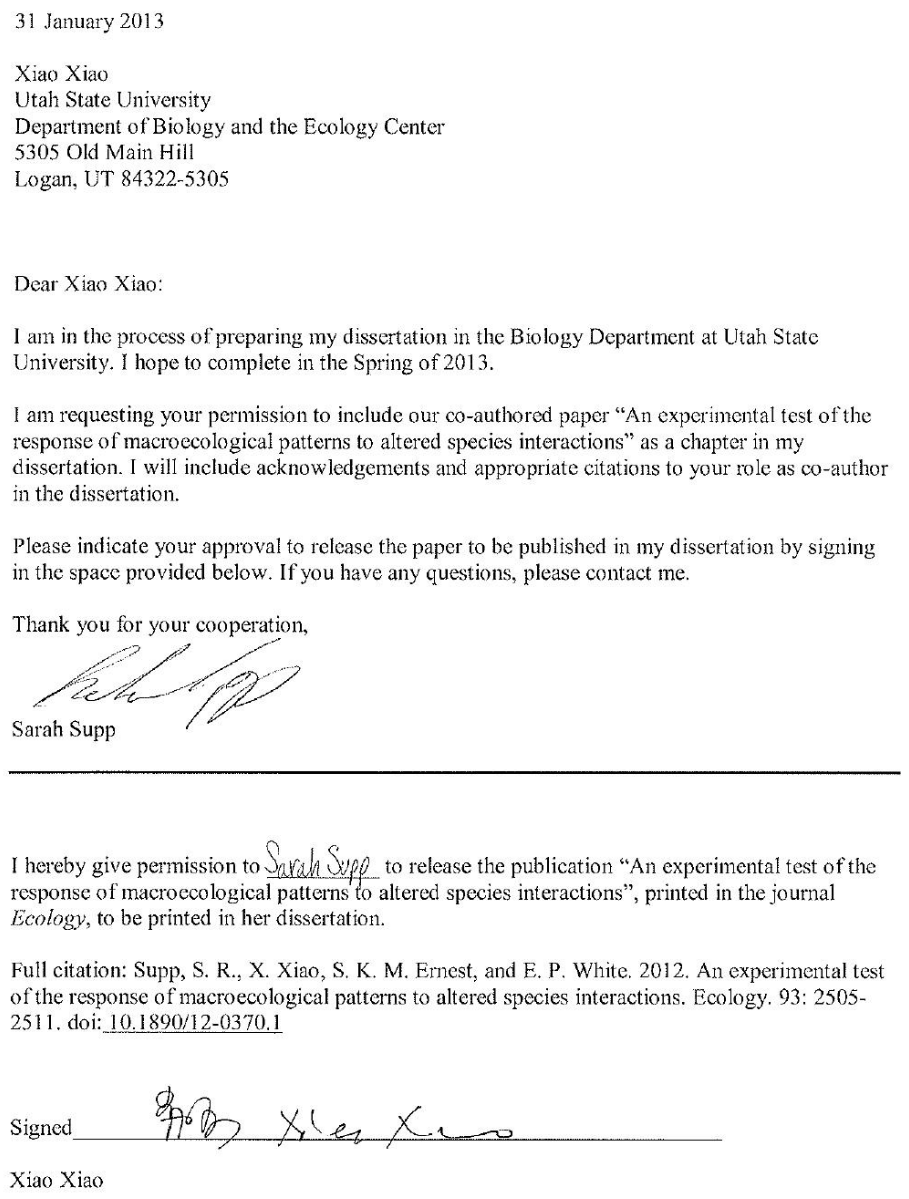
Sarah Supp

I hereby give permission to Sarah R. Supp to reprint the requested article in her dissertation with the following acknowledgment:

Full citation: Supp, S. R., X. Xiao, S. K. M. Ernest, and E. P. White. 2012. An experimental test of the response of macroecological patterns to altered species interactions. Ecology. 93: 2505-2511. doi: 10.1890/12-0370.1

Signed_____ ____
Date_____2/4/13_____________
Fee___________none________

Appendix L. Non-committee coauthor (Xiao Xiao) release form for Chapter 3



31 January 2013

Xiao Xiao
Utah State University
Department of Biology and the Ecology Center
5305 Old Main Hill
Logan, UT 84322-5305

Dear Xiao Xiao:

I am in the process of preparing my dissertation in the Biology Department at Utah State University. I hope to complete in the Spring of 2013.

I am requesting your permission to include our co-authored paper "An experimental test of the response of macroecological patterns to altered species interactions" as a chapter in my dissertation. I will include acknowledgements and appropriate citations to your role as co-author in the dissertation.

Please indicate your approval to release the paper to be published in my dissertation by signing in the space provided below. If you have any questions, please contact me.

Thank you for your cooperation,

Sarah Supp

I hereby give permission to Sarah Supp to release the publication "An experimental test of the response of macroecological patterns to altered species interactions", printed in the journal *Ecology*, to be printed in her dissertation.

Full citation: Supp, S. R., X. Xiao, S. K. M. Ernest, and E. P. White. 2012. An experimental test of the response of macroecological patterns to altered species interactions. Ecology. 93: 2505-2511. doi: 10.1890/12-0370.1

Signed Xiao Xiao

Xiao Xiao

CURRICULUM VITAE

Sarah R. Supp

Utah State University
Department of Biology and the Ecology Center
5305 Old Main Hill
Logan, UT 84322-5305

tel: (435) 757 – 2979 • **email:** sarah.supp@usu.edu or sarah@weecology.org
twitter: @srsupp • **url:** http://weecology.org/people/sarahsupp/Sarah_Supp

EDUCATION

2007 – 2013	Ph.D. in Ecology *Dissertation:* Local and regional drivers of biodiversity: From life-history traits to system-level properties Department of Biology, Utah State University – Logan, UT *Advisor*: S. K. Morgan Ernest
2007	B.S. Biology, *magna cum laude*, minors in Chemistry and Spanish Valparaiso University – Valparaiso, IN *Advisor*: Laurie S. Eberhardt

PUBLICATIONS

1. **Supp, S. R.**, X. Xiao, S. K. M. Ernest, and E. P. White. 2012. An experimental test of the response of macroecological patterns to altered species interactions. Ecology. 93: 2505-2511. doi: 10.1890/12-0370.1
2. Cobbold, S. M. and **S. R. Supp.** 2012. Patch shape alters spider community structure: links between microhabitat choice and sensitivity to increased edge habitat. Journal of Insect Conservation. 4: 581-589.
3. Thibault, K. M., **S. R. Supp,** M. Giffin, E. P. White and S. K. M. Ernest. 2011. Species composition and abundance of mammalian communities. Ecology. 92: 2316.
4. **Supp, S. R.** and E.P. White. 2010. Measures of journal quality should separate reviews from original research. Ideas in Ecology and Evolution. 3: 16-19.
5. O'Donnell, R. **S.R. Supp** and S. M. Cobbold. 2010. Hindrance of conservation biology by delays in the submission of manuscripts. Conservation Biology. 24: 615-620.

MANUSCRIPTS IN PREPARATION

1. **Supp, S. R.**, and S. K. M. Ernest. *in prep*. Do system-level properties respond to environmental change? Biodiversity and the species abundance distribution.
2. **Supp, S. R.**, D.N. Koons and S. K. M. Ernest. *in prep*. Life history trade-offs among core and transient species regulate local diversity and community structure.

PRODUCTS

1. Portal-rodent-dispersal: Accompanies the Supp, Koons, and Ernest project examining individual-level rodent trap data for a 10-year time series at the Portal Project. Includes data and code to replicate analyses and figures. https://github.com/weecology/portal-rodent-dispersal/
2. Experimental-rads: Accompanies the Supp and Ernest project examining change in the rank-abundance distribution (rad), species richness, total abundance, and species composition in a wide variety of manipulated terrestrial animal communities. Includes data and code to replicate analyses and figures. https://github.com/weecology/experimental-rads/
3. PortalExperimentalMacroeEco: Accompanies the Supp, Xiao, Ernest, and White publication in Ecology (doi: 10.1890/12-0370.1). Includes data and code to replicate analyses and figures from the paper. https://github.com/sarahsupp/PortalExperimentalMacroeEco/
4. METE: Python-based tool for fitting and modeling the Maximum Entropy Theory of Ecology. https://github.com/weecology/METE
5. Experiments and the Rank Abundance Distribution (Slides from 2012 Ecological Society of America Conference). Figshare.http://dx.doi.org/10.6084/m9.figshare.95835
6. Experimental evidence suggests that richness and total abundance primarily determine macroecological patterns (slide deck from 2011 Ecological Society of America Conference). Figshare. http://dx.doi.org/10.6084/m9.figshare.95850
7. Online Presence for graduate students (presentation from 7 December 2012 Utah State University Ecolunch). Prezi. http://prezi.com/yugz4zgdo3qh/onlinepresence/

RESEARCH EXPERIENCE

2007-2012	**Graduate Research Assistant**. Long-term monitoring and manipulation of a desert ecosystem. S. K. Morgan Ernest, P.I.
2010	**Graduate Research Assistant**. Advancing macroecology using informatics and entropy maximization. Ethan P. White, P.I.
2009	**Graduate Research Assistant**. Mammalian community database. Ethan P. White, P.I.
2007	**ASIANetwork Research Fellow**. Water quality in east central China and northwest Indiana: issues, perceptions, and approaches for resolution. Jonathan Schoer, P.I.
2006-2007	**Undergraduate Research**. Tree community diversity influences on feeding preferences of yellow-bellied sapsucker (*Sphyrapicus varius*) in northwestern Indiana. Laurie S. Eberhardt, P.I.

TEACHING EXPERIENCE

2012	**Co-instructor**. Software Carpentry Bootcamp (Washington University at St. Louis)
2012	**Instructor**. Evolution (Utah State University)
2012	**Teaching Assistant**. Software Carpentry Bootcamp (Utah State

	University and Software Carpentry)
2012	**Teaching Assistant**. Introduction to R (Utah State University and The Utah Department of Wildlife Resources)
2011	**Guest Lecturer**. Macroecology (Utah State University) “Macroecology and Conservation”
2011	**Guest Lecturer**. Evolution (Utah State University. “Speciation and Systematics”
2011	**Outreach**. Grades K-6 Science Lesson. (District 33, Hastings, NE) “What is a Scientist?”
2010	**Teaching Assistant**. Evolution (Utah State University)
2008	**Teaching Assistant**. Ornithology (Utah State University)
2007	**Teaching Assistant**. Human Physiology (Utah State University)
2007	**Undergraduate Teaching Assistant**. Field Biology (Valparaiso University)
2007	**Undergraduate Teaching Assistant**. Science of the Indiana Dunes (Valparaiso University)
2006	**Undergraduate Teaching Assistant**. Ecology (Valparaiso University)
2004 – 2007	**Outreach**. Earthtones environmental education team (Valparaiso University)

RELATED PROFESSIONAL EXPERIENCE AND TRAINING

2012-2014	Elected Co-chair for Gordon Research Seminar – Unifying Ecology Across Scales, 2014 at the University of New England
2012	Teaching Software Carpentry studygroup. teaching.software-carpentry.org – a group committed to teaching scientists how to program
2010-2011	Advanced Programming for Biologists. Utah State University
2010	Ecology Center Director Student Search Committee. Utah State University.
2009	Hantavirus Safety Training. Utah State University.
2009-2010	Ecology Seminar Series Committee Co-Chair. Utah State University.
2008-2011	Biology Department Student Representative. Utah State University.
2008-2010	Ecology Seminar Series Committee Member and Graduate Student Host. Utah State University.
2008-2010	Biology Graduate Student Association President. Utah State University.
2008	Introduction to ArcGIS interactive course with ESRI Certification. Utah State University.
2006 – 2007	Laboratory Assistant, Department of Biology. Valparaiso University Valparaiso, IN. Prepare avian specimens for storage and lab use.
2006	Resource Management. Indiana Dunes National Lakeshore, Porter, IN and the Student Conservation Association.
2004 – 2005	Mosquito Abatement Specialist. Department of Parks and Recreation Department. Hastings, NE.

MEDIA

O'Donnell *et al.* 2010 highlighted in:

Dolgin, E. 2009. Endangered papers. Nature. 461: 831. doi: 10.1038/nj7265-831c.

Dolgin, E. 2010. Research Remand. The Scientist. http://www.the-scientist.com/?articles.view/articleNo/27889/title/Research-remand/

SELECTED PRESENTATIONS

Supp, S. R. 8 November 2012. Moving macroecology forward with novel experimental approaches. Washington University at St. Louis. *Invited seminar.*

Supp, S. R., Ernest, S.K.M. 2012. Testing the drivers of the species-abundance distribution: the relative importance of composition and state variables. Ecological Society of America AnnuaL Meeting. Portland, OR. *Oral presentation.*

Supp, S. R., Ernest, S.K.M. 2012. Experimentally testing the drivers of the species-abundance distribution: the relative importance of composition and state variables. Gordon Research Conference – Metabolic Basis of Ecology, Biddeford, ME. *Invited poster.*

Supp, S. R., Ernest, S.K.M. 2012. Experimentally testing the drivers of the rank abundance distribution – sensitivity to anthropogenic change? Gordon Research Seminar – Metabolic Basis of Ecology, Biddeford, ME. *Invited presentation.*

Supp S. R., Xiao, X, Ernest, S.K.M., White, E.P. 2011. Experimentally altering biotic interactions has different effects on static and dynamic macroecological patterns. Ecological Society of America Annual Meeting. Austin, TX. *Oral presentation.*

Supp, S. R., O'Donnell, R. P, Cobbold, S. M. 2010. Hindrance of conservation biology by delays in the submission of manuscripts. Student Conference on Conservation Science. Cambridge, UK. *Poster.*

Mohlman, S. R. and Ernest, S. K. M. 2009. Predator influences on prey community structure in a long-term experimental rodent-plant system. Ecological Society of America Annual Meeting. Albuquerque, NM. *Poster.*

Mohlman, S. R. and Ernest, S. K. M. 2009. Pocket mouse invasion influences desert plant community structure in place of absent Kangaroo rats. American Society of Mammalogist Annual Meeting. Fairbanks, AK. *Poster.*

Mohlman, S. R., O'Donnell, R. P., Cobbold, S. M. 2008. Is the progress of conservation biology hindered by delays in the submission of conservation manuscripts? Faculty and Graduate Student Research Symposium, Utah State University. Logan, UT. *Poster.*

Mohlman, S. R., Field, J., Schoer, J. 2008. Water quality in east central China and northwest Indiana: issues, perceptions, and approaches for resolution: Part II. ASIANetwork Annual Conference. San Antonio, TX. *Poster.*

Eberhardt, L., **Mohlman, S. R.**, Zuercher, R., Lute-Kulaga, M. 2007. Yellow-bellied sapsucker (*Sphyrapicus varius*) feeding preferences for *Carya ovata* in relation to species diversity in Northwest Indiana woods. Indiana Dunes Research Forum. Highland, IN. *Poster.*

GRANTS AND AWARDS

2013	Graduate Researcher of the Year Nomination, Biology Department, Utah State University
2012-2013	School of Graduate Studies Fellowship, Utah State University
2012-2013	Ecology Center Assistantship, Utah State University
2012	National Science Foundation Postdoctoral Research Fellowship, “Macroecology of Global Change: Assessment of body size pattern response to anthropogenic stressors”, ***in review***
2012	Graduate Student Senate Travel Grant, Utah State University
2012	Center for Women and Gender Travel Grant, Utah State University
2012	Ecology Center Travel Grant, Utah State University
2012	Ecology Center Travel Grant, Utah State University
2010	James A. and Patty MacMahon Scholarship, Utah State University
2010	Biology Department Travel Grant, Utah State University
2010	Ecology Center Travel Grant, Utah State University
2009	Ecology Center Travel Grant, Utah State University
2008	Biology Department Travel Grant, Valparaiso University
2008	Board of Directors’ Award for Exceptional Student Research, Valparaiso University
2007	ASIANetwork Research and Travel Grant
2007	Phi Beta Kappa, Valparaiso University
2006-2007	National SMART Grant
2006	Lumina Award for Outstanding Scholarship, Valparaiso University
2006	National Residence Hall Honorary, Valparaiso University
2005	Sigma Delta Pi National Spanish Honor Society
2003-2007	Presidential Scholarship, Valparaiso University
2003-2007	Dean’s list, Valparaiso University