Title: Maintenance of community function through compensation breaks down over time in a desert rodent community

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Original submission: This submission analyzes long-term data on rodent community abundance and energy use from the Portal Project. Sections of this timeseries have been analyzed in numerous other publications, but this is the first to analyze data from 2007-2020 on compensation on experimental and control plots.

No prior publication: This submission is posted as a preprint on bioRxiv at [bioRxiv].

Animal welfare: Rodent censuses were conducted with IACUC approval, most recently under protocol 201808839_01 at the University of Florida.

Open research: All data and code to reproduce these analyses are archived on Zenodo at https://doi.org/10.5281/zenodo.5544362 and https://doi.org/10.5281/zenodo.5539881.

Analytic methods: All analyses were conducted in R version 4.0.3.

Abstract

Understanding the ecological processes that maintain community function in systems experiencing species loss, and how these processes change over time, is key to understanding the relationship between community structure and function and predicting how communities may respond to perturbations in the Anthropocene. Using a 30-year experiment on desert rodents, we show that the impact of species loss on community-level energy use has changed dramatically over time, due to changes in both species composition and in the degree of functional redundancy among the same set of species. Although strong compensation, initially driven by the dispersal of functionally redundant species to the local community, occurred in this system from 1996-2010, since 2010, compensation has broken down due to decreasing functional overlap within the same set of species. Simultaneously, long-term changes in sitewide community composition due to niche complementarity have decoupled the dynamics of compensation from the overall impact of species loss on community-level energy use. These results highlight the importance of explicitly long-term, metacommunity, and eco-evolutionary perspectives on compensatory dynamics, zero-sum constraints, and the link between species-level fluctuations and community function in a changing world.

Key words: community function, compensation, zero-sum dynamic, environmental fluctuations, functional redundancy

Introduction

Determining the extent to which community-level properties are affected by species loss, and how and why this changes over time, is key for understanding how communities are structured and how community function may respond to future perturbations (Gonzalez and Loreau 2009). When species are lost from a community, their contributions to community function are also directly lost (Bannar-Martin et al. 2018). Community function may be maintained, however, if the remaining species in a community have similar functional traits to the lost species, allowing those species to compensate for the decline in function directly caused by species loss - i.e., functional redundancy (Walker 1992, 1995; Ernest and Brown 2001; Rosenfeld 2002; Gonzalez and Loreau 2009). When compensation via functional redundancy occurs among consumers with a common resource base, it is consistent with a zero-sum competitive dynamic, in which resources not used by one species are readily absorbed by competitors, and any increases in the abundance of one species must come at the direct expense of others (Van Valen 1973; Ernest et al. 2008).

Because the response of system-level function to species loss is partially determined by degree of functional redundancy in a community, processes that cause functional redundancy to change over time can have important consequences for the long-term maintenance of ecosystem function following species loss. Shifts in species composition (e.g., colonization events) may buffer community function against species loss, if a community gains species that are functionally similar to the species that are lost (Ernest and Brown 2001; Leibold et al. 2017). The ability of colonization to supply functionally redundant species depends on the species (and traits) present in the broader metacommunity, and on the rate of dispersal supplying appropriate species to local communities (Leibold et al. 2017). Even without the addition of new species and

traits, however, functional redundancy within a consistent set of coexisting species may fluctuate over time. While, in theory, functional redundancy may occur via the special case of complete niche neutrality (where functionally redundant species do not differ in any aspects of the niche; Hubbell 2001), it may also occur in niche-structured systems that contain species that share some traits but differ along other niche axes (Thibault et al. 2010). In these systems, if functionally-similar, but non-identical, species respond to environmental change in similar ways, functional overlap can be maintained or even strengthened. However, if niche differences cause species to respond differently to changing conditions, the degree of functional overlap between those species may decline, resulting in a breakdown in compensation (Loreau 2004; Fetzer et al. 2015). As the dynamics of both metacommunity processes and changing environmental conditions produce changes in functional redundancy in a community over time, the extent to which a community can compensate for species loss - and the strength of zero-sum competition for limiting resources - may also be dynamic and context-dependent.

Despite logical conceptual support, and evidence from experimental microcosms (Fetzer et al. 2015), there is little empirical documentation of how, and through which mechanisms, temporal changes in functional redundancy modulate the effect of species loss on ecosystem function in natural assemblages. Although relatively plentiful, observational data cannot unambiguously detect compensation through functional redundancy, and even short-term experiments may not be sufficient to capture temporal variation in compensation (Ernest and Brown 2001; Houlahan et al. 2007). In contrast, long-term manipulative experiments are uniquely suited to address this question. In long-term experiments in which key species are removed from a community over an extended period of time, the impact of species loss on community function can be directly quantified by comparing community function between

complete and manipulated assemblages. As metacommunity dynamics and environmental conditions shift over time, long-term monitoring can reveal how these processes contribute to changes in functional redundancy and ecosystem function across different time periods. Due to the financial and logistical resources required to maintain and monitor whole-community manipulations over long timescales, these experiments are rare in natural systems representative of realistic evolutionary, geographic, and environmental constraints (Hughes et al. 2017).

Here, we use a 30-year experiment on desert rodents to investigate how shifts in functional redundancy alter the effect of species loss on community function over time. In this study, kangaroo rats (*Dipodomys* spp.), which are the largest and competitively dominant species in the rodent community, have been removed from a subset of experimental plots to explore how the loss of key species affects community function, measured as community-level metabolic flux ("total energy use", or *Etot*; Ernest et al. 2019). For systems of consumers with a shared resource base, such as the granivorous rodents that make up this community, *Etot* reflects the total amount of resources being processed by an assemblage, and is an important metric of community function (Lawton 1994; Ernest and Brown 2001). Long-term monitoring of this experiment has documented repeated shifts in the habitat and species composition of this system, resulting in distinct time periods characterized by different habitat conditions and configurations of the rodent community (Christensen et al. 2018). Abrupt reorganization events in community composition occurred in 1996 and in 2010, associated with the establishment and subsequent decline of the pocket mouse *Chaetodipus baileyi*. *C. baileyi* is similar in size, and presumably other traits, to kangaroo rats, and its establishment in 1996 drove a pronounced increase in compensation due to functional redundancy between *C. baileyi* and kangaroo rats (Ernest and Brown 2001; Thibault et al. 2010). Over the course of this experiment, the habitat at the study

site has transitioned from desert grassland to scrub, driving a shift in baseline rodent community composition away from kangaroo rats and favoring other, smaller, granivores (Ernest et al. 2008). By making comparisons across these time periods, we explored how changes in community composition, and functional overlap among the same set of species, have contributed to changes in how species loss has impacted *Etot* over time.

Methods

All analyses were conducted in R version 4.0.3 (R Core Team 2020). Data and code are available at https://doi.org/10.5281/zenodo.5544362 and https://doi.org/10.5281/zenodo.5539881.

The Portal Project

The Portal Project consists of a set of 24 fenced experimental plots located approximately 7 miles east of Portal, AZ, USA, on unceded land of the Chiricahua Apache. Beginning in 1977, kangaroo rats (*Dipodomys spectabilis, D. merriami,* and *D. ordii*) have been experimentally excluded from a subset of these plots (exclosures), while all other rodents are allowed access through small holes cut in the plot fencing. Control plots, with larger holes, are accessible to all rodents, including kangaroo rats. Rodents on all plots are censused monthly. For additional details on the site and methodology of the Portal Project, see Ernest et al. (2019).

Data

We use data for 4 control and 5 exclosure plots from February 1988 until January 2020. The experimental treatments for some plots have changed over time, and we used the subset of plots that have had the same treatments for the longest period of time (Ernest et al. 2019). We broke this timeseries into three time periods corresponding to previously-documented major transitions in the rodent community: 1) February 1988 to June 1997; 2) July 1997 to January 2010, which spans from the first census period in which *C. baileyi* was captured on all exclosure

plots at the site until the most recent reorganization event; and 3) from January 2010 until January 2020, when data collection was interrupted by the COVID-19 pandemic (Christensen et al. 2018; Bledsoe and Ernest 2019). For each individual rodent captured, we estimated the individual-level metabolic rate as 5.69 * ($m^{0.75}$), where m is body mass in grams (White et al. 2004). We calculated treatment and species-level energy use as the sum of the appropriate individuals' metabolic rates. All data were accessed using the R package *portalr* (Christensen et al. 2019).

Rodent community energy use

For all variables, we combined data for all plots within a treatment in each monthly census period and calculated treatment-level means. This is necessary to calculate compensation, and we treated other variables in the same way to maintain consistency. To measure the overall impact of kangaroo rat removal on *Etot*, we calculated a "total energy ratio" as the ratio of treatment-level *Etot* for kangaroo-rat exclosure plots relative to unmanipulated control plots, i.e. $Etot_E/Etot_C$ where $Etot_E$ and $Etot_C$ are total energy use on exclosures and controls, respectively (Thibault et al 2010; Bledsoe and Ernest 2019). The total energy ratio is distinct from energetic compensation, which we defined as the proportion of the energy made available by removing kangaroo rats from the community that is taken up via compensatory increases in energy use by small granivores (all granivorous species other than kangaroo rats; *Baiomys taylori, C. baileyi, Chaetodipus hispidus, Chaetodipus intermedius, Chaetodipus penicillatus, Perognathus flavus, Peromyscus eremicus, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys fulvescens, Reithrodontomys megalotis,* and *Reithrodontomys montanus*). We calculated this as $(SG_E - SG_C)/KR_C$, where SG_E and SG_C are the amount of energy used by small granivores on exclosure and control plots, respectively, and KR_C is the amount of energy used by kangaroo rats

on control plots (Ernest and Brown 2001). To compare these variables across time periods, we used generalized least squares models (the R package *nlme*; Pinheiro et al. 2020), accounting for temporal autocorrelation, using the form *response ~ time period + CORCAR1(census period)*, and calculated estimates and contrasts using the R package *emmeans* (Lenth 2021). To evaluate change in baseline community composition over time, we calculated the proportion of treatment-level energy use accounted for by kangaroo rats on control plots in each census period ($KR_C/Etot_C$). Because proportional abundance is bounded 0-1 and is therefore not appropriate for generalized least squares, we compared values across time periods using a generalized linear model with a quasibinomial link function of the form *response ~ time period*. Finally, we calculated the proportional energy use accounted for by *C. baileyi,* specifically, on exclosure and control plots in each census period ($CB_E/Etot_E$ and $CB_C/Etot_C$, respectively). *C. baileyi* was not present at the site prior to 1996, and we restricted the analysis of *C. baileyi* proportional energy use to July 1997-2020. We compared *C. baileyi* proportional energy use over time and across treatments using a quasibinomial generalized linear model of the form *response ~ time period * treatment.*

Results

The impact of kangaroo rat removal on *Etot* has changed repeatedly over time, through a combination of abrupt shifts in compensation associated with *C. baileyi*, and long-term changes in baseline community composition sitewide (Figure 1). The first shift occurred around 1996, when *C. baileyi* - which had not previously been observed at the site - established in the community (Figure 1D; see also Ernest and Brown 2001). *C. baileyi* rapidly became dominant on exclosure plots and dramatically increased energetic compensation (Figure 1B), from an average of 19% (95% interval 9-29%) from 1988-1996 to an average of 55% (46-63%; contrast $p <$

0.001; for complete results of all models, see Appendix 1) from 1996-2010. With *C. baileyi*'s addition to the community, the total energy ratio (on exclosures relative to controls; Figure 1A) increased from 30% (20-39%) to 68% (60-77%, contrast $p < 0.001$). In the second shift, beginning around 2010, *C. baileyi*'s abundance sitewide dropped precipitously (Figure 1D). *C. baileyi*'s proportional energy use dropped from an average of 72% (70-75%) to 25% (22-28%, contrast $p < 0.001$) on exclosure plots, and from 12% (10-14%) to essentially 0 on control plots (contrast $p < 0.001$). Other species of small granivore did not make compensatory gains to offset the decline in *C. baileyi* (Figure 1B). As a result, energetic compensation declined from an average of 55% (46-63%) to 22% (12-32%, contrast $p < 0.001$), a level not significantly different from the 19% (9-29%, contrast $p = .9$) observed prior to *C. baileyi*'s establishment at the site. Somewhat paradoxically, while the total energy ratio also dropped following *C. baileyi*'s decline, from an average of 68% (60-77%) from 1996-2010 to 46% (37-56%, contrast $p = 0.002$) from 2010-2020, it remained higher than its average of 30% (20-39%, contrast $p = 0.04$) from 1988-1996 (Figure 1A). Over the course of the experiment, rodent community composition shifted sitewide, such that in later years, kangaroo rats have accounted for a lower proportion of baseline *Etot* than they did at the beginning of the study (Figure 1C). From 1988-1996, kangaroo rats accounted for 92% (90-94%) of *Etot* on controls; in later time periods, this dropped to an average of approximately 70% (1988-1996 compared to later time periods, $p < 0.001$; 1996-2010 and 2020-2020 not significantly different, $p = .86$). Because the proportion of *Etot* directly lost to kangaroo rat removal was smaller from 2010-2020 than from 1988-1996, the total energy ratio was higher from 2010-2020 than it was from 1988-1996 - even though there was not a detectable difference between the two time periods in the proportion of lost energy being offset through energetic compensation.

Discussion

The dynamics of rodent community energy use at Portal illustrate that the role of functional redundancy in buffering community function against species loss fluctuates over time, due to changes in both species composition and in the degree of functional overlap among the same species. The 1996 increase in compensation, driven by *C. baileyi*'s establishment at the site, was a clear and compelling instance of colonization from the regional species pool overcoming a dispersal constraint on functional redundancy (Ernest and Brown 2001; Leibold et al 2017). Although the small granivore species originally present in the community did not possess the traits necessary to compensate for kangaroo rats, *C. baileyi* supplied those traits and substantially restored community function on exclosure plots. In contrast, following the community reorganization event in 2010, *C. baileyi* remained present in the community, but ceased to operate as a functional replacement for kangaroo rats. This is consistent with fluctuating conditions modulating the degree of functional redundancy between similar, but non-identical, competitors. Kangaroo rats and *C. baileyi* are relatively similar in size and are demonstrably capable of using similar resources. However, *C. baileyi* prefers different, shrubbier microhabitats than kangaroo rats, and the two groups have been observed to replace each other in adjacent habitats (Rosenzweig and Winakur 1969; M'Closkey 1982; Price 1978). We suggest that this study site, which has historically been dominated by kangaroo rats, constitutes marginal habitat for *C. baileyi*, and that, while conditions from 1996-2010 aligned sufficiently with *C. baileyi*'s requirements to create appreciable functional redundancy between kangaroo rats and *C. baileyi*, conditions since 2010 have caused this redundancy to break down. *C. baileyi*'s decline occurred immediately following a period of low plant productivity and low rodent abundance community-wide (Appendix 2; Christensen et al. 2018). In the decade after, the site experienced

two long and severe droughts interspersed with an exceptionally wet period (Appendix 2; Christensen et al. 2018). These extreme conditions may themselves have limited *C. baileyi's* fitness at the site, or the community-wide low abundance event may have temporarily overcome incumbency effects and triggered a community reorganization tracking longer-term habitat shifts (Thibault and Brown 2008; Christensen et al. 2018). Regardless of the proximate cause of *C. baileyi*'s decline, the fact that *C. balieyi* remains in the community, but no longer compensates for kangaroo rats, illustrates that changing conditions can have profound effects on community function by modulating the degree of functional redundancy within a consistent set of species.

While changes in compensation over time have contributed to changes in community function in this system, changes in compensation alone do not fully account for the long-term changes in the overall impact of kangaroo rat removal on *Etot*. Specifically, although the ratio of *Etot* on exclosure plots relative to control plots declined coinciding with the breakdown in compensation associated with *C. baileyi*, it remained higher than the levels observed prior to 1997 (Figure 1A). This difference in exclosure *Etot* between the first and last time periods cannot be explained by an increase in compensation, as compensation from 2010-2020 approximated pre-1997 levels (Figure 1B). Rather, the increase in *Etot* on exclosure plots relative to control plots was the result of a long-term decrease in the contribution of kangaroo rats to *Etot* sitewide. Because kangaroo rats accounted for a smaller proportion of *Etot* on control plots from 2010-2020 than they did prior to 1997, their removal had a smaller impact on community function – even though there was not an increase in the degree to which small granivores compensated for their absence. In fact, the relatively consistent levels of compensation achieved in the decades preceding and following *C. baileyi*'s dominance at the site suggest a relatively stable, and limited, degree of functional overlap between kangaroo rats and the original small granivores

(i.e., excluding *C. bailyei*). Niche complementarity, combined with changing habitat conditions, may partially explain how small granivores have come to account for a larger proportion of community *Etot* over time, but have not increased their capacity to exploit resources usually controlled by kangaroo rats. It is well-documented that, while kangaroo rats readily forage in open microhabitats where predation risk can be relatively high, smaller granivores rely on vegetation cover as an antipredator defense and preferentially forage in sheltered microhabitats (Kelt 2011). Over the course of this experiment, the habitat at this study site has transitioned from an arid grassland to a shrubland (Brown et al. 1997). As the landscape availability of open and sheltered microhabitats shifted, small granivores may have gained access to a larger proportion of resources and increased their share of *Etot* sitewide. However, kangaroo rats may have continued to use resources predominately located in the remaining open areas – resources that would have remained inaccessible to smaller granivores, even on plots where kangaroo rats were removed. The long-term reduction in the impact of kangaroo rat removal on community function, driven by niche complementarity and consistent niche partitioning, contrasts with the temporary compensatory dynamic driven by functional redundancy with *C. baileyi*. Although changes in the overall effect of species loss are sometimes treated interchangeably with compensation (e.g. Ernest and Brown 2001 compared to Thibault et al. 2010, Bledsoe and Ernest 2019), especially at short timescales, it is important to recognize that multiple distinct pathways modulate the long-term impacts of species loss on community function. Particularly in strongly niche-structured systems, such as the desert granivores studied here, complementarity effects and fluctuations in functional redundancy may occur simultaneously, with complex and potentially counterintuitive outcomes for community-level function.

Overall, the decadal-scale changes in energy use among the Portal rodents underscore the importance of long-term metacommunity dynamics to the maintenance of community function following species loss (see also Leibold et al. 2017). Although a single colonization event may be enough to allow for temporary compensation via functional redundancy, as conditions fluctuate, species that are capable of compensating under some conditions may no longer perform that function. Particularly if limiting similarity prevents similar competitors from specializing on precisely the same habitats (Rosenfeld 2002), this type of temporary, context-dependent compensation may be common. To maintain compensation for species loss over time, multiple colonization events, supplying species that are functionally redundant under different conditions, may be required. Depending on dispersal rates and the composition of regional species pools, repeated colonization events tracking changing conditions may be unlikely or even impossible. At Portal, dispersal limitation introduced a 20-year lag between the initiation of the experiment and the beginning of energetic compensation driven by *C. baileyi*. Theoretically, another species capable of compensating for kangaroo rats, and better-suited to conditions at the site since 2010, could colonize the site and restore compensation – but it is unclear whether such a species exists or how long it might take for it to disperse to the site. More generally, as ecosystems globally undergo reductions in habitat connectivity and regional beta diversity, and move into novel climatic spaces, maintenance of community function through functional redundancy may become increasingly rare and fragile (Dornelas et al. 2014; Williams and Jackson 2007).

Finally, the long-term variability in functional redundancy documented here adds important nuance to our understanding of how zero-sum dynamics operate in natural assemblages. Theories invoking zero-sum dynamics, and tests for compensatory dynamics in

empirical data, often treat a zero-sum dynamic as a strong and temporally consistent constraint on population dynamics (Hubbell 2001; Houlahan et al. 2007). In this framing, any resources made available through species loss should immediately be taken up by other species. This is not consistent with the dynamics that occur at Portal, as there have been extended periods of time when there are substantial resources available on exclosure plots that are not being used by any rodent species. Rather, the dynamics at Portal are more consistent with a zero-sum constraint operating at metacommunity, or, more broadly, evolutionary scales (Van Valen 1973; Terry and Rowe 2015; Leibold et al. 2017). Over short timescales, or within a closed local assemblage, niche differences may weaken zero-sum effects, especially under fluctuating conditions. However, over larger temporal and spatial scales, dispersal or evolution may supply new species equipped to take advantage of available resources - either through functional redundancy with species that have been lost, or niche complementarity allowing them to exploit novel niches. Moving forward, a long-term, metacommunity, and even macroevolutionary approach may be necessary to fully understand how zero-sum constraints manifest in community dynamics; how functional redundancy and niche complementarity jointly contribute to dynamics of community function; and how, and when, community-level properties are maintained in the face of species extinctions and changing conditions over time.

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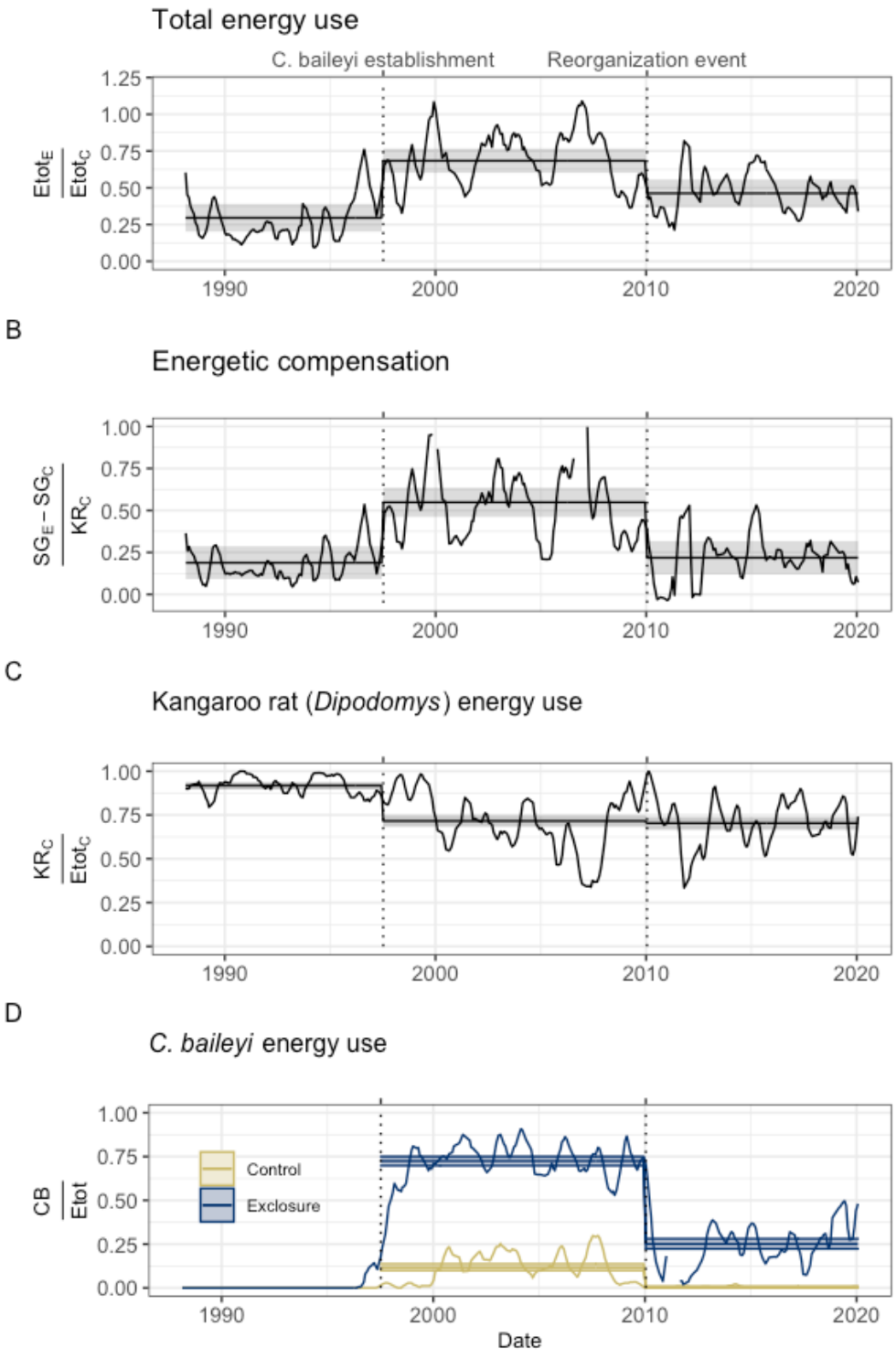
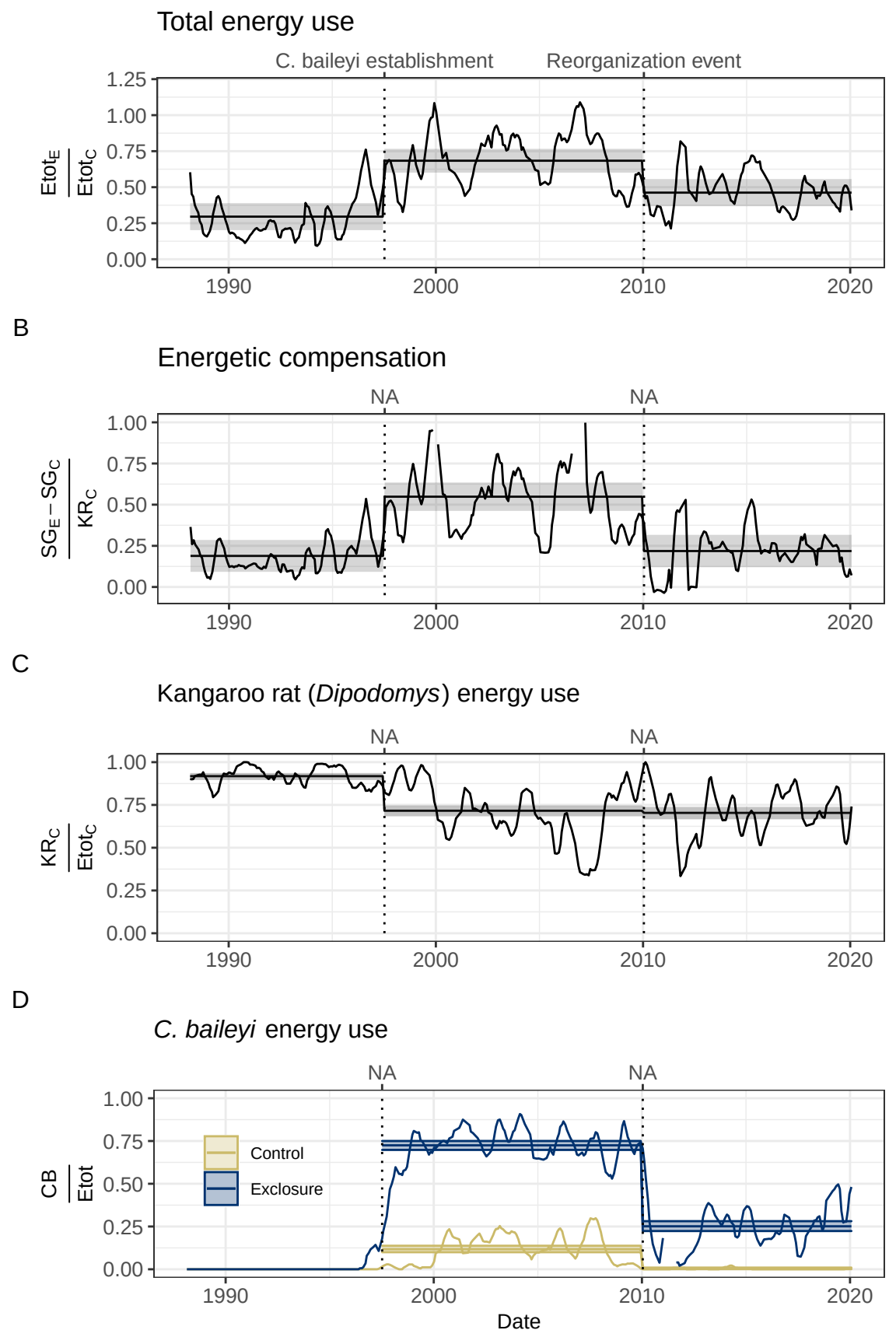
Figure legends

Figure 1. Dynamics of energy use and rodent community composition over time. Lines represent 6-month moving averages of energetic compensation (a), the ratio of energy use on exclosure plots to control plots (b), and the share of community energy use accounted for by kangaroo rats on control plots (c), and by *C. baileyi* (d), on control (gold) and exclosure (blue) plots. Dotted vertical lines mark the boundaries between time periods used for statistical analysis. Horizontal lines are time-period estimates from generalized least squares (a, b) and generalized linear (c, d) models, and the semitransparent envelopes mark the 95% confidence or credible intervals.

Figure 1


Total energy use
C. baileyi establishment
Reorganization event
EtotE / EtotC
1.25
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
B
Energetic compensation
SGE – SGC / KRC
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
C
Kangaroo rat (Dipodomys) energy use
KRC / EtotC
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
D
C. baileyi energy use
CB / Etot
Control
Exclosure
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
Date


Total energy use
C. baileyi establishment
Reorganization event
$\frac{Etot_E}{Etot_C}$
1.25
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
B
Energetic compensation
NA
NA
$\frac{SG_E - SG_C}{KR_C}$
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
C
Kangaroo rat (*Dipodomys*) energy use
NA
NA
$\frac{KR_C}{Etot_C}$
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
D
C. baileyi energy use
NA
NA
$\frac{CB}{Etot}$
Control
Exclosure
1.00
0.75
0.50
0.25
0.00
1990
2000
2010
2020
Date