1 **Title:** Maintenance of community function through compensation breaks down over time in a

2 desert rodent community

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18   **Abstract**

19   Understanding the ecological processes that maintain community function in systems

20   experiencing species loss, and how these processes change over time, is key to understanding the

21   relationship between community structure and function and predicting how communities may

22   respond to perturbations in the Anthropocene. Using a 30-year experiment on desert rodents, we

23   show that the impact of species loss on community-level energy use has changed repeatedly and

24   dramatically over time, due to 1) the addition of new species to the community, and 2) a

25   reduction in functional redundancy among the same set of species. Although strong

26   compensation, initially driven by the dispersal of functionally redundant species to the local

27   community, occurred in this system from 1997-2010, since 2010, compensation has broken

28   down due to decreasing functional overlap within the same set of species. Simultaneously, long-

29   term changes in sitewide community composition due to niche complementarity have decoupled

30   the dynamics of compensation from the overall impact of species loss on community-level

31   energy use. Shifting, context-dependent compensatory dynamics, such as those demonstrated

32   here, highlight the importance of explicitly long-term, metacommunity, and eco-evolutionary

33   perspectives on the link between species-level fluctuations and community function in a

34   changing world.

35   **Key words:** community function, compensation, zero-sum dynamic, environmental fluctuations,

36   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 (e.g. total productivity or resource use) are also directly lost. Community function may be maintained, however, if in the new community context, species that remain perform similar functions to the species that were lost, and 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. Colonization events may buffer community function against species loss, if a community gains species that perform similar functions to the species that were 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).

59   Even without the addition of new species and traits, however, functional redundancy

60   within a consistent set of coexisting species may fluctuate over time. While, in theory, functional

61   redundancy may occur via the special case of complete niche neutrality (e.g. Hubbell 2001), it

62   may also occur in niche-structured systems that contain species that share some traits but differ

63   along other niche axes (Thibault et al. 2010). In these systems, if similar, but non-identical,

64   species respond to environmental change in similar ways, functional overlap can be maintained

65   or even strengthened. However, if niche differences cause species to respond differently to

66   changing conditions, the degree of functional overlap between those species may decline,

67   resulting in a breakdown in compensation (Loreau 2004; Fetzer et al. 2015). Over time, as

68   metacommunity dynamics and changing environmental conditions modulate functional

69   redundancy within a community, the extent to which community function is robust to species

70   loss - and the strength of zero-sum competition - may also be dynamic and context-dependent.

71   Despite logical conceptual support, and evidence from experimental microcosms (Fetzer

72   et al. 2015), there is little empirical documentation of how, and through which mechanisms,

73   temporal changes in functional redundancy modulate the effect of species loss on ecosystem

74   function in natural assemblages. Although relatively plentiful, observational data cannot

75   unambiguously detect compensation through functional redundancy, and even short-term

76   experiments may not be sufficient to capture temporal variation in compensation (Ernest and

77   Brown 2001; Houlahan et al. 2007). In contrast, long-term manipulative experiments are

78   uniquely suited to address this question. In long-term experiments in which key species are

79   removed from a community over an extended period of time, the impact of species loss on

80   community function can be directly quantified by comparing community function between

81   complete and manipulated assemblages. As metacommunity dynamics and environmental

82   conditions shift over time, long-term monitoring can reveal how these processes contribute to

83   changes in functional redundancy and ecosystem function across different time periods. Due to

84   the financial and logistical resources required to maintain and monitor whole-community

85   manipulations over long timescales, these experiments are rare in natural systems representative

86   of realistic evolutionary, geographic, and environmental constraints (Hughes et al. 2017).

87   Here, we use a 30-year experiment on desert rodents to investigate how shifts in

88   functional redundancy alter the effect of species loss on community function over time. In this

89   study, kangaroo rats (*Dipodomys* spp.), the largest and competitively dominant species in the

90   rodent community, have been removed from a subset of experimental plots to explore how the

91   loss of key species affects community function, measured as community-level metabolic flux

92   ("total energy use", or *Etot*) or total biomass (Ernest et al. 2019). For systems of consumers with

93   a shared resource base, such as this community of granivorous rodents, *Etot* reflects the total

94   amount of resources being processed by an assemblage, and total biomass directly reflects

95   standing biomass. Both are important metrics of community function (Lawton 1994; Ernest and

96   Brown 2001). Long-term monitoring of this experiment has documented repeated shifts in the

97   habitat and species composition of this system, resulting in distinct time periods characterized by

98   different habitat conditions and configurations of the rodent community (Christensen et al.

99   2018). Abrupt reorganization events in community composition occurred in 1997 and in 2010,

100 associated with the establishment and subsequent decline of the pocket mouse *Chaetodipus*

101 *baileyi*. *C. baileyi* is similar in size, and presumably other traits, to kangaroo rats, and its

102 establishment in 1996-97 drove a pronounced increase in compensation due to functional

103 redundancy between *C. baileyi* and kangaroo rats (Ernest and Brown 2001; Thibault et al. 2010).

104 Over the course of this experiment, shifting environmental conditions have caused the habitat at

105   the study site to transition from desert grassland to scrub, driving a shift in baseline rodent

106   community composition away from kangaroo rats and favoring other, smaller, granivores

107   (Brown et al. 1997; Ernest et al. 2008). By making comparisons across these time periods, we

108   explored how shifts in community composition and functional overlap among the same species

109   have contributed to long-term changes in the effect of species loss on community function.

110   **Methods**

111   *The Portal Project*

112   The Portal Project consists of a set of 24 fenced experimental plots located approximately

113   7 miles east of Portal, AZ, USA, on unceded land of the Chiricahua Apache. Beginning in 1977,

114   kangaroo rats (*Dipodomys spectabilis, D. merriami,* and *D. ordii*) have been experimentally

115   excluded from a subset of these plots (exclosures), while all other rodents are allowed access

116   through small holes cut in the plot fencing. Control plots, with larger holes, are accessible to all

117   rodents, including kangaroo rats. Rodents on all plots are censused via monthly bouts of live-

118   trapping.Each individual captured is identified to species and weighed. For additional details on

119   the site and methodology of the Portal Project, see Ernest et al. (2019).

120   *Data*

121   We used data for control and exclosure plots from February 1988 until January 2020. The

122   experimental treatments for some plots have changed over time, and we used the subset of plots

123   that have had the same treatments for the longest period of time (Ernest et al. 2019). Four control

124   plots, and five exclosure plots, met these criteria. In order to achieve a balanced sample, we

125   randomly selected four exclosure plots for analysis. We divided the timeseries into three time

126   periods defined by major transitions in the rodent community surrounding the establishment and

127   decline of *C. baileyi* (Ernest and Brown 2001; Christensen et al. 2018). The first time period

128   (February 1988-June 1997) precedes *C. baileyi*'s establishment at site. We defined *C. baileyi*'s

129   establishment date as the first census period in which *C. baileyi* was captured on all exclosure

130   plots (following Bledsoe and Ernest, 2019). During the second time period (July 1997-January

131   2010), *C. baileyi* was abundant on both exclosure and control plots. This time period ended with

132   a reorganization event in which *C. balieyi* became scarce sitewide. We used January 2010, the

133   midpoint of the 95% credible interval for the date of this reorganization event as estimated in

134   Christensen et al. (2018), as the end date for this time period. The last time period spans from

135   Feburary 2010-January 2020. For each individual rodent captured, we estimated the individual-

136   level metabolic rate using the scaling relationship between individual body mass and metabolic

137   rate $b = 5.69 * (m^{0.75})$, where m is body mass in grams and b is metabolic rate (for details, see

138   White et al. 2004). We calculated treatment and species-level energy use as the sum of the

139   appropriate individuals' metabolic rates, and total biomass as the sum of individuals' body mass

140   measurements.

141   *Statistical analysis of rodent community energy use and biomass*

142   Here, we describe analyses for energy use. For biomass, we repeated these analyses

143   substituting biomass values for energy use throughout. For all variables, we combined data for

144   all plots within a treatment in each monthly census period and calculated treatment-level means.

145   This is necessary to calculate compensation, and we treated other variables in the same way to

146   maintain consistency. A provisional plot-level analysis yielded qualitatively equivalent results

147   (Appendix S1). To measure the overall impact of kangaroo rat removal on *Etot*, we calculated a

148   "total energy ratio" as the ratio of treatment-level *Etot* for kangaroo-rat exclosure plots relative to

149   unmanipulated control plots, i.e. $Etot_E/Etot_C$ where $Etot_E$ and $Etot_C$ are total energy use on

150   exclosures and controls, respectively (Thibault et al 2010; Bledsoe and Ernest 2019). This ratio is

151　distinct from compensation, which we defined as the proportion of the energy made available by

152　kangaroo rat removal taken up via compensatory increases in energy use by small granivores (all

153　granivores other than kangaroo rats; *Baiomys taylori, C. baileyi, Chaetodipus hispidus,*

154　*Chaetodipus intermedius, Chaetodipus penicillatus, Perognathus flavus, Peromyscus eremicus,*

155　*Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys fulvescens, Reithrodontomys*

156　*megalotis,* and *Reithrodontomys montanus*). We calculated this as $(SG_E - SG_C)/KR_C$, where SG_E

157　and SG_C are the amount of energy used by small granivores (SG) on exclosure and control plots,

158　respectively, and KR_C is the amount of energy used by kangaroo rats (KR) on control plots

159　(Ernest and Brown 2001). To compare these variables across time periods, we used generalized

160　least squares models (GLS; the R package *nlme*; Pinheiro et al. 2020) of the form (SG_E –

161　$SG_C)/KR_C \sim$ *time period*, for compensation, and $Etot_E/Etot_C \sim$ *time period*, for the total energy

162　ratio. We included a continuous-time autoregressive temporal autocorrelation term to account for

163　temporal autocorrelation between values from monthly census periods within each multi-year

164　time period (for details of model selection, see Appendix S2). To evaluate change in baseline

165　community composition over time, we calculated the proportion of treatment-level energy use

166　accounted for by kangaroo rats on control plots in each census period ($KR_C/Etot_C$). Proportional

167　energy use is bounded 0-1 and is therefore not appropriate for GLS, so we compared values

168　across time periods using a binomial generalized linear model (GLM) of the form $KR_C/Etot_C \sim$

169　*time period*. Finally, we calculated the proportional energy use accounted for by *C. baileyi* (CB)

170　on exclosure and control plots in each census period ($CB_E/Etot_E$ and $CB_C/Etot_C$, respectively). *C.*

171　*baileyi* was not present at the site prior to 1996, and we restricted the analysis of *C. baileyi*

172　proportional energy use to the second two time periods. We compared *C. baileyi* proportional

173　energy use over time and across treatments using a binomial GLM of the form $CB_E/Etot_E \sim$ *time*

174 *period + treatment*. For all models, we calculated estimated means and 95% confidence or

175 credible intervals for time-period (and, for *C. baileyi*, treatment) level values, and contrasts

176 between time periods (and, for *C. baileyi*, treatments), using the R package *emmeans* (Lenth

177 2021). Analyses were conducted in R 4.0.3 (R Core Team 2020). Data and code are archived at

178 https://doi.org/10.5281/zenodo.5544362 and https://doi.org/10.5281/zenodo.5539881.

179 **Results**

180   The impact of kangaroo rat removal on community function has changed repeatedly

181 over time, through a combination of abrupt shifts in compensation associated with *C. baileyi*, and

182 long-term changes in baseline community composition sitewide (Figure 1). These dynamics are

183 qualitatively identical whether function is measured as total energy use (Figure 1; Appendix S2)

184 or total biomass (Appendix S3). The first shift coincided with *C. baileyi*'s establishment in the

185 community beginning in 1996-97 (Figure 1D). *C. baileyi* rapidly became dominant on exclosure

186 plots and dramatically increased compensation (Figure 1B). From 1997-2010, small granivores

187 compensated for an average of 58% of kangaroo rat energy use on control plots (95% interval

188 48-67%), an increase from an average of 18% from 1988-1997 (95% interval 8-29%; contrast *p*

189 < 0.001; for complete results of all models, see Appendix S2) from 1997-2010. With *C. baileyi*'s

190 addition to the community, the total energy ratio (on exclosures relative to controls; Figure 1A)

191 increased from 30% (20-40%) to 71% (62-79%, contrast *p* < 0.014). In the second shift,

192 beginning around 2010, *C. baileyi*'s abundance sitewide dropped precipitously (Figure 1D). *C.*

193 *baileyi*'s proportional energy use dropped from an average of 72% (65-80%) to 26% (18-35%,

194 contrast *p* < 0.001) on exclosure plots, and from 11% (6-16%) to essentially 0 on control plots

195 (contrast *p* < 0.001). Other species of small granivore did not make compensatory gains to offset

196 the decline in *C. baileyi* (Figure 1B). As a result, compensation declined from an average of 58%

197   (48-67%) to 28% (17-38%, contrast $p = 0.002$), a level not significantly different from the 18%

198   (8-29%, contrast $p = .44$) observed prior to *C. baileyi*'s establishment at the site. Somewhat

199   paradoxically, while the total energy ratio also dropped following *C. baileyi*'s decline, from an

200   average of 71% (62-79%) from 1997-2010 to 50% (40-60%, contrast $p = 0.0056$) from 2010-

201   2020, it remained higher than its average of 30% (20-40%, contrast $p = 0.0144$) from 1988-1997

202   (Figure 1A). Over the course of the experiment, community composition shifted sitewide. In

203   later years, kangaroo rats accounted for a lower proportion of baseline *Etot* than they did at the

204   beginning of the study (Figure 1C). From 1988-1997, kangaroo rats accounted for 92% (87-97%)

205   of *Etot* on controls; after 1997, this dropped to an average of approximately 70% (1988-1997

206   compared to later time periods, both $p = .0004$; 1997-2010 and 2020-2020 not significantly

207   different, $p = .976$). Because the proportion of *Etot* directly lost to kangaroo rat removal was

208   smaller from 2010-2020 than from 1988-1997, the total energy ratio was higher from 2010-2020

209   than it was from 1988-1997 - even though there was not a detectable difference between the two

210   time periods in the proportion of lost energy being offset through compensation.

211   **Discussion**

212   The dynamics of rodent community energy use at Portal illustrate that the role of

213   functional redundancy in buffering community function against species loss fluctuates over time,

214   due to changes in both species composition and in the degree of functional overlap among the

215   same species. The 1997 increase in compensation, driven by *C. baileyi*'s establishment at the

216   site, was a clear and compelling instance of colonization from the regional species pool

217   overcoming limitations on functional redundancy (Ernest and Brown 2001; Leibold et al 2017).

218   Although the small granivore species originally present in the community did not possess the

219   traits necessary to compensate for kangaroo rats, *C. baileyi* supplied those traits and

220   substantially, but incompletely, restored community function. In contrast, following the

221   community reorganization event in 2010, *C. baileyi* remained present in the community, but

222   ceased to operate as a partial functional replacement for kangaroo rats. This is consistent with

223   fluctuating conditions modulating functional redundancy between similar, but non-identical,

224   competitors. Kangaroo rats and *C. baileyi* are relatively similar in size and are demonstrably

225   capable of using similar resources. However, *C. baileyi* prefers different, shrubbier microhabitats

226   than kangaroo rats, and the two groups have been observed to replace each other in adjacent

227   habitats (Ernest and Brown 2001). We suggest that this study site, which has historically been

228   dominated by kangaroo rats, constitutes marginal habitat for *C. baileyi*, and that, while

229   conditions from 1997-2010 aligned sufficiently with *C. baileyi*'s requirements to create

230   appreciable functional redundancy between kangaroo rats and *C. baileyi*, conditions since have

231   caused this redundancy to break down. *C. baileyi*'s decline occurred immediately following a

232   period of low plant productivity and low rodent abundance community-wide, and in the decade

233   following, the site experienced two long and severe droughts (Appendix S4; Christensen et al.

234   2018). These extreme conditions may themselves have limited *C. baileyi's* fitness at the site, or

235   the community-wide low abundance event may have temporarily overcome incumbency effects

236   and triggered a community shift tracking longer-term habitat trends (Thibault and Brown 2008;

237   Christensen et al. 2018). Regardless of the proximate cause of *C. baileyi*'s decline, the fact that

238   *C. baileyi* remains in the community, but no longer compensates for kangaroo rats, illustrates

239   that changing conditions can have profound effects on community function by modulating the

240   degree of functional redundancy within a consistent set of species.

241   While changes in compensation have contributed to changes in community function in

242   this system, changes in compensation alone do not fully account for the long-term changes in the

243   overall impact of kangaroo rat removal on *Etot*. Since 2010, although the ratio of *Etot* on

244   exclosure plots relative to control plots declined coinciding with the breakdown in compensation

245   associated with *C. baileyi*, it remained higher than the levels observed prior to 1997 (Figure 1A).

246   This difference between the first and last time periods cannot be explained by an increase in

247   compensation, as compensation from 2010-2020 was not greater than pre-1997 levels (Figure

248   1B). Rather, the increase in *Etot* on exclosure plots relative to control plots was the result of a

249   long-term decrease in the contribution of kangaroo rats to *Etot* sitewide. Because kangaroo rats

250   accounted for a smaller proportion of *Etot* on control plots from 2010-2020 than they did prior to

251   1997, their removal had a smaller impact on community function – even though there was not an

252   increase in the degree to which small granivores compensated for their absence. In fact, the

253   comparable levels of compensation achieved in the decades preceding and following *C. baileyi*'s

254   dominance at the site suggest a relatively stable, and limited, degree of functional overlap

255   between kangaroo rats and the original small granivores (i.e., excluding *C. bailyei*). Niche

256   complementarity, combined with changing habitat conditions, may partially explain this

257   phenomenon. It is well-documented that, while kangaroo rats readily forage in open

258   microhabitats where predation risk can be relatively high, smaller granivores preferentially

259   forage in sheltered microhabitats as an antipredator tactic (Kelt 2011). Over the course of this

260   experiment, the habitat at this study site has transitioned from an arid grassland to a shrubland

261   (Brown et al. 1997). As sheltered microhabitats became more widespread, small granivores may

262   have gained access to a larger proportion of resources and increased their share of *Etot* sitewide.

263   However, kangaroo rats may have continued to use resources in open areas, which would have

264   remained inaccessible to smaller granivores even on exclosure plots. The long-term reduction in

265   the impact of kangaroo rat removal on community function, driven by niche complementarity

266 and consistent niche partitioning, contrasts with the temporary compensatory dynamic driven by

267 functional redundancy with *C. baileyi*. Although changes in the overall effect of species loss are

268 sometimes treated interchangeably with compensation (e.g. Ernest and Brown 2001 compared to

269 Thibault et al. 2010), it is important to recognize that multiple distinct pathways modulate the

270 long-term impacts of species loss on community function. Particularly in strongly niche-

271 structured systems, complementarity effects and fluctuations in functional redundancy may occur

272 simultaneously, with complex and counterintuitive impacts on community function.

273   Overall, the decadal-scale changes in energy use among the Portal rodents underscore the

274 importance of long-term metacommunity dynamics to the maintenance of community function

275 following species loss (see Leibold et al. 2017). Although a single colonization event may allow

276 for temporary compensation via functional redundancy, as conditions shift, species that once

277 compensated may no longer perform that function (see also Isbell et al. 2011). Particularly if

278 limiting similarity prevents similar competitors from specializing on precisely the same habitats

279 (Rosenfeld 2002), temporary, context-dependent compensation may be common. To maintain

280 compensation over time, multiple colonization events, supplying species that are functionally

281 redundant under different conditions, may be required. Depending on dispersal rates, and the

282 diversity and composition of regional species pools, this may be unlikely or even impossible. At

283 Portal, dispersal limitation introduced a 20-year delay in the compensatory response driven by *C.*

284 *baileyi*. Theoretically, a new species capable of compensating for kangaroo rats, and better-

285 suited to conditions at the site since 2010, could restore compensation under present conditions –

286 but it is unclear whether this species exists or if it can disperse to this site. As ecosystems

287 globally undergo reductions in habitat connectivity and regional beta diversity, and enter novel

288   climatic spaces, maintenance of community function via functional redundancy may grow

289   increasingly rare and fragile (Dornelas et al. 2014; Williams and Jackson 2007).

290   Finally, the long-term variability in functional redundancy documented here adds

291   important nuance to our understanding of how zero-sum dynamics operate in natural

292   assemblages. Theories invoking zero-sum dynamics, and tests for compensatory dynamics in

293   empirical data, often treat a zero-sum dynamic as a strong and temporally consistent constraint

294   (Hubbell 2001; Houlahan et al. 2007). In this framing, any resources made available via species

295   loss should immediately be taken up by other species. This is not consistent with the dynamics

296   that occur at Portal, which has seen extended periods of time when resources are available on

297   exclosure plots but are not used. Rather, these results are more consistent with a zero-sum

298   constraint operating at metacommunity or evolutionary scales (Van Valen 1973; Terry and Rowe

299   2015; Leibold et al. 2017). Over short timescales, or within a closed local assemblage, niche

300   differences may weaken zero-sum effects, especially under fluctuating conditions. However,

301   over larger temporal and spatial scales, dispersal or evolution may supply new species equipped

302   to use available resources - via either functional redundancy, or niche complementarity allowing

303   them to exploit novel niches. A long-term, metacommunity, and even macroevolutionary

304   approach may be necessary to fully understand how zero-sum constraints, functional

305   redundancy, and niche complementarity contribute to the maintenance of community-level

306   function in the face of species extinctions and changing conditions over time.

307   **Acknowledgements**

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401 **Figure legends**

402 **Figure 1.** Dynamics of energy use and rodent community composition over time. Lines represent

403 the ratio of total energy use on exclosure plots to control plots (a), 6-month moving averages of

404 energetic compensation (b), and the share of community energy use accounted for by kangaroo

405 rats on control plots (c), and by *C. baileyi* (d), on control (gold) and exclosure (blue) plots.

406 Dotted vertical lines mark the boundaries between time periods used for statistical analysis.

407 Horizontal lines are time-period estimates from generalized least squares (a, b) and generalized

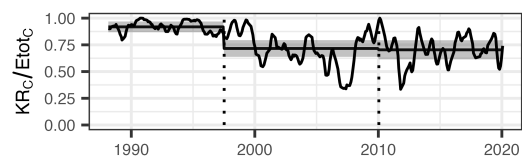408 linear (c, d) models, and the semitransparent envelopes mark the 95% confidence or credible

409 intervals.

410

411
412

a. Total energy use ratio
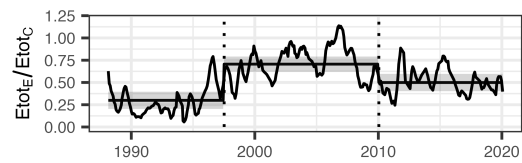
b. Energetic compensation
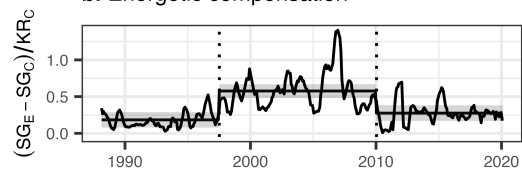
c. Kangaroo rat proportional energy use

d. *C. baileyi* proportional energy use

Control
Exclosure

Date