1 **Temporal changes in species composition affect a ubiquitous species' use of habitat patches**

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24 **Abstract**

25 Across landscapes, shifts in species composition often co-occur with shifts in structural or abiotic

26 habitat features, making it difficult to disentangle the role of competitors and environment on

27 assessments of patch quality. Using 22 years of rodent community data from a long-term

28 experiment, we show that a small, ubiquitous granivore (*Chaetodipus penicillatus*) shifted its use

29 of different experimental treatments with the invasion of a novel competitor, *C. baileyi*. Changes

30 in population metrics such as residency, probability of movement between patches, and the

31 arrival of new individuals in patches resulted in changes in which treatment supported the

32 highest abundances of *C. penicillatus*. Our results suggest that the invasion of a new species

33 worsened the quality of the originally preferred treatment, probably through its impacts on

34 resource availability. Paradoxically, the invader also increased *C. penicillatus'* use of the less

35 preferred treatment, potentially through shifts in the competitive network on those plots.

36 **Key words**: habitat selection, patch quality, patch preference, species composition

37

38 **Introduction**

39   Species often exist in landscapes consisting of a patchwork of habitats, some of which are

40 conducive to a species' survival and reproduction and others which are less suitable. Building

41 upon intraspecific habitat selection (Fretwell & Lucas 1970) and optimal patch use theory

42 (Charnov 1976, Brown 1988), numerous studies have shown that interspecific habitat selection

43 can act as a potential mechanism of species coexistence (e.g., Grant 1971, Schoener 1974,

44 Morris 1989, Morris 2003). Landscape heterogeneity creates niche opportunities (Comins &

45 Noble 1985) while variability in patch connectivity supports scenarios where populations can be

46 rescued from extinction by dispersal (Brown & Kodric-Brown 1977) or where species can find

47   isolated refuges when they would otherwise be driven extinct (Sedell et al. 1990). However,

48   changes in patch conditions can also take place through time (Ernest et al. 2008), resulting in

49   patches that vary in their suitability for a species as conditions change. Despite the fact that

50   population dynamics and regional processes (i.e., dispersal, colonization, extinction) are

51   inherently both spatial and temporal, temporal variation in patches is rarely incorporated into

52   studies on patch preference.

53   While many studies on habitat selection focus on differences between patches in

54   structural habitat (e.g., vegetation structure) or abiotic conditions (e.g., temperature, soil

55   conditions), species density and composition can also affect patch preference (Grant 1971,

56   Morris 1989, Danielson & Gaines 1987, Abramsky et al. 1992). Understanding a species'

57   response to species composition is complicated because shifts in species composition often co-

58   occur across landscapes with shifts in structural or abiotic habitat features (Whittaker 1967, Tews

59   et al. 2004). Species may be less abundant or absent from certain patches, but whether that

60   absence is due to the patch having an incompatible environment, the isolation of the patch from

61   other patches, the presence of superior competitors, or a combination of any of the above reasons

62   is often unclear. Thus, in determining how a species uses the landscape through time, it is often

63   difficult to disentangle the roles of structural or abiotic habitat qualities from species interactions

64   (Grant 1971, Kraft et al. 2015).

65   In this study, we use time-series data from a desert rodent community in southeastern

66   Arizona, USA, to show how both spatial and temporal variation in the species composition in

67   patches affect species and their use of habitat patches. Our system has both control plots (all

68   rodents have access) and manipulated plots in which kangaroo rats, the behaviorally dominant

69   genus in the system, are selectively excluded. Recent studies have shown only minimal impacts

70   of the treatment on the plant community (Supp et al. 2012); thus, this system creates a landscape

71   with patches of differing quality due primarily to differences in rodent species composition.

72   In the mid-1990s, a species of large pocket mouse (*Chaetodipus baileyi*) colonized and

73   exhibited a preference for kangaroo rat exclosures. Here, we ask how the patch preference of a

74   small, subdominant pocket mouse, *C. penicillatus*, across this landscape of patches with and

75   without kangaroo rats was impacted by the arrival of the larger pocket mouse, *C. baileyi*.

76   Because congeners are expected to compete more strongly due to their shared evolutionary

77   history, we hypothesized that 1) *C. penicillatus* use of treatment would change with the

78   establishment of *C. baileyi,* 2) the magnitude of change would be correlated with *C. baileyi*

79   abundance, and 3) *C. penicillatus* residency, probability of moving between treatments, and

80   recruitment of new individuals would show corresponding changes with the establishment of *C.*

81   *baileyi*.

82

83   **Methods**

84   ***Study System and Data***

85   We used a 22-year time series (1988 – 2010) of capture-mark-recapture rodent data

86   collected from the Portal Project to assess how *C. penicillatus* responded to the arrival of a novel

87   competitor, *C. baileyi*, through time. While *C. penicillatus* has been caught at the site throughout

88   the time series, *C. baileyi* was first caught at the site in 1995. Over the next decade, *C. baileyi*

89   became a dominant species in the system; in the late 2000s, however, *C. baileyi's* population

90   crashed and did not rebound (Appendix S1: Fig. S4). While *C. baileyi* individuals continue to be

91   caught occasionally, the species is no longer dominant (see Appendix S1 for more details).

92   The Portal Project is a long-term experimental system (Brown 1998) located in the

93   Chihuahuan desert near Portal, Arizona, USA, on colonized land of the Chiricahua Apache now

94   under the jurisdiction of the U.S. Bureau of Land Management. The site consists of 24 50x50 m

95   fenced plots with three treatments. In control plots ($n = 10$), holes cut in the fence are large

96   enough to allow all rodent species access while full rodent removal plots ($n = 6$) have no gates.

97   Kangaroo rat exclosures ($n = 8$) have small holes in the fences which allow passage of all rodents

98   except for kangaroo rats (*Dipodomys* genus), which are behaviorally dominant in the system

99   (Brown & Heske 1990).

100   In this study, we primarily use data from 18 plots—controls and kangaroo rat

101   exclosures—though we include data from full removals in calculations of residency and

102   probability of movement between treatments to increase estimate accuracy. Each plot consists of

103   49 evenly-spaced permanent trapping stations in a 7x7 grid. Rodent abundance and composition

104   data are collected monthly using Sherman live traps (Ernest et al. 2018). We identify trapped

105   individuals to species, measure and record size and sex characteristics, and give each rodent an

106   individualizing marker (previously toe and ear tags, now exclusively passive integrated

107   transponder (PIT) tags).

108   We only use data through 2010 because this is when *C. baileyi* was no longer dominant

109   in the system. Including additional data through 2014 (treatments for many plots were changed

110   in early 2015) produced qualitatively similar results (Appendix S1: Fig. S1-S3).

111   ***Patch use of C. penicillatus in response to C. baileyi abundance***

112   We assessed changes in relative abundance of *C. penicillatus* between control plots and

113   kangaroo rat exclosures by fitting a linear model along the 1:1 line of mean *C. penicillatus* per

114   plot by year in kangaroo rat exclosures against control plots. We then fit a linear generalized

115   least squares model (*nlme*, Pinheiro et al. 2018) of mean *C. baileyi* per plot by year against the

116   resulting residuals from the previous model, accounting for temporal autocorrelation (see

117   supplements), to evaluate how *C. penicillatus'* habitat use shifted with increases in *C. baileyi*

118   abundance.

Population-level metrics of C. penicillatus

120   For *C. penicillatus* in each treatment, we calculated apparent survival (*S*), transition

121   probability (Ψ), and the average number of new individuals per treatment. Both survival and

122   transition probability were estimated through a multistate capture-mark-recapture model using

123   the *RMark* package, an R interface for the MARK software (White & Burnham 1999, Laake

124   2013). Different strata represented treatment types, and each time step was a trapping period. We

125   designated each time period as being either before or after the establishment of *C. baileyi*; the

126   first trapping period in which *C. baileyi* was caught in all eight kangaroo rat exclosures (July

127   1997) was used as the differentiating time point. We assumed that recapture probabilities (*p*)

128   were equal between the treatments. Our data do not allow for differentiation between permanent

129   emigration and death, so these two processes are not differentiated in our survival estimates; we

130   believe that any differences in apparent survival are driven primarily by emigration and,

131   therefore, will hereafter refer to this metric as residency. We used Program CONTRAST, a

132   program designed specifically for comparing survival estimates (Hines & Sauer 1989), to run

133   chi-squared tests to determine the significance of differences in residency and transition

134   probabilities between *C. baileyi* establishment and treatments.

135   We calculated the number of new *C. penicillatus* individuals, defined as individuals

136   caught and given identification tags for the first time, in each treatment. Using mean new *C.*

137   *penicillatus* individuals per plot by year, we ran a linear mixed effects model (*nlme*, Pinheiro et

138   al. 2018) to assess the interaction between treatments and *C. baileyi* establishment.

139   ***System-level aspects of patch preference***

140   Changes in species composition can have substantial effects on the energy use in a

141   system (Ernest & Brown 2001). To determine how this aspect of ecosystem functioning might

142   have contributed to *C. penicillatus* use of patches through time, we calculated the ratio of total

143   energy use per year between the kangaroo rat exclosures and controls (*portalr*, Yenni et al.

144   2018).

145   ***Analyses***

146   All analyses were performed using R 3.5.0 (R Core Team 2018). Data and code are

147   available on GitHub (https://github.com/bleds22e/PP_shifts).

148

149   **Results**

150   ***Patch use of C. penicillatus in response to C. baileyi abundance***

151   After its arrival in 1995, *C. baileyi* increased in abundance until the late 2000s (Fig. 1a)

152   and was found far more frequently on the kangaroo rat exclosures than the control plots

153   (Appendix S1: Fig. S4). *C. penicillatus'* preferences for the two treatment types also shifted

154   through time (Fig. 1b). *C. penicillatus* had higher average abundance in the kangaroo rat

155   exclosure plots before *C. baileyi* arrived. During the time *C. baileyi* was established, however, *C.*

156   *penicillatus* had an even higher average abundance on controls. *C. penicillatus's* preference for

157   control plots increased with increases in *C. baileyi* abundance (Fig. 1c; y = -0.14x + 0.40, df =

158   16, RSE = 0.40, p < 0.001).

159   ***Population-level metrics of C. penicillatus***

160   Residency of *C. penicillatus* depended on treatment and *C. baileyi* status ($\chi^2 = 10.72$, df =

161   3, p = 0.01). Before *C. baileyi* colonized the site, residency for *C. penicillatus* was significantly

162   higher on kangaroo rat exclosures than on controls (Fig. 2a). This difference completely

163   disappeared after *C. baileyi* established, at which point residency became statistically

164   indistinguishable between treatments.

165   The transition probability of *C. penicillatus* also depended on treatment and *C. baileyi*

166   status ($\chi^2 = 16.53$, df = 3, p < 0.001). The probability of a *C. penicillatus* individual moving from

167   a kangaroo rat exclosure to a control plot was low, regardless of *C. baileyi* establishment (Fig.

168   2b). When a *C. penicillatus* individual moved before *C. baileyi*'s arrival, it was more likely to

169   move from a control plot to a kangaroo rat exclosure. Afterwards, however, the probability of a

170   *C. penicillatus* individual moving from a control plot to a kangaroo rat exclosure was not only

171   significantly lower than before *C. baileyi* establishment but also significantly lower than the

172   probability of movement in the other direction (Fig. 2b).

173   The significant interaction between treatments and *C. baileyi* establishment in new (i.e.,

174   untagged) *C. penicillatus* individuals also supports changes in patch preference (Fig. 2c). Before

175   the arrival of *C. baileyi*, kangaroo rat exclosures had significantly higher numbers of new

176   individuals appearing ($F_{1,389} = 24.87$, p < 0.001); after *C. baileyi* established in the system, new

177   individuals were consistently found on control plots in higher average numbers until the period

178   of *C. baileyi* decline in the late 2000s.

179   ***System-level aspects of patch preference***

180   Prior to *C. baileyi* fully establishing in the system, the energy on kangaroo rat exclosures

181   was only a fraction of that on control plots (Fig. 3). With the arrival of *C. baileyi*, however, the

182   average energy on kangaroo rat exclosure plots reached over 80% of the energy used on control

183   plots, even with *C. penicillatus* individuals moving to the control plots.

184

185   **Discussion**

186   Our results suggest that the arrival of a congener changed perceptions of patch quality for

187   one of the abundant rodent species in our ecosystem, *C. penicillatus.* Changes in patch use can

188   be driven by perceived declines in an individual's current patch or perceived increases in quality

189   in another patch. Increases in new *C. penicillatus* individuals on the controls and declines in

190   residency on kangaroo rat exclosures suggest that both of these mechanisms may have occurred

191   with the arrival of *C. baileyi*, ultimately shifting patch use by *C. penicillatus*.

192   Declines in the perceived quality of kangaroo rat exclosures—as evidenced by declines in

193   *C. penicillatus* residency—could have been caused by changes in resource availability after the

194   arrival of *C. baileyi* (Fig. 1). Before *C. baileyi* established, rodent energy use on the kangaroo rat

195   exclosures was never more than half of that found in the control plot (Fig. 3). With the

196   preferential establishment of *C. baileyi* on the kangaroo rat exclosures, however, the energy ratio

197   between the exclosure and control plots increased considerably. If patches have roughly the same

198   amount of resources, patches with lower rates of energy use should have more resources that are

199   not being fully exploited (MacArthur & Pianka 1966). Because the two species are congeners,

200   niche similarities due to a shared evolutionary history may have increased the possibility of

201   substantive overlap in their resource preferences. Thus, the colonization of *C. baileyi* on

202   kangaroo rat exclosures may have had a substantive effect on rates of resource use on those

203   plots, thus altering foraging and fitness expectations for *C. penicillatus*. This could explain the

204   corresponding declines in residency for *C. penicillatus* (Fig. 2a) on kangaroo rat exclosures.

205   However, while this explains why kangaroo rat exclosures may have been perceived as worse

206   environments after the arrival of C. baileyi, this does not explain why controls were suddenly

207   able to support higher numbers of *C. penicillatus*.

208   Greater increases in abundances of *C. penicillatus* on controls than on kangaroo rat

209   exclosures suggest that *C. penicillatus* perceived improvements in the quality of those patches.

210   Since *C. penicillatus'* residency and transition probabilities were similar between treatments after

211   the arrival of *C. baileyi*, increases in abundance appear to be due to higher numbers of new

212   individuals arriving on controls (Fig. 2c). These new individuals could be due to increases in

213   birth rates, immigration rates or juvenile survivorship or decreases in juvenile dispersal rates, but

214   we unfortunately do not have the data to discern the source of the new individuals.

215   Higher immigration rates into some patches over others can reflect differences in

216   distances to source populations (i.e., mass effects or source-sink dynamics; Holt 1985, Pulliam

217   1988) or active decisions by individuals based on their expected fitness or resource intake rate in

218   a patch, which is indicative of density-dependent habitat selection (e.g., Grant 1971, Brown &

219   Munger 1985, Morris 1987, Abramsky et al. 1992, Morris & MacEachern 2010). Because our

220   patches are interspersed in a matrix that is suitable habitat for *C. penicillatus*, all patches should

221   be equidistant from a *C. penicillatus* source population. We also see no reason *C. penicillatus*

222   should perceive control plots as improved based on abiotic conditions, habitat structure, or

223   resource availability. At the scale of the site, all plots experience the same weather and our

224   measure of rodent energy use suggests that resource availability on the two plot types is very

225   similar (Fig 3). Furthermore, while the site has experienced vegetation changes (Brown 1998),

226   there is no indication that this has differed by treatment (Ernest 2001).

227   The movement of *C. penicillatus* to control plots after the establishment of *C. baileyi*

228   presents an interesting dilemma. If there were ecological opportunities (e.g., resource

229   availability, territory, etc.) for *C. penicillatus* in the control plots after *C. bailey* become

230   established on the kangaroo rat exclosures, why was *C. penicillatus* not utilizing that space

231   previously? After *C. baileyi* established in the system, control plots tended to have a higher

232   abundance of competitors (*Dipodomys spp.* and *C. baileyi*) than kangaroo rat exclosures ($p <$

233   0.001, Appendix S1: Fig. S5), making density-dependent habitat selection an unlikely

234   explanation. Coexistence theory provides another interesting possibility. Resource competitors

235   that would be unable to coexist if they interacted only with each other can actually benefit each

236   other when they share a common competitor (Levine 1976, Stone & Roberts 1991, Allesina and

237   Levine 2011). At our site, while *C. baileyi* showed a preference for kangaroo rat exclosures over

238   controls, they were still present on control plots in considerable numbers (Fig. S1; Thibault and

239   Brown 2008). Both natural history and observed dynamics at our site have shown that *C. baileyi*

240   also competes with kangaroo rats (Thibault and Brown 2008), probably due to its similar size

241   and dietary overlap (Reichman 1975). Thus, in this "enemy of my enemy is my friend" scenario,

242   the shifts in the competitive network caused by adding *C. baileyi* to controls may have

243   paradoxically improved conditions on control plots for *C. penicillatus,* leading to higher vital

244   rates, more new individuals, and higher abundances on controls.

245   Species' perceptions of patch quality can vary depending on a variety of factors, such as

246   resource availability (MacArthur & Pianka 1966), biotic interactions (Grant 1971, Abramsky et

247   al. 1992), and other habitat properties (Brown 1988). Changes in patch quality and selection can

248   also affect communities and metacommunities through landscape-level processes (e.g., dispersal,

249   colonization/extinction; Pulliam & Danielson 1991, Resetarits & Silberbush 2016). In this study,

250   we used an experimental long-term study to show how species invasion and resulting shifts in

251   the species composition can affect a species' perception of patch quality and patch preference.

252   This is not to suggest that changes in structural habitat or abiotic factors do not impact patch

253   preference; much work in landscape ecology and metacommunity theory has shown that they can

254   (Leibold & Chase 2018); rather, we use time series and experimentally manipulated patches to

255   tease apart the effects of species composition from those of structural or abiotic habitat

256   differences, changes which frequently occur together spatially. This method allows us to still

257   assess spatial use patterns—a key aspect of metacommunity theory—while also allowing

258   changes through time to inform our observations. We suggest that time is a key component in

259   any holistic study of patch preference in community structure and metacommunity dynamics.

260

261   **Acknowledgments**

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270   **Literature Cited**

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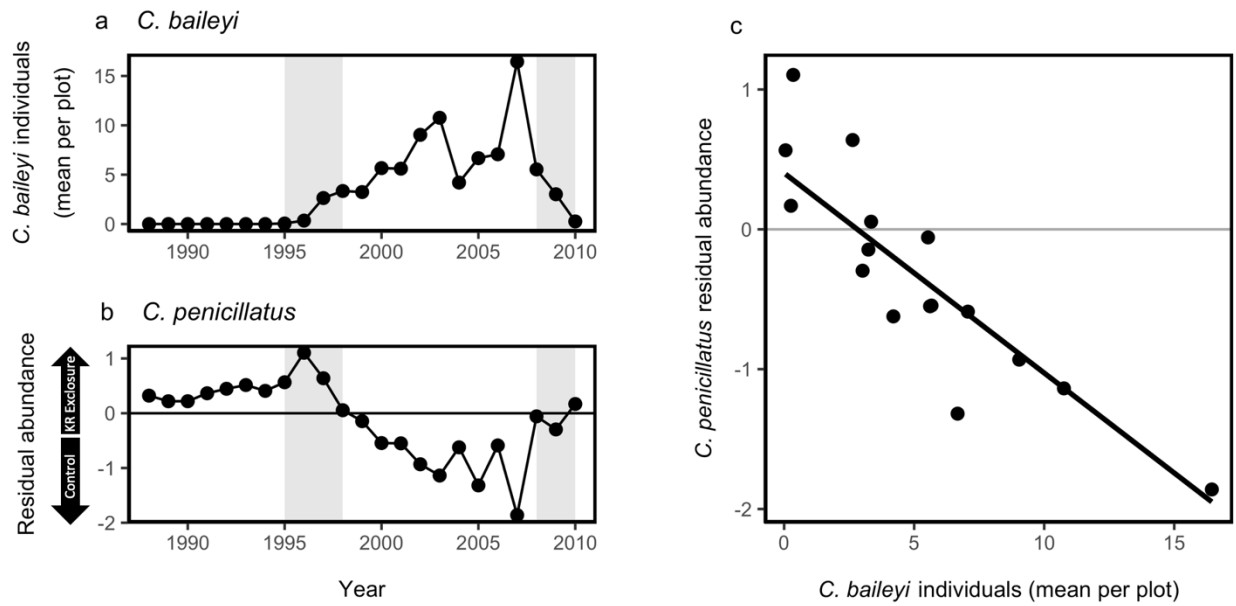362   http://doi.org/10.5281/zenodo.1492721.

363   **Figure Legends**

364   **Figure 1:** Relationship between *C. penicillatus* abundances on treatments and *C. baileyi*

365   abundance. (a) Average number of *C. baileyi* individuals per plot through time. (b) The

366   difference between mean *C. penicillatus* individuals per treatment through time. The zero line

367   indicates equal numbers of *C. penicillatus* on both treatments. Points are residuals from a linear

368   model run against a 1:1 line of mean *C. penicillatus* abundance on kangaroo rat exclosures

369   against controls. Above the zero line (positive residuals) indicates higher mean *C. penicillatus*

370   abundance on kangaroo rat exclosures; below the line (negative residuals) are higher mean *C.*

371   *penicillatus* on controls. In (a) and (b), grey bars indicate the colonization period (1995-1998)

372   and subsequent decline (2008-2010) of *C. baileyi.* (c) Generalized least squares regression of *C.*

373   *penicillatus* differences from equal (y-axis from [a]) against mean *C. baileyi* individuals per plot

374   per year (y-axis from [b]). As mean *C. baileyi* abundances increase, the mean abundance of *C.*

375   *penicillatus* shifts from more individuals on kangaroo rat exclosures to more on controls.
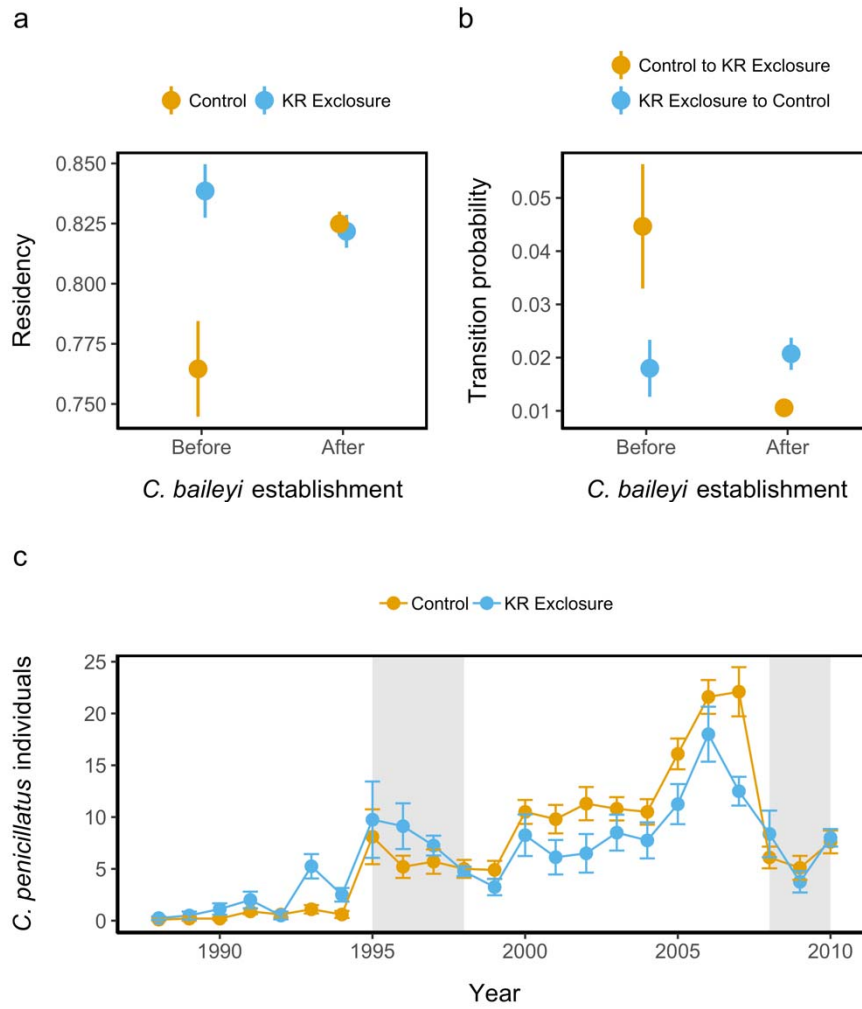
376

377   **Figure 2.** Population-level metrics of *C. penicillatus* by treatment type. (a) Residency of *C.*

378   *penicillatus* by treatment and *C. baileyi* establishment in the system. (b) Probability of *C.*

379   *penicillatus* individuals moving from one treatment to the other, also based on *C. baileyi*

380   establishment. (c) Mean new *C. penicillatus* individuals per plot through time. Grey bars indicate

381   the period of establishment (1995-1998) and subsequent decline (2008-2010) of *C. baileyi.*

382

383   **Figure 3.** Ratio of total rodent energy in kangaroo rat exclosures to controls though time. Grey

384   bars indicate establishment (1995-1998) and subsequent decline (2008-2010) of *C. baileyi.*
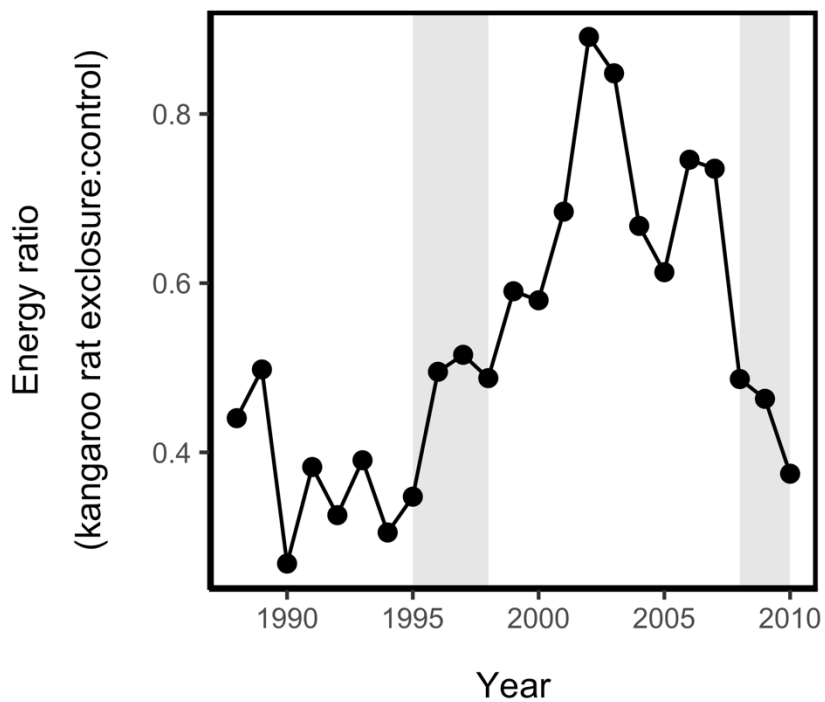
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385 **Figure 1**

386 **Figure 2**

a

b

c

387

388

389   **Figure 3**

390