1   **Temporal changes in species composition affect a ubiquitous species' views of patch quality**

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9   **Abstract**

10   Metacommunity theory, particularly the patch dynamics archetype, suggests that an organism's

11   perspective of patch quality can depend solely on the local competitive environment. Across

12   landscapes, however, shifts in species composition often co-occur with shifts in habitat, making

13   it difficult to disentangle the role of competitors and environment on assessments of patch

14   quality. Using 26 years of rodent community time-series data, we show that perception of patch

15   quality by a small, ubiquitous granivore (*Chaetodipus penicillatus*) shifted with both spatial and

16   temporal changes in species composition. In the mid-1990s, *C. baileyi*, a novel competitor,

17   colonized and the study site. *C. penicillatus* patch preference shifted with increasing abundance

18   of *C. baileyi*, including corresponding changes in estimated survival, probability of movement

19   between patches, and the arrival of new individuals in patches. Changes in energy use on patches

20   due to the establishment of *C. baileyi* point to a potential mechanism for the differences in patch

21   quality perceived by *C. penicillatus*. These results demonstrate that experimental time-series data

22   can be used to examine how changes in species composition and, specifically, changes in the

23   competitive landscape, can affect perception of patch quality and patch preference.

24   **Key words**: metacommunity, patch heterogeneity, patch preference, species composition

25

26   **Introduction**

27   Species often exist on continuous landscapes consisting of a patchwork of habitats, some

28   of which are conducive to a species' survival and reproduction and others which are less suitable.

29   The long-term persistence of a species on one of these landscapes is a function of both its

30   interactions with other species within suitable patches and the ability of it and its enemies to

31   move across this landscape (Huffaker 1958, Ricklefs 1987). One framework developed to study

32   such scenarios is metacommunity theory (Leibold et al. 2004). A metacommunity is a group of

33   interacting communities (or "localities") connected by dispersal (Wilson 1992, Leibold et al.

34   2004). One of the most useful aspects of the metacommunity framework is the ability to

35   simultaneously consider multiple processes that are acting at different scales. Within patches,

36   multiple populations of species interact, and mechanisms of species coexistence play an

37   important role. These local communities, however, are also connected to each other at a larger

38   scale where regional processes (e.g., dispersal, colonization and extinction events, and landscape

39   heterogeneity) become increasingly important. Two main messages have emerged from

40   metacommunity theory since its formal proposal by Leibold et al. (2004): 1) metacommunities

41   represent the interaction of local and regional processes and the scales at which they operate, and

42   2) *some* type of patch heterogeneity remains an integral assumption to the vast majority of work

43   on metacommunities (Leibold & Chase 2018).

44   Landscape heterogeneity in patches is important for maintaining diverse

45   metacommunities. Variability in environmental conditions creates niche opportunities (Comins

46   & Noble 1985), while variability in patch connectivity supports scenarios where populations can

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

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48   find isolated refuges when they would otherwise be driven extinct (Sedell et al. 1990).

49   Metacommunity ecology often focuses on spatial patterns in heterogeneity—differences between

50   patches in habitat (e.g., vegetation structure) or abiotic conditions (e.g., temperature, soil

51   conditions). However, changes in patch conditions can also take place through time (Azeria &

52   Kolasa 2008, Ernest et al. 2008), resulting in patches that may vary in their suitability for a

53   species as conditions change in the future. Despite the fact that population dynamics and regional

54   processes (i.e., dispersal, colonization, extinction) are inherently both spatial *and* temporal,

55   temporal variation in patch heterogeneity is not frequently incorporated into the metacommunity

56   framework.

57   An organism's perspective on the quality of a patch not only depends on the

58   environmental conditions of a patch but also the local competitive environment (i.e.,

59   colonization-competition trade-offs; Levins & Culver 1971, Tilman 1994). For example, two

60   patches of equivalent environment may differ considerably in their suitability for a species based

61   solely on the presence or absence of a dominant competitor (Durant 1998). Because

62   metacommunities are embedded in dynamic landscapes, the impact of a dominant competitor on

63   a subdominant species' patch preferences may also vary over time depending on the resource-

64   supply rates or shifts in the competitive hierarchy (Tilman 1982, Amarasekare et al. 2004).

65   Understanding a species' perception of biotically-induced changes in patch quality over time is

66   complicated because shifts in species composition often co-occur across landscapes with shifts in

67   habitat (MacArthur et al. 1966, Whittaker 1967, Tews et al. 2004). Species may be less abundant

68   or absent from certain patches, but whether that absence is due to the patch having an

69   incompatible environment, the isolation of the patch from other patches, the presence of superior

70   competitors, or a combination of any of the above reasons is often unclear. Thus, the role of

71   shifting biotic conditions in determining how a species views the patchy landscape is often

72   difficult to disentangle (Kraft et al. 2015).

73   To understand how shifts in species composition can alter a species' perception of patch

74   quality, we can leverage long-term experiments manipulating the presence of dominant species

75   across patches. If conducted at a small enough spatial scale, these species manipulations are

76   independent of landscape-level changes in environmental conditions that often are correlated

77   with changes in species composition. In this study, we use time-series data from a desert rodent

78   community in southeastern Arizona, USA, to show how both spatial *and* temporal variation in

79   the competitive biotic landscape affect species and their perception of patch quality. Our system

80   has both control plots (all rodents have access) and manipulated plots in which kangaroo rats, the

81   behaviorally dominant genus in the system, are selectively excluded. Recent studies have shown

82   only minimal impacts of the treatment on the plant community (Supp et al. 2012, Christensen et

83   al. 2018); thus, this system creates a landscape with patches differing in quality due primarily to

84   differences in rodent species composition caused by the removal of the dominant competitor,

85   kangaroo rats. In the mid-1990s, this competitive landscape was altered when a species of large

86   pocket mouse (*Chaetodipus baileyi*) colonized. It rapidly became one of the most abundant

87   species at the site for over two decades but exhibited a preference for kangaroo rat exclosure

88   plots. Here, we ask how the patch preference of a small, subdominant pocket mouse, *C.*

89   *penicillatus*, across this landscape of patches with and without kangaroo rats was impacted by

90   the change in the competitive landscape with the arrival of the larger pocket mouse, *C. baileyi*.

91

92   **Methods**

93   *Study System and Data*

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94   We used a 26-year time series (1988 – 2014) of capture-mark-recapture rodent data

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

96   competitor, *C. baileyi*, through time. The Portal Project, started in 1977, is a long-term

97   experimental system (Brown et al. 1998) located in the Chihuahuan desert near Portal, Arizona,

98   USA, on colonized land of the Chiricahua Apache now under the jurisdiction of the U.S. Bureau

99   of Land Management. The site consists of 24 50x50 m fenced plots with three treatment types. In

100   control plots ($n = 10$), holes cut in the fence are large enough to allow all rodent species access

101   while full rodent removal plots ($n = 6$) have no gates. Kangaroo rat exclosures ($n = 8$) have small

102   holes in the fences which allow passage of all rodents except for kangaroo rats (*Dipodomys*

103   genus), which are behaviorally dominant in the system (Brown & Heske 1990). Each plot

104   consists of 49 evenly-spaced permanent trapping stations in a 7x7 grid. Rodent abundance and

105   composition data are collected monthly using Sherman live traps (Ernest et al. 2018). We

106   identify trapped individuals to species, measure and record size and sex characteristics, and give

107   each rodent an individualizing marker. In the past, toe and ear tags were used to mark

108   individuals, but we now exclusively use passive integrated transponder (PIT) tags. We excluded

109   data collected after 2014 because the treatments for many plots changed in early 2015.

110

111   *Analyses*

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

113   GitHub (https://github.com/weecology/PortalData; https://github.com/bleds22e/PP_shifts).

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115   *Patch preference of C. penicillatus in response to C. baileyi abundance*

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116   To determine how *C. penicillatus* abundance in control plots and kangaroo rat exclosures

117   differed from equal through time, we fit a linear model along the 1:1 line of mean *C. penicillatus*

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

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

120   resulting residuals from the previous model to demonstrate how *C. baileyi* mean abundance

121   relates to *C. penicillatus'* plot treatment preferences. Accounting for temporal autocorrelation did

122   not significantly improve the model (see supplemental material for details).

123

124   *Population-level metrics of C. penicillatus*

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

126   probability (Ψ), and the average number of new individuals per plot type. Both survival and

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

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

129   2013). Different strata represented treatment types, and each time step was a trapping period. We

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

131   system; the first trapping period in which *C. baileyi* was caught in all eight kangaroo rat

132   exclosures (July 1997) was used as the differentiating timepoint. In the model, we assumed that

133   recapture probabilities (*p)* were equal between the plot types. Additionally, it should be noted

134   that our data does not allow for differentiation between permanent emigration and death, and,

135   therefore, these two processes are not differentiated in our survival estimates. We used Program

136   CONTRAST, a program designed specifically for comparing survival estimates (Hines & Sauer

137   1989), to run chi-squared tests to determine if differences in survival and transition probabilities

138   between *C. baileyi* establishment and treatment types were statistically significant.

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

140   caught and given an identification tags, for the first time,in each treatment type. We then

141   calculated mean and standard error of new *C. penicillatus* individuals per plot by year by

142   treatment type.

143

144   *System-level aspects of patch preference*

145   Changes in species composition have been shown to have substantial effects on the

146   energy use in a system (Ernest & Brown 2001). To determine how this aspect of ecosystem

147   functioning might have contributed to how *C. penicillatus* view the quality of patches through

148   time, we calculated the ratio of total rodent biomass per year between the kangaroo rat

149   exclosures and control plots (*portalr*; Yenni et al. 2018).

150

151   **Results**

152   *Patch preference of C. penicillatus in response to C. baileyi abundance*

153   After its arrival in the mid-1990s, *C. baileyi* increased in abundance until the late 2000's

154   (Fig. 1a) and was found far more frequently on the kangaroo rat exclosures than the control plots

155   (Fig. S1). *C. penicillatus'* preferences for the two treatment types also shifted through time (Fig.

156   1b). *C. penicillatus* had higher average abundance in the kangaroo rat exclosure plots before *C.*

157   *baileyi* arrived. During the time *C. baileyi* was established, however, *C. penicillatus* had a higher

158   average abundance on control plots. *C. penicillatus's* preference for control plots increased with

159   increases in *C. baileyi* abundance (Fig. 1c; y = -0.163x + 0.662, df = 20, RSE = 0.46, p <0.05).

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161   *Population-level metrics of C. penicillatus*

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162   Estimated survival of *C. penicillatus* showed significant differences between treatment

163   types and *C. baileyi* status (χ^2 = 15.22, df = 3, p = 0.002). Before *C. baileyi* colonized the site,

164   estimated survival for *C. penicillatus* was significantly higher on kangaroo rat exclosures than on

165   controls (Fig. 2a). This difference completely disappears after *C. baileyi* becomes established, at

166   which point estimated survival becomes statistically indistinguishable between treatment types.

167   The transition probability of *C. penicillatus* also showed significant differences between

168   treatment types and *C. baileyi* status (χ^2 = 12.44, df = 3, p = 0.006). The probability of a *C.*

169   *penicillatus* individual moving from a kangaroo rat exclosure to a control plot was low,

170   regardless of *C. baileyi* establishment (Fig. 2b). When a *C. penicillatus* individual moved before

171   *C. baileyi*'s arrival, it was more likely to move from a control plot to a kangaroo rat exclosure.

172   Afterwards, however, the probability of a *C. penicillatus* individual moving from a control plot

173   to a kangaroo rat exclosure was not only significantly lower than before *C. baileyi* establishment

174   but also significantly lower than the probability of movement in the other direction (Fig. 2b).

175   The differences in arrival of new (i.e., untagged) *C. penicillatus* individuals on the two

176   treatments also support changes in patch preference (Figure 2c). Before the arrival of *C. baileyi*,

177   kangaroo rat exclosures had, on average, slightly higher numbers of new individuals appearing.

178   After *C. baileyi* established in the system, new individuals were consistently found on control

179   plots in higher average numbers until the period of *C. baileyi* decline in the late 2000s.

180

181   *System-level aspects of patch preference*

182   Prior to *C. baileyi* fully establishing in the system, the biomass on kangaroo rat exclosure

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

184   the average biomass on kangaroo rat exclosure plots reached over 80% of the biomass found on

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

186

187   **Discussion**

188   If a species changes its patch preference due to changes in the competitive landscape,

189   there should be detectable effects on population metrics such as apparent survival, patch choice,

190   and the probability of movement between patch types (Morris & Davidson 2000, Gurnell et al.

191   2004). Our results show responses in all of these metrics, indicating that *C. penicillatus*

192   perceived a substantive change in the suitability of kangaroo rat exclosures with the colonization

193   of *C. baileyi*. Before the arrival of *C. baileyi*, *C. penicillatus* was disproportionately found in

194   kangaroo rat exclosures and exhibited higher survival, lower transition probabilities, and a larger

195   influx of new individuals than on the control plots. After the arrival and establishment on *C.*

196   *baileyi* on the kangaroo rat exclosures, however, *C. penicillatus* was found disproportionately in

197   control plots (Fig. 1), a higher number of new individuals were detected on control plots (Fig

198   2c), and survivorship and transition probabilities converged between plot types (Fig 2ab). Thus,

199   with the arrival of *C. baileyi*, kangaroo rat exclosures shifted from high quality patches to

200   patches of a similar, or even slightly lower, quality as control plots. Because all patches are in

201   more-or-less the same habitat (Supp et al. 2012, Christensen et al. 2018), this approach allowed

202   us to disentangle effects of community composition from habitat differences on perception of

203   patch quality by effectively eliminating the habitat changes that often coincide with changes in

204   species composition.

205   Our results provide some insights into the mechanisms that led to higher *C. penicillatus*

206   numbers on control plots once *C. baileyi* established on kangaroo rat exclosures. Higher *C.*

207   *penicillatus* abundances on control plots after *C. baileyi's* establishment seems due to more new

208   individuals being caught on control plots (Fig. 3). However, once *C. penicillatus* individuals

209   established territories on control plots, similar apparent survivorship and transition probabilities

210   on treatments and controls suggest they perceived little difference between these plot types after

211   *C. baileyi* colonized. We do not know whether the higher numbers of new individuals on control

212   plots were due to higher birth rates, higher juvenile survivorship, lower juvenile dispersal rates,

213   or higher immigration rates for controls. Shifts in control plot birth rates, juvenile survivorship,

214   or juvenile emigration rates would suggest that conditions on control plots had improved; we are

215   not aware of any mechanisms, however, that would improve the quality of control plots without

216   also improving the nearby kangaroo rat exclosures. Instead, we suspect that dispersing

217   individuals from the surrounding matrix of desert habitat were preferentially deciding to enter

218   control plots rather than *C. baileyi*-dominated kangaroo rat exclosures.

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

220   distances to source populations (i.e., mass effects or source-sink dynamics; Schmida & Wilson

221   1985, Holt 1985, Pulliam 1988) or active decisions by individuals based on their expected fitness

222   or resource intake rate in a patch (e.g., Ideal Free Distribution, optimal foraging; Fretwell &

223   Lucas 1970, Charnov 1976). Because our patches are interspersed in a matrix that is suitable

224   habitat for *C. penicillatus*, all patches should be equidistant from a *C. penicillatus* source

225   population. However, the colonization of *C. baileyi* on kangaroo rat exclosures had a substantive

226   effect on rates of resource use on those plots, which may have altered foraging and fitness

227   expectations for *C. penicillatus*. Before *C. baileyi* established in the system, rodent biomass of

228   the kangaroo rat exclosures was never more than half of that found in the control plot (Fig. 3).

229   With the preferential establishment of *C. baileyi* on the kangaroo rat exclosures, however, the

230   biomass ratio between the exclosure and control plots increased considerably. In addition to

231   demonstrating the impact that the establishment of one species can have on the entire system, the

232   biomass ratio nearing equal helps shed light on why the arrival of *C. baileyi* caused *C.*

233   *penicillatus's* clear shifts in patch preference (Fig. 1). The changes in biomass also correspond to

234   changes in energy use in the system (Ernest & Brown 2001). If patches have roughly the same

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

236   not being fully exploited (MacArthur & Pianka 1966). As the biomass and, subsequently, energy

237   use in the plot types neared equal, the kangaroo rat exclosures were no longer overtly preferable,

238   and *C. penicillatus* showed corresponding changes in patch preferences (e.g., changes in survival

239   rates, Fig. 2a). As resource availability became more similar, the importance of resource

240   availability in discriminating among patches may have diminished and allowed other factors to

241   influence the decision-making process of *C. penicillatus*. One possibility is that niche similarities

242   between *C. penicillatus* and its congener, *C. baileyi*, made establishing territories on plots with

243   *C. baileyi* more difficult, or simply less appealing, for dispersing *C. penicillatus* individuals.

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

245   resource availability (MacArthur & Pianka 1966), biotic interactions (Durant 1998, Gurnell et al.

246   2004), and other habitat properties (Brown 1988, Butler et al. 2005). In many systems, changes

247   in species composition correspond to changes in habitat (MacArthur et al. 1966, Whittaker 1967,

248   Tews et al. 2004). Therefore, teasing apart the effects of species composition and habitat

249   properties on a species' perception of patch quality can prove challenging. In this study, we show

250   that experimental time-series data can be used to help elucidate how changes in species

251   composition and, specifically, changes in the competitive landscape, can affect perception of

252   patch quality and patch preference. This is not to suggest that changes in habitat or abiotic

253 factors do not impact patch preference; much work in landscape ecology and metacommunity

254 theory has shown that they can (Leibold & Chase 2018); rather, we use time series and

255 experimentally manipulated patches to tease apart the effects of species composition from those

256 of habitat, changes which frequently occur together spatially (Durant 1998, Tews et al. 2004).

257 This method allows us to still assess spatial use patterns—a key aspect of metacommunity

258 theory—while also allowing changes through time to inform our observations. We suggest that

259 time is a key component in any holistic study of patch preference in metacommunity dynamics.

260

261 **Acknowledgments**

268

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Figure Legends

Figure 1: Relationship between *C. penicillatus* abundances on treatments and *C. baileyi* abundance. (a) Average number of *C. baileyi* individuals per plot through time. (b) The difference between mean *C. penicillatus* individuals per treatment type through time. The zero line indicates equal numbers of *C. penicillatus* on both treatments. Points are residuals from a linear model run against a 1:1 line of mean *C. penicillatus* abundance on kangaroo rat exclosures against control plots. Above the zero line (positive residuals) indicates higher mean *C. penicillatus* abundance on kangaroo rat exclosures; below the line (negative residuals) are higher mean *C. penicillatus* on control plots. In (a) and (b), grey bars indicate the colonization period (1995-1998) and subsequent decline (2008-2010) of *C. baileyi.* (c) Generalized least squares regression of *C. penicillatus* differences from equal (y-axis from (a)) against mean *C. baileyi* individuals per plot per year (y-axis from (b); $y = -0.163x + 0.662$, df = 20, RSE = 0.46, p <0.05). As mean *C. baileyi* abundances increase, the mean abundance of *C. penicillatus* shifts from more individuals on kangaroo rat exclosures to more on control plots.

Figure 2. Population-level metrics of *C. penicillatus* by treatment type. (a) Estimated survival of *C. penicillatus* by treatment type and *C. baileyi* establishment in the system. (b) Probability of *C. penicillatus* individuals moving from one treatment type to the other, also based on *C. baileyi* establishment. (c) Mean new *C. penicil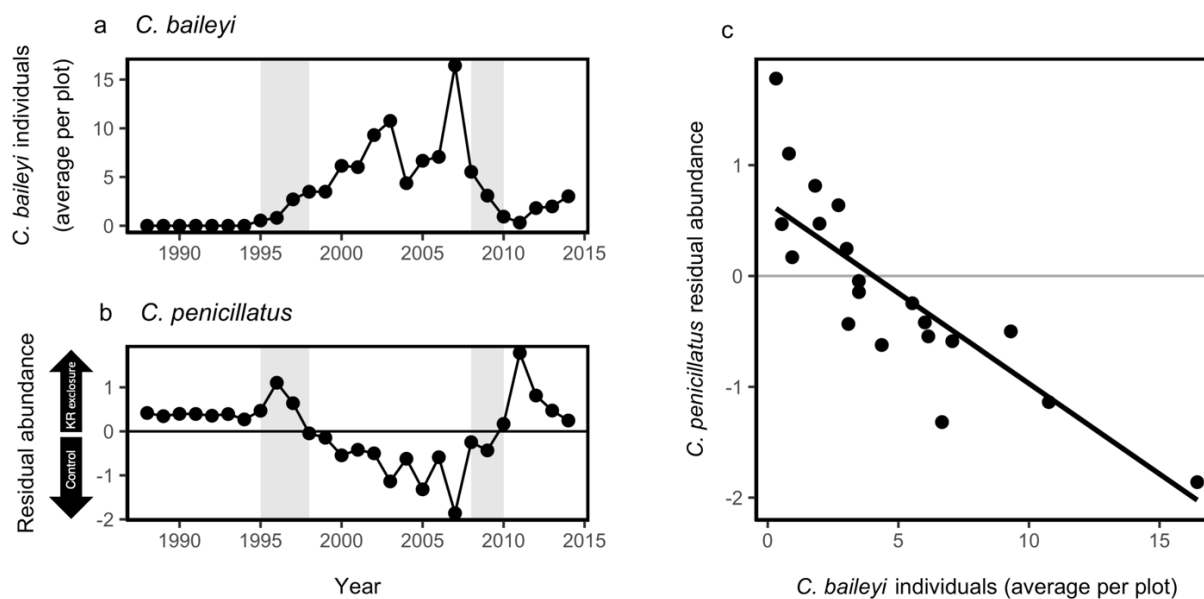latus* individuals per plot through time. Grey bars indicate the period of establishment (1995-1998) and subsequent decline (2008-2010) of *C. baileyi.*

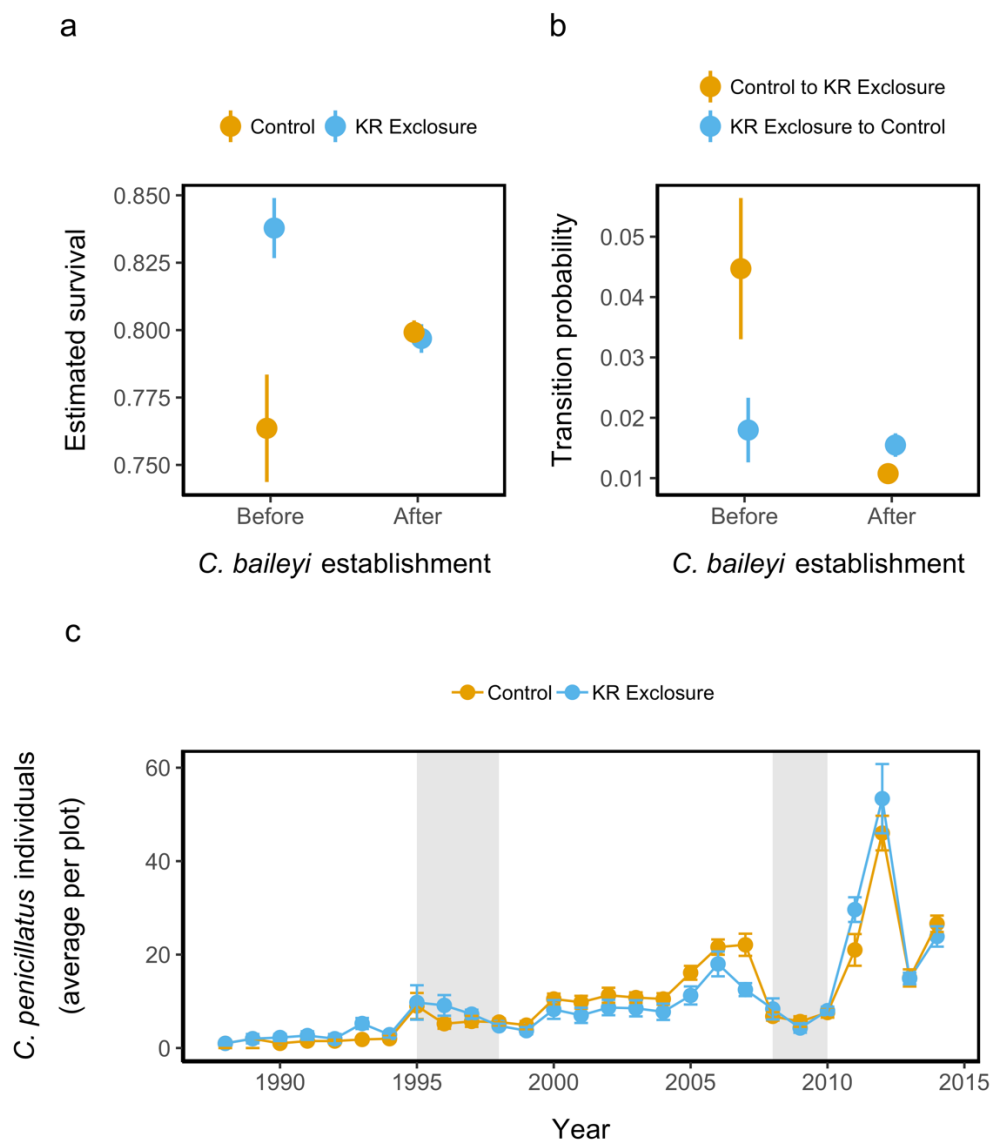**Figure 3.** Ratio of total rodent biomass in kangaroo rat exclosures to control plots though time. Grey bars indicate establishment (1995-1998) and subsequent decline (2008-2010) of *C. baileyi.*
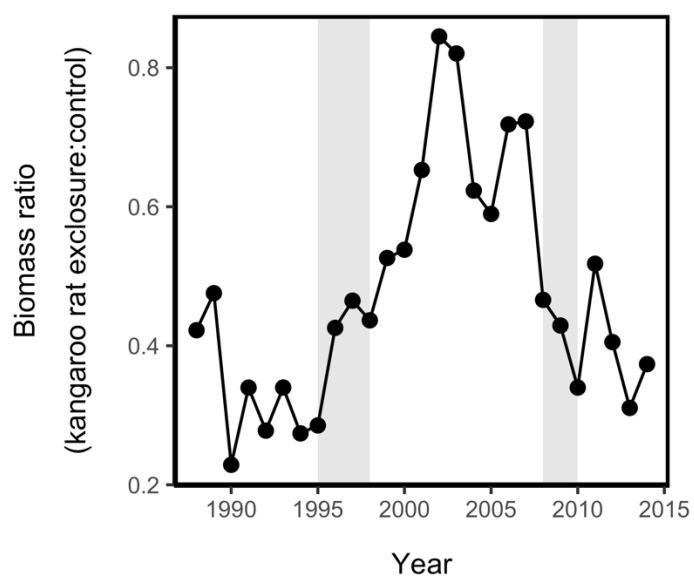
390   **Figure 1**

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392   **Figure 2**

a

b

c

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395   **Figure 3**

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