1 **Using life history trade-offs to understand core-transient structuring of a small mammal**

2 **community**

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Abstract

An emerging conceptual framework suggests that communities are composed of two main groups of species through time: core species that are temporally persistent, and transient species that are temporally intermittent. Core and transient species have been shown to differ in spatiotemporal turnover, diversity patterns, and importantly, survival strategies targeted at local vs. regional habitat use. While the core-transient framework has typically been a site-specific designation for species, we suggest that if core and transient species have local vs. regional survival strategies across sites, and consistently differ in population-level spatial structure and gene flow, they may also exhibit different life-history strategies. Specifically, core species should display relatively low movement rates, low reproductive effort, high ecological specialization and high survival rates compared to transient species, which may display a wider range of traits given that transience may result from source-sink dynamics or from the ability to emigrate readily in a nomadic fashion. We present results from 21 years of capture-mark-recapture data in a diverse rodent community, evaluating the linkages between temporal persistence, local abundance, and trade-offs among life-history traits. Core species at our site conservatively supported our hypotheses, differing in ecological specialization, survival and movement probabilities, and reproductive effort relative to transient species. Transient species exhibited a wider range of characteristics, which likely stems from the multiple processes generating transience in local communities, such as source-sink dynamics at larger regional scales or nomadic life history strategies. We suggest that trait associations among core-transient species may be similar in other systems and warrants further study.

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Introduction

50   A pervasive characteristic of ecological communities is that they tend to be composed of a

51   few common species and many rare ones. Traditionally, ecologists have assumed that particular

52   structuring processes are equally important for explaining patterns of abundance among all

53   species in a community. Alternately, species abundances have been modeled as a product of

54   spatially linked metapopulations or metacommunities (e.g., Hanski 1982; Gaston and Lawton

55   1989; Gotelli 1991; Urban and Skelly 2006). An emerging view posits that species occurring at a

56   site can be sorted into two different groups that should be modeled differently based on temporal

57   patterns of occupancy (Magurran and Henderson 2003): core species that display high temporal

58   persistence (i.e. present most years) and transient species that exhibit low temporal persistence

59   (i.e. present only occasionally). Core species tend to account for most of the abundance or

60   biomass within a particular community. The richness of core species is better predicted by local

61   environmental conditions, presumably reflecting the need for strong local adaptation to

62   outcompete other species and maintain highly abundant, persistent populations in a specific

63   habitat (Ulrich and Ollik 2004; Belmaker 2009; Coyle et al 2013). In contrast, transient species

64   tend to be rare, and their richness in a local community is better predicted by regional factors (e.g.

65   spatial heterogeneity, regional species pool), presumably because dispersal is a critical process

66   allowing those species to immigrate into particular habitats (Costello & Myers 1996; Milstead et

67   al. 2007; Henderson and Magurran 2014). Because core species at a site require a strong match

68   between their niche requirements and local environmental conditions to maintain populations

69   whereas immigration is the primary process governing the presence of transient species, the core-

70   transient framework suggests that the spatial and temporal scale of processes influencing the two

71   groups should differ.

72   Although transient species move into a local site from other habitat patches on the

73   landscape, and thus suggests the importance of habitat connectivity and linked populations within

74   a given time frame, the core-transient framework is fundamentally distinct from its spatial analog,

75   the core-satellite framework (Hanski 1982). The core-transient framework assigns species based

76   on temporal persistence at a single site (e.g., the fraction of years where present; Magurran and

77   Henderson 2003; Ullrich and Ollik 2004, Vergnon et al. 2009; Coyle et al. 2013), whereas the

78   core-satellite framework asigns species based on spatial patterns of occurrence across a regional

79   metapopulation (e.g., the fraction of sites in the region where present; Hanski 1982). For example,

80   a species could be identified as regionally "core" because it inhabits a high fraction of habitat

81   patches, but be identified as temporally "transient" at a single site that it inhabits infrequently

82   across a time-series. Here, we use "core" and "transient" to refer to species' occupancy within a

83   time-series of a single site.

84   Core-transient research has primarily focused on differences between temporally defined

85   groups at a site in how they respond to the same environment. However, if core and transient

86   species differ in the importance of local and regional processes in maintaining populations at a

87   site, they may also differ in the ecological and evolutionary drivers ultimately determining their

88   presence, abundance and diversity (Magurran and Henderson 2003; Dolan *et al.* 2009, Coyle *et*

89   *al.*2013, Connolly et al. 2014). While little research has focused on this question *per se*, a rich

90   literature on metapopulations, metacommunities, and the evolution of dispersal suggest that core

91   and transient species could indeed experience different pressures that would select for different

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92 ecologies or life history strategies. Core species must successfully compete in, and adapt to, their

93 local biotic and abiotic environment. As such, core species that are strongly governed by local

94 ecological processes experience strong local co-evolutionary pressures with their biotic and

95 abiotic environment (McCauley 2007). Species that are highly adapted to a particular

96 environment can evolve reduced dispersal tendencies in part because of the cost of moving into a

97 maladaptive environment (Kisdi 2002). Limited gene flow through reduced dispersal among

98 populations enhances the role of local natural selection and adaptation for core species (Hanski

99 1982, McPeek and Holt 1992; Kisdi 2002; Urban *et al.* 2008). By focusing on using local habitat

100 and reducing the tendency to disperse, core species must also be able to persist through acclimate

101 environmental conditions. This likely involves specialized behaviors or traits to allow persistence

102 under poor conditions (Hanski 1982, Clutton-Brock 1991, Ghalambor & Martin 2000, Kisdi

103 2002).

104 The ecological and evolutionary pressures on transient species are more complicated.

105 Although there is only one way to be core, there are two primary processes that may generate

106 transient species within a local community, each with different resulting expectations of the eco-

107 evolutionary pressures imposed. One process that can generate transients in a local community is

108 source-sink dynamics (e.g., Hanski 1982). Source-sink transients are species that are core at other

109 sites on the landscape through time, but not in the focal site. Because they are well-adapted

110 elsewhere and immigration from the adapted source population should swamp local adaption to

111 the new environment (Holt and Gaines 1992; Lenormand 2002; Kawecki and Holt 2002; Kawecki

112 2008), we would expect source-sink transients to retain many of the same general life history

113 characteristics as core species – except with low temporal occupancy.

114 In contrast to source-sink transients, some transients may form short-term reproducing

115 populations before disappearing and potentially reappearing later via immigration. Processes that

116 could generate this type of transient include opportunistic tracking of shifting resources across a

117 region (e.g. Weins 2001; Roshier and Reid 2003; Milstead et al. 2007; Jonzen et al. 2011) or

118 competition-colonization tradeoffs (e.g., Diamond 1974; Kneitel and Chase 2004). Both cases

119 create what we will call nomadic transients – individuals that form reproducing populations for

120 short periods of time in a local habitat before moving elsewhere on the landscape. Nomadism

121 results from irregular, non-sedentary behavior, and differs from migration in that movements may

122 be made at any time of year following any path (e.g., no fixed breeding grounds, low home range

123 stability), and may occupy a large portion of the animal's life (Baker 1978; Roshier and Reid

124 2003). Nomadic transients are strongly governed by regional ecological processes with high

125 levels of movement across the landscape that reflects demographic processes or spatial

126 rearrangement in response to changing conditions though time (O'Donnell 2001; Roshier and

127 Reid 2003).

128 Increased individual movement may impact the long-term evolutionary dynamics of

129 nomadic transient species if: 1) high gene flow homogenizes gene pools and inhibits local

130 adaptation (Urban *et al.* 2008) or 2) intermediate gene flow increases the capacity for local

131 adaptation in unstable habitats via novel subsidies from the regional gene pool (Roshier and Reid

132 2003; Urban and Skelly 2006; Loeuille and Leibold 2008). Both the high gene flow and

133 intermediate gene flow scenarios suggest that on average transient species should be less adapted

134 to local biotic and abiotic conditions than core species. Because they are less well adapted to local

135 conditions, they are expected to be at a competitive disadvantage, except for their ability to

136 exploit novel conditions in unstable environments. If nomadic transient species depend on a

137 regional life history strategy that requires the ability to track suitable environmental conditions

138 and use heterogeneous landscapes, then they should be strongly associated with traits that enable

139 them to traverse non-ideal habitat patches and to colonize new suitable habitat patches as they

140 arise (McCauley 2007). Increased dispersal ability and movement rates come with costs that may

141 include increased mortality risk and increased time and energetic expenditure (Murray 1967;

142 Hanski 1982; Waser 1985; Rousset and Gandon 2002). To maximize fitness amidst such costs, it

143 may be optimal for nomadic transient species to trade-off survival investment toward increased

144 reproductive allocation (*e.g.*, Clutton-Brock 1991; Stearns 1992) and they may have thus evolved

145 associations with life-history traits such as low survival probability, high fecundity, early age of

146 primiparity, and resource or habitat generalism (Diamond 1974; Charlesworth 1980).

147   The core-transient framework can thus provide a key connection of the slow-fast theory of

148 life history evolution (Ricklefs and Wikelski 2002; Sibly and Brown 2007) with movement and

149 habitat use strategies. From theoretical and empirical studies on dispersal, metapopulations, and

150 metacommunities, we might expect a life history strategy for core species focused on local-scale

151 coexistence to include low movement rates, low mortality rates, high immune function, limited

152 gene flow among populations, high specialization for local conditions, and decreased fecundity.

153 Source-sink transients should show similar trait correlations as core species, except that they

154 should exhibit lower abundances and temporal persistence and have little genetic differentiation

155 between source and sink populations (Gaggiotti 1996). For nomadic transients, we expect the

156 opposite set of characteristics from core species. Nomadic species at a site should generally be

157 expected to have higher movement rates, be able to reproduce in a wider range of habitats, exhibit

158 increased fecundity, higher gene flow among populations, but lower survival (Mueller and Fagan

159 2008; Baguette et al. 2013). While this possible link between the core-transient framework and

160   life-history traits is intriguing, there has been no empirical evaluation, especially examining

161   correlations in traits across species within the same community.

162   We use 21-years of data from a diverse desert rodent community containing information

163   on movement, mark-recapture rates, and reproduction to test aspects of the hypothesis that core

164   species have fundamentally different life-history strategies than transient species as expected

165   from differences in local vs. regional habitat use. We predict that core species will generally be

166   associated with relatively low movement rates, high survival rates, and low fecundity. We predict

167   that transient species will display a mixture of traits, depending on whether they are source-sink

168   or nomadic transients, but generally have more incidence of high movement rates, low survival

169   rates, high fecundity, and resource or habitat generalism (Figure 1).

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171   **Materials and Methods**

172   *Study site and data*

173   We evaluated the relationship between life history traits and core-transient status at our

174   site using 21 years (1989-2009) of capture-mark-recapture (CMR) data for rodents from a long-

175   term experimental site in the Chihuahuan desert in southeastern Arizona (the Portal Project field

176   site; Ernest *et al.* 2009). The study site consists of 24, 0.25 ha fenced plots (50 m X 50 m). Each

177   month, year-round, plots are trapped on a grid consisting of 49 evenly spaced permanent stakes

178   to survey the rodent community and to maintain experimental treatments. Four gates cut into

179   each side of the fenced plots allow free passage of rodents in and out of plots. Large-bodied and

180   behaviorally dominant kangaroo rats (*Dipodomys spp.*) have enlarged auditory bullae that make

181   it possible to selectively exclude them from plots that have a smaller gate size (n=8). Total

182   rodent removal plots have no gates (n=6), while control plots (n=10) have relatively large gates

183   that allow all species access (Brown 1998). Rodents are known to follow barriers until a path

184   opens (Singleton et al. 1998), ensuring that plot gates are discovered, and there are not

185   significant differences in species colonization of the plots compared to the natural landscape

186   (Brown and Maurer 1985). Upon capture, each individual was marked by toe clipping, ear tags

187   or with a permanent, subcutaneous passive integrated transponder (PIT) tag that allowed it to be

188   uniquely identified upon capture. For each captured individual, we recorded species, sex,

189   reproductive status, hind foot length, weight, and individual PIT tag. For our analysis, we right-

190   censored data from individuals after the point that they were captured on total rodent removal

191   plots, or from kangaroo rat individuals captured on kangaroo rat removal plots because these

192   individuals were subsequently removed from the study site.

193   Since the small mammal community includes diverse species (n=21) representing a suite

194   of different feeding guilds and life history strategies (Table 1), our site is ideal for evaluating

195   certain traits associated with core and transient species in 3 main feeding guilds: granivores

196   (n=15), folivores (n=4) and carnivores (n=2). At our site, species across the three guilds have a

197   wide range of body sizes (4-280 g) and divergent evolutionary histories (Bininda-Edmonds et al.

198   2007), leading to differing levels of adaptation to the arid environment, which results in them

199   being differently suited to local and regional habitat use strategies. During 1989-1999,

200   individuals were marked using ear and toe tags, and during 2000-2009, individuals were mainly

201   marked with PIT tags. We conducted extensive data cleaning and error checking to ensure that

202   potential problems in the data (*e.g.*, duplicate tags, uncertainty in sex or species) were resolved.

203   In cases where the data with identical tags could be clearly partitioned into unique individuals,

204   we assigned new unique tag numbers to each individual. In cases where data could not be clearly

205 partitioned into individuals, or where species identity was questionable, the data were excluded

206 from analysis.

207 Core and transient species status was assigned based on temporal persistence, as defined

208 by the proportion of years that each species was present (1989-2009) on control plots at our site.

209 Species that were present in at least 2/3 of the years (≥0.66) were considered core (*sensu* Coyle

210 *et al.* 2013). Species that were present less than 1/3 of the years (≤0.33) were considered

211 transient. All other species were considered intermediate temporal status.

Movement, Survival, and Fecundity

213 Using individual-level recapture data, we assessed movement characteristics for each

214 species. Here, we define individual movement at each time-step relative to the individual's

215 previous capture location, and not in a geographic context defined by the individual's birthplace,

216 burrow, or location relative to other individuals. We were unable to measure geographic

217 dispersal (e.g., relative to natal location) using our dataset, but we assume that patterns of

218 individual movement (including maintenance, breeding, foraging, and exploratory movements)

219 are correlated with and encompassed by dispersal, which is an outcome of movement (Roshier

220 and Reid 2003). Locations of the permanently marked trap stakes were recorded in 2010 using

221 ProMark3 GPS Units with error < 2 cm. We recorded the distance in meters between trap stakes

222 among chronologically ordered capture histories for each individual. For each species, we binned

223 the individual movement data by 6-meter increments that roughly represent the distance between

224 stakes (with bin 1 representing distance 0-3 meters, or recapture at the same stake), and plotted

225 the data in histograms. For each species, we calculated the modal distance and the mean plus one

226 standard deviation of the log (Y+1) transformed data to determine a species-level benchmark at

227 which each movement distribution transitions into long-distance movements. We chose this

228   transformation to meet the assumptions of normality and because there are many 0 m movements

229   (Sokal and Rohlf 2012). For each species, these histograms provide insight into the frequency at

230   which individuals move short versus long distances. Using the combined individual movement

231   distances of the core species within each feeding guild (granivore, folivore, and carnivore), we

232   set the mean plus one standard deviation of log(Y+1) transformed data as our guild-level

233   benchmark defining a short versus a long distance movement to compare across all species. We

234   used this method because home range size likely differs based on trophic group (Mace and

235   Harvey 1983).

236   To more thoroughly evaluate life-history relationships between movement and apparent

237   survival, conditional on recapture probability, we used a multistate capture-mark-recapture

238   (CMR) modeling approach in Program Mark version 7.0 (White and Burnham 1999, White and

239   Cooch 2012) through the R programming environment 3.0.2 (R Core Development Team 2012)

240   and package RMark (Laake and Rexstad 2008; Laake *et al.* 2012). To address our questions of

241   whether core and transient species differ in apparent survival (Φ), recapture (p), and movement

242   probabilities (ψ), we used a two-state model where all species were first recorded in state 1, and

243   were switched to state 2 (or from state 2 back to state 1) conditional on the distance between

244   trapping stakes upon recapture being greater than the guild-level benchmark defining short

245   distance movements. In this two-state CMR model, transitioning between states indicates long

246   distance movement, and staying in the same state indicates short distance movement, conditional

247   on apparent survival and recapture probabilities. We defined apparent survival probability as the

248   probability that an individual alive in trapping period i survived and did not emigrate from the

249   entire study area by trapping period $i+1$. We defined recapture probability at trapping period $i+1$

250   as the probability that a live individual anywhere on the study area was recaptured in a trap. All

251 probabilities were measured over a time scale of approximately one month, the time between

252 trapping events. To address inconsistencies in the data, we controlled for omitted trap periods

253 (when trapping did not occur or the site was only partially trapped) by fixing recapture

254 probability to zero for those occasions. It should be noted that we could not differentiate between

255 permanent emigration and death, which may affect interpretation of our survival estimates. Thus,

256 low apparent survival probabilities may indicate low actual survival, high permanent emigration

257 from the entire study area, or both. We evaluated each species separately in RMark to estimate

258 apparent survival, recapture, and transition probabilities (White and Cooch 2012), except for

259 transient granivores, which we grouped together because there were not enough captures to

260 analyze species separately. Pooling data for all species into a single dataset, and designating

261 species or strategies with factors, led to an extremely large CMR dataset that prohibited

262 computational analysis using MARK and RMark. We thus used post hoc analyses to compare the

263 estimates for core versus intermediate and transient species. For further details on our RMark

264 analysis, please refer to our code, which is maintained online in a public GitHub repository along

265 with the data (https://github.com/weecology/portal-rodent-dispersal) and is available in the

266 online supplement.

267   To assess reproductive effort for each species, we tracked the reproductive history for

268 captured individual females within each calendar year. We considered females with enlarged

269 and/or red nipples or who were pregnant (researcher could feel embryos) to be actively

270 reproducing. If a female was marked in reproductive condition during consecutive trapping

271 periods, we assumed it to be a single reproductive event. Reproductive condition recorded across

272 non-consecutive trapping periods was considered as multiple reproductive events. We used data

273 from females because males display reproductive signals for a larger portion of the year, and

274 male reproductive status does not necessarily indicate recent copulation or reproductive success.

275 For each species, we also recorded litter size and number of litters per year from the literature

276 (Hoffmeister 1986).

277 To compare the life-history traits among groups, we standardized the data and results to

278 account for different units ($[(x - mean(x))/sd(x)]$) and controlled for the influence of

279 phylogenetic relatedness on our results (Felsenstein 1985). We used a generalized least squares

280 model to test for the correlation of traits and trait trade-offs with phylogenetic relatedness (APE,

281 Paradis et al. 2004; Geiger, Harmon et al. 2008; picante, Kembel et al. 2010) based on a

282 published mammalian phylogeny (Bininda-Emonds et al. 2007; PhyloOrchard, O'Meara et al.

283 2013) and using the assumption of linear decrease in trait covariance (bm gls; Brownian motion

284 model). We also compared species using a linear regression and PCA biplots to determine the

285 relative influences of temporal status, feeding guild, and phylogenetic relatedness on movement

286 patterns and life history traits.

287

288 **Results**

289 *Core-transient species designation*

290 During the 21-year study period, we captured 12,651 individuals from the 21 species

291 included in the analysis (Table 1). Based on the proportion of years that each species was

292 present, we placed species into three temporal persistence categories (Figure 2) consisting of 10

293 core (*Dipodomys ordii, D. merriami, Chaetodipus baileyi, C. penicillatus, Perognathus flavus,*

294 *Peromyscus eremicus, Reithrodontomys megalotis, Neotoma albigula, Onychomys torridus,* and

295 *O. leucogaster*), 7 transient species (*C. hispidus, C. intermedius, Peromyscus leucopus, R.*

296 *montanus, R. fulvescens, Baiomys taylori,* and *Sigmodon ochrognathus*), and 4 intermediate

297 species (*D. spectabilis, Peromyscus maniculatus, S. fulviventer,* and *S. hispidus*). Granivores and

298 folivores were represented across all three persistence categories, but both carnivorous species

299 were designated "core" (Table 1). We removed *Chaetodipus hispidus* from our main

300 comparisons because there were only 10 individuals with recaptures and we could not run

301 multistate CMR models on such a small sample. Since transient species were rarely captured at

302 the site and thus do not have enough data points for robust statistical analysis, we focus our

303 results on the comparison between core and non-core species, where non-core refers to

304 intermediate and transient species grouped together, generally.

305 *Movement, Survival, and Fecundity*

306   For all the species, movement distances between recaptures were strongly unimodal and

307 left-skewed. Transient and intermediate species generally had a longer tail on their movement

308 distributions than core species and distributions for many non-core species had a secondary

309 mode, suggesting more long-distance movements, larger home ranges, and possible emigration

310 off-site (Table 1, Figure 3; Figure A1). Transient species that had few long-distance movements

311 may be attributed to high mortality, low detectability on the site, low recapture due to rapid

312 movement off the site, or a combination of these. Core species tended to move shorter distances

313 (median species-level movement benchmark; core=42.91 meters [29.96-152.45]; non-core=65.24

314 [24.70-365.01]. Among granivores, core species had a lower frequency of moving a relatively far

315 distance away from the previous trap location (median benchmark=41.50 m) than intermediate

316 (median benchmark=72.42 m) or transient granivore species (median benchmark=63.42 m;

317 Table 1). Among folivores, the core species *N. albigula* generally moved shorter distances

318 (benchmark=39.76 m) than the intermediate (benchmark=53.31 m) and transient species (mean

319 benchmark=91.85 m; Table 1). Core guild-level movement benchmarks were used to

320   parameterize the CMR model and differed across trophic groups (benchmark$_\text{granivore}$=36.70;

321   benchmark$_\text{folivore}$=39.76; benchmark$_\text{carnivore}$=88.07).

322   When using the two-state CMR model in Mark to compare apparent survival, recapture,

323   and movement probabilities among core and transient species, differences were most pronounced

324   among core granivores versus transient and intermediate granivores (Table 1; Table S1). On

325   average, core species had a lower probability of moving a long distance (mean ψ_core=0.14 [range

326   0.03-0.37]), but higher recapture (p_core=0.39 [range 0.21-0.63]) and apparent survival

327   probabilities (mean Φ_core=0.76 [range 0.63-0.84]) than non-core species (mean $\psi_\text{non-core}$=0.25

328   [range 0.02-0.86], mean $p_\text{non-core}$=0.35 [range 0.07-0.66], mean $\Phi_\text{non-core}$=0.67 [range 0.45-0.83]).

329   Reproductive results from the field data were best explained by phylogeny. For all

330   species in *Heteromyidae* (5 core and 3 non-core), the majority of captured females were never

331   recorded in reproductive condition (Table 1; Figure A2). However, despite generally much lower

332   abundance, species in *Cricetidae* were observed in reproductive condition more often. For

333   example, nearly 50% of *Peromyscus eremicus* (core) and *P. maniculatus* (non-core) were

334   recorded in reproductive condition at least once per year (Table 1) and *N. albigula* (core) females

335   were often found in reproductive condition. However, *Sigmodon* (non-core) females were almost

336   never recorded as reproductive (Table 1). The lack of observed reproduction may suggest that

337   *Sigmodon* rarely reproduce at the site or that sampling error associated with the small number of

338   captures affected our results. *Onychomys* (core) females were rarely captured when reproductive,

339   but other data suggest that *O. torridus* may reproduce multiple times per year (Table 1, Table 2).

340   *Phylogeny and Trade-offs*

341   PCA results suggested that species can be grouped in multivariate space by their traits

342   and core-transient status (Figure 4), and that traits appear to be strongly conserved within family

343 (Figure A3). Phylogeny (family) was a significant predictor of ψ (linear model; lm (ψ~family),

344 p=0.016, r^2=0.28), Φ (lm (Φ~family), p=0.006, r^2=0.35), and mean abundance (lm

345 (abundance~family), p=0.004, r^2=0.37), but not for the proportion of years a species was present.

346 Mean abundance was positively related to the proportion of years a species was present in the

347 study area when phylogeny was controlled for (bm gls, p=0.005). Body size was not a significant

348 predictor for the proportion of years present, mean abundance, survival, reproduction, or

349 movement (bm gls, p >> 0.05). We did not detect strong movement-survival trade-offs or

350 movement-reproduction trade-offs in this community using linear regression or phylogenetic

351 methods (Figures A4, A5). There was a relationship between observed modal movement distance

352 and temporal persistence (lm(distance mode ~ proportion years present), p=0.03, r^2=0.23; bm

353 gls, p=0.05) where species that persisted longer moved shorter distances.

354

355 **Discussion**

356   Our study provides the first test, to our knowledge, of whether life-history traits are

357 associated with the temporal persistence patterns of species in a community. Life-history traits

358 were generally conserved within evolutionary lineages, which in our system are also related to

359 higher or lower degrees of adaptation to desert environments. Our results provide some

360 indication that life history traits are also linked to the core-transient structure among species at

361 our site. Analysis of the movement, survival and reproduction data indicated that core species at

362 our site moved relatively short distances and had higher apparent survival rates than intermediate

363 and transient species, consistent with our predictions. Core species were generally more

364 abundant than transient or intermediate species, which may suggest greater competitive

365 dominance or ecological specialization. Transient species at our site exhibited lower apparent

366 survival and moved longer distances, on average, than core species, but the range of estimates

367 within this group varied widely. We interpret the high variation in survival and movement

368 estimates across species within the intermediate and transient groups as support for the idea that

369 this heterogeneous group includes both source-sink and nomadic transients. Among traits, we did

370 not detect strong movement-survival trade-offs, and too few reproductive events were observed

371 to test for survival-reproduction trade-offs.

372   Other research at our site also supports the idea that our core and transient species have

373 different effects on community structure and resource use. Core species that exhibit high self-

374 investment, strong competitive ability, and strong local adaptation are also expected to

375 successfully exploit most of the available resources at a local site (Kneitel and Chase 2004). The

376 most abundant core species at our site are indeed responsible for the majority of resource

377 consumption (Thibault et al. 2004), are behaviorally dominant (*Dipodomys* spp.; Reichmann and

378 Price 1993), and have cascading impacts on rodent and plant communities (Brown and Heske

379 1990; Heske *et al.* 1994; Valone and Schutzenhofer 2007). Pocket mice (*Chaetodipus* spp.),

380 another group of core species, become dominant in the absence of kangaroo rats (Ernest and

381 Brown 2001). Therefore, it is generally true in this system that species with lower movement,

382 higher survivorship, and potentially lower reproductive rates are also the competitively dominant

383 species responsible for the majority of resource consumption (Thibault et al. 2004).

384   The life-history estimates for transient and intermediate species (n=11) generally

385 supported our hypotheses. We expected that results for this group of species would exhibit broad

386 interspecific variation because of the presence of both nomadic and source-sink transients.

387 Unfortunately, it is not possible to definitively distinguish between these groups using our data,

388 but using a combination of our results and the well-studied natural history of these species, we

389   can make some informed predictions. Species that exhibited trait correlations more similar to

390   core species could be source-sink transients (Lenormand 2002; Kawecki 2008), or could be

391   undergoing local extinction (Gibson et al. 1999). Because they are core somewhere else, source-

392   sink transients may generally be inferior competitors that temporarily colonize in response to

393   resource pulses and density dependent dispersal at other locations, both of which could create a

394   source-sink dynamic over time (Heske *et al.* 1994; Thibault *et al.* 2004; Milstead et al. 2007).

395   *Dipodomys* and *Chaetodipus* species that were not core at our site are either undergoing local

396   extinction due to directional habitat change (*D. spectabilis*; Valone et al. 2002, Thibault et al.

397   2004) or are not adapted to the habitat at our site (*C. intermedius* and *C. hispidus*; Hoffmeister

398   1986; Paulson 1988, Williams et al. 1993) and their occasional presence can likely be attributed

399   to temporary dispersal from nearby source populations (Wilson and Ruff 1999). At our site,

400   *Sigmodon* and *Reithrodontomys* are prairie-adapted species (Webster and Jones 1982;

401   Hoffmeister 1986) that usually arrive during years and seasons where climatic conditions lead to

402   higher than normal grass cover (Thibault *et al.* 2004). During our study period these species had

403   relatively low abundance and were rarely recorded in reproductive condition – strong evidence

404   that our site represents a habitat sink for these populations. Species that exhibited trait

405   correlations different from core species could be nomadic transients. *Peromyscus maniculatus*

406   and *leucopus* at our site were generally rare, moved longer distances more often, potentially

407   reproduce multiple times per year, and use a wider resource base than the core species

408   (Hoffmeister 1986; Wilson and Ruff 1999), evidence that these species could readily colonize

409   new locations. In addition, *Baiomys taylori* seem to be dependent on high ground cover, and thus

410   requiring populations to nomadically track habitats receiving more than the usual amount of

411   water (Wilson and Ruff 1999). Thus, through these two different processes, source-sink and

412   nomadic transient species maintain presence in the regional metacommunity and comprise a

413   dynamic component of the local community.

414   The core-transient framework, integrated with an eco-evolutionary viewpoint, suggests

415   that core and transient species may be responsible for maintaining different aspects of ecosystem

416   function at a local site. Because of their higher local adaptation and stronger ability to exploit

417   resources under local conditions, core species may be particularly important for maintaining

418   ecosystem function (Grime 1998; Henderson and Magurran 2014). In contrast, because of their

419   higher movement rates, transient species may be particularly important for maintaining local

420   diversity through time and in response to disturbance (Dornelas et al 2014, Henderson and

421   Magurran 2014; Supp and Ernest 2014). Our site exhibits high annual composition turnover

422   while generally maintaining species richness (Brown et al. 2001, Goheen et al. 2005), which

423   indicates a role for nomadic transients in the regional metacommunity that can opportunistically

424   fill empty niches and thus maintain community-level species richness. Our results suggest that

425   species with locally adapted traits well suited to maximizing ecosystem functions related to

426   resource use may also have lower movement rates. If so, this relationship between traits and

427   movement patterns may be particularly important to explore in a metacommunity context.

428   The core-transient and core-satellite frameworks are merely two different ways of

429   considering commonness and rarity in ecological systems. Temporal patterns of species

430   persistence at a site depend on environmental filtering and competitive processes (Magurran and

431   Henderson 2003; Coyle et al. 2013), but also partially depend on spatial patterns of habitat

432   heterogeneity and movement between linked populations (Hanski 1982; Grime 1998; Gibson et

433   al. 1999). A difficulty in linking the two ideas is that they define commonness and rarity in two

434   different ways – species are categorized by occupancy of a regionally defined area (core-

435 satellite) or species are categorized by occupancy of a single site through time (core-transient).

436 Combining the two frameworks would require modeling patch occupancy in the region through

437 time, while allowing for core-satellite switching (e.g., Gaston and Lawton 1989, Gotelli 1991),

438 and assigning core-transient species for each site across the time-series. Presumably, such a

439 model would lead to several new categories of species: (a) regionally core species that remain

440 core throughout the time-series and are temporally core at sites in which they occur, (b)

441 regionally core species that switch to satellite species in poor years (e.g., experience local

442 population crashes) or that display enhanced occupancy in good years (e.g., experience density

443 dependent dispersal), and are mixed across sites as temporally core or transient, (c) satellite

444 species that are temporally core in sites in which they occur, (d) satellite species that switch to

445 regionally core in high resource years (e.g. irruptive dynamics), and are mixed across sites as

446 temporally core or transient, (e) satellite species that switch the sites they occupy through time,

447 and thus are temporally transient across the sites in which they occur (e.g., nomadism).

448 Synthetically understanding the characteristics of species that display different or overlapping

449 syndromes of commonness (e.g., locally abundant, high regional occupancy, and/or high

450 temporal persistence) or rarity (locally rare, low regional occupancy, and/or low temporal

451 persistence) remains a critical area for future research in community ecology.

452   Assessing whether there are life history implications for species using local versus

453 regional scale processes for population maintenance is challenging. Long-term mark-recapture

454 data that provides information on movement, survival, and reproduction rates across an entire

455 community, including rare species, is very difficult data to obtain. Despite the shortcomings of

456 our data, our results suggest that core and transient species may differ not only in their temporal

457 persistence, but also in their use of landscapes, traits for resource use, and structure of their life

458   histories. If other studies support our findings, it suggests that core-transient species traits should

459   be modeled separately to understand how these groups might respond differently to

460   environmental change. Core and source-sink transient species generally associated with low

461   levels of gene flow or that are unable to track shifts in the location of suitable habitat across the

462   landscape, would be predicted to undergo catastrophic decline under environmental changes that

463   alter local conditions long-term (*e.g.* temperature, resource availability). Alternately, nomadic

464   transient species that emigrate readily and exhibit high levels of gene flow among populations

465   would be predicted to exhibit relatively small change in response to the same scenario. In the

466   drive to better understand the response of biodiversity to perturbations, a temporal perspective of

467   species demographics and persistence represents a critical link in identifying the linkages

468   between local and regional richness patterns and predicting community response to change.

469

470   **Acknowledgements**

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659 **Tables**

660 **Table 1.**

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Species	Guild	Status	N	Mean mass (g)	Mean num. reproduction events/year	Movement benchmark (m)	Φ (std. error)	p (std. error)	Ψ (std. error)
Dipodomys merriami	Gran.	Core	1972	43.64	0.52	33.13	0.80 (0.00)	0.60 (0.01)	0.06 (0.00)
D. ordii	Gran.	Core	1030	48.32	0.47	30.35	0.75 (0.01)	0.63 (0.01)	0.03 (0.00)
D. spectabilis	Gran.	Intermed.	41	115.01	0.21	24.70	0.83 (0.02)	0.66 (0.04)	0.02 (0.01)
Chaetodipus baileyi	Gran.	Core	2063	31.77	0.40	29.96	0.84 (0.00)	0.56 (0.01)	0.04 (0.00)
C. penicillatus	Gran.	Core	2818	17.01	0.40	44.33	0.83 (0.00)	0.21 (0.00)	0.06 (0.02)
C. hispidus	Gran.	Transient	10	31.74	0.43	16.49	--	--	--
C. intermedius	Gran.	Transient	20	18.46	0.14	33.96	0.79 (0.05)	0.25 (0.07)	0.06 (0.04)
Perognathus flavus	Gran.	Core	648	8.12	0.54	41.50	0.78 (0.01)	0.23 (0.01)	0.06 (0.01)
Peromyscus eremicus	Gran.	Core	479	21.47	0.53	107.18	0.63 (0.02)	0.32 (0.02)	0.37 (0.04)
Pe. maniculatus	Gran.	Intermed.	398	21.41	0.46	120.13	0.62 (0.02)	0.28 (0.03)	0.53 (0.05)
Pe. leucopus	Gran.	Transient	77	22.41	0.24	56.05	0.46 (0.06)	0.44 (0.11)	0.12 (0.06)
Reithrodontomys megalotis	Gran.	Core	1180	10.71	0.23	95.17	0.63 (0.01)	0.27 (0.01)	0.33 (0.20)
R. montanus	Gran.	Transient	18	9.01	0.67	365.01	0.72 (0.14)	0.07 (0.06)	0.86 (0.15)
R. fulvescens	Gran.	Transient	11	13.90	1.50	63.42	0.81 (0.05)	0.63 (0.08)	0.22 (0.08)
Baiomys taylori	Gran.	Transient	106	8.76	0.26	70.65	0.63 (0.05)	0.22 (0.05)	0.12 (0.05)
Sigmodon hispidus	Foliv.	Intermed.	268	88.84	0.12	39.56	0.45 (0.04)	0.38 (0.06)	0.08 (0.03)
S. fulviventer	Foliv.	Intermed.	151	66.01	0.07	67.06	0.66 (0.03)	0.35 (0.04)	0.14 (0.03)
S. ochrognathus	Foliv.	Transient	27	55.55	0.37	91.85	0.70 (0.07)	0.21 (0.07)	0.31 (0.14)
Neotoma albigula	Foliv.	Core	255	167.05	0.66	39.76	0.79 (0.01)	0.33 (0.02)	0.10 (0.02)
Onychomys torridus	Carn.	Core	952	23.81	0.49	80.87	0.76 (0.01)	0.42 (0.01)	0.09 (0.01)
O. leucogaster	Carn.	Core	127	30.16	0.54	152.45	0.77 (0.02)	0.37 (0.03)	0.27 (0.04)

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663 **Table 1. Summary of species traits from the field data.** Species-level trait details summarizing

664 feeding guild, core-transient status, total number of individuals tracked through the study (N),

665 mean body mass across all recorded weights, mean yearly reproductive effort, and species-level

666 benchmarks defining where each movement distribution transitions into long-distance

667 movements. Yearly reproductive effort was estimated by taking weighted average of the number

668 of individual females marked as reproductive 0-4 times per year. -- indicates that we could not

669 generate multistate CMR estimates due to small sample size (N ≤10).

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692 **Table 2.**

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Species	Status	Litter size	Mean litter size	Number of litters per year	Typical breeding months
*Dipodomys ordii**	Core	2-3	2.37	1-2	February-July
*D. merriami**	Core	2-3	2	1-2	March-October
*Chaetodipus baileyi**	Core	1-6	3.6	--	April-August
*C. penicillatus**	Core	2-8	4.72	1	April-August
*Perognathus flavus**	Core	1-6	4	1	April-August
*Peromyscus eremicus**	Core	1-4	2.53	1-4[†]	Year-round
*Reithrodontomys megalotis**	Core	3-7[†]	3.6	1-10	Year-round
Neotoma albigula	Core	1-4	1.95	≥ 1	Year-round
Onychomys torridus	Core	2-5	3.45	--	March-October
O. leucogaster	Core	3-5	4	--	March-September
*D. spectabilis**	Intermed.	1-3	2.1	1-2	January-August
P. maniculatus	Intermed.	1-6	4.29	2-4[†]	Year-round
Sigmodon hispidus	Intermed.	2-10	5.6	1-9	Year-round
S. fulviventer	Intermed.	4-6[†]	--	--	Year-round
*C. hispidus**	Transient	4-7[†]	--	1-2[†]	--
*C. intermedius**	Transient	1-7	3.94	--	March-July
*P. leucopus**	Transient	2-5	3.61	>1[†]	February-October
*R. montanus**	Transient	1-9[†]	4[†]	--	Year-round[†]
*R. fulvescens**	Transient	2-4	--	--	Year-round
*Baiomys taylori**	Transient	1-5[†]	2.49	1-9	Year-round
S. ochrognathus	Transient	2-6	--	--	Year-round[†]

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709 **Table 2. Summary of reproductive life-history traits.** Data from Hoffmeister (1986), with

710 missing data filled from Wilson and Ruff (1999)[†]. Dashes (--) indicate no data from either

711 reference. Species marked with an asterisk (*) are directly competing for resources in the

712 granivore feeding guild.

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Figure Legends

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

offs. Temporal persistence is predicted to be correlated with life-history traits including survival,

reproduction, movement patterns, and resource use.

Figure 2. The proportion of years and the mean proportion of months that a species was

present in the study period (1989-2009). We designated core (≥0.66), intermediate (<0.66 and

>0.33) and transient (≤0.33) status based on the proportion of years only. Two-letter

abbreviations refer to the species names (*B. taylori,* BA; *C. baileyi,* PB; *C. hispidus,* PH; *C.*

intermedius, PI; *C. penicillatus,* PP; D. *merriami,* DM; *D. ordii*, DO; *D. spectabilis*, DS; *N.*

albigula, NA; *O. leucogaster,* OL; *O. torridus,* OT; *P. flavus,* PF; *Pe. eremicus,* PE; *Pe.*

leucopus, PL; *Pe. maniculatus,* PM; *R. flavescens,* RF; *R. megalotis,* RM; *R. montanus*, RO; *S.*

fulviventer, SF; *S. hispidus,* SH; *S. ochrognathus,* SO).

Figure 3. Histograms grouped by temporal persistence for the distances at which

individuals were recaptured each month. Note that the y-axes are the percent of observations

for each bin, but that there is a large difference in total number of individuals captured in each

group, that is not represented in the histograms (but see Table 1).

Figure 4. PCA biplot with confidence ellipses for temporal persistence. The relationship of

movement (Psi and benchmark), mean number of observed reproductive events for individuals of

each species per year (fecundity), apparent survival (Phi), recapture rates (p), mean abundance,

and the proportion of years a species was present (persistence). Two letter abbreviations refer to

744   species names as presented in Figure 2. PCA axes 1 and 2 explained a total 64.6% of the
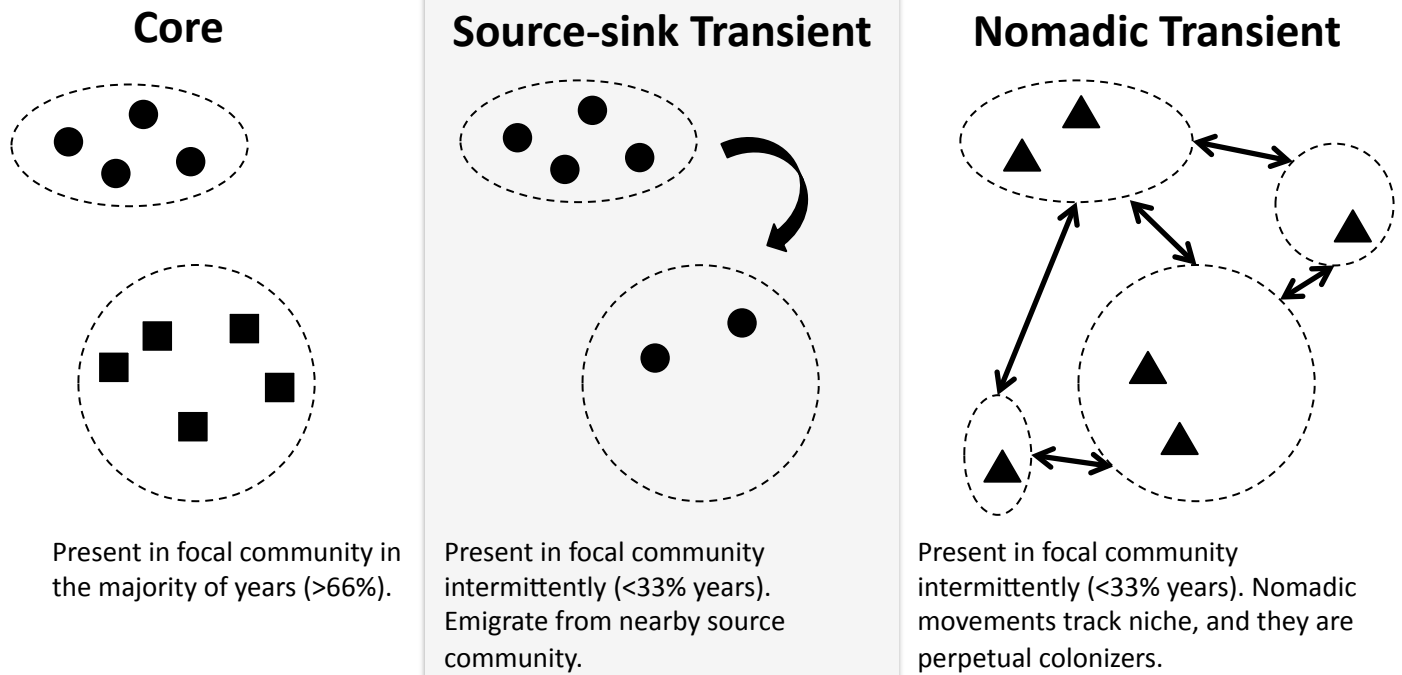
745   variation.

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747   **Appendix A.** Additional figures supporting the analyses and results in the manuscript.

748   **Supplementary Material.** Zip file containing the code and data for replicating the analyses.

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Figure Legends for Appendix A and the Supporting Information

Figure A1. Panels showing the species-level movement distances calculated from the recapture data. Two-letter species name abbreviations are as follows from Figure 2.

Figure A2. Observed yearly reproductive effort for individuals of each species from the field study. The y-axis represents the proportion females that we tracked that were recorded in reproductive condition 0-4 times per calendar year (no individuals were recorded as having > 4 reproductive events within a calendar year). Two-letter species name abbreviations are as follows from Figure 2.

Figure A3. PCA biplot with confidence ellipses for phylogenetic relatedness at the family level. The relationship of movement (Psi, benchmark), mean number of reproductive events individuals of a species had per year (fecundity), apparent survival (Phi), recapture rates (p), mean abundance, and the proportion of years a species was present (persistence). Two letter abbreviations refer to species names as presented in Figure 2. PCA axes 1 and 2 explained a total of 64.6% of the variation.

Figure A4. Apparent survival estimates (Φ) shown against the log(Y+1) distance (benchmark) moved for each species and probability of moving a relatively long distance (ψ) as estimated using RMark. The plotted variables have been standardized. Points represent core (pink circles), intermediate (green triangles) and transient (blue squares) species.
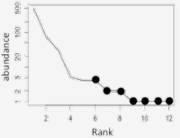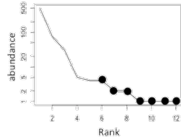
Figure A5. Movement estimates (benchmark, ψ) shown against fecundity for each species. Evidence for a reproduction-movement trade-off is not statistically significant. The plotted variables have been standardized. Points represent core (pink circles), intermediate (green triangles) and transient (blue squares) species.
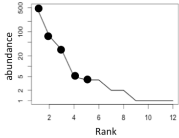
Figure A6. Relationship between the CMR estimates for apparent survival (Phi), movement (Psi) and recapture (p) probability from the CMR analysis for each species, plotted with error bars representing standard error for each estimate. Points represent core (pink), intermediate (green) and transient (blue) species. Note that the transient species have the largest error bars.

File S1. Zip file containing the code and data for replicating the analyses. Code and data are also found in a public GitHub repository (https://github.com/weecology/portal-rodent-dispersal).

Figure 1

Core	Source-sink Transient	Nomadic Transient
Present in focal community in the majority of years (>66%).	Present in focal community intermittently (<33% years). Emigrate from nearby source community.	Present in focal community intermittently (<33% years). Nomadic movements track niche, and they are perpetual colonizers.

Species fall along a continuum of traits and temporal persistence

Core	Source-sink Transient	Nomadic Transient
Highly adapted to habitat/resources in focal community	Adapted to habitat/resources in source community, but not necessarily to focal community	Habitat/resource generalist that opportunistically colonizes in response to available niches
Generally dominant and abundant in focal community	May become abundant for short time periods, but are generally rare	May become abundant for short time periods, but are generally rare
Competitively dominant	Competitively inferior	Competitively inferior
Self investment Strategy High survival Low fecundity	High survival in source community Lower survival in focal community Low fecundity	Offspring investment Strategy Low survival High fecundity
Strong fidelity to "home"	Colonize population sinks in response to density dependent dynamics in source community	Strong colonizers
Movements tied strongly to defending home resources/territory. Reduced movement.	Movements tied strongly to obtaining and defending home territory. Reduced movement.	Movements tied to obtaining resources and exploring available territory/niches. Increased movement tendencies.
Relatively low gene flow among populations	Relatively low gene flow among populations	Intermediate to high gene flow among populations

Circular habitat is "focal" community. Dashed lines represent that communities are open. Core-transient designation is a concept defined within a focal community, but we hypothesize that temporal persistence should be linked to traits.
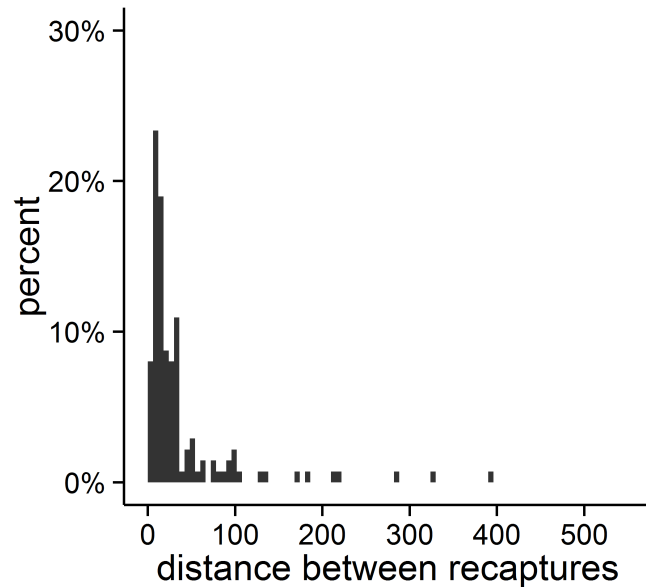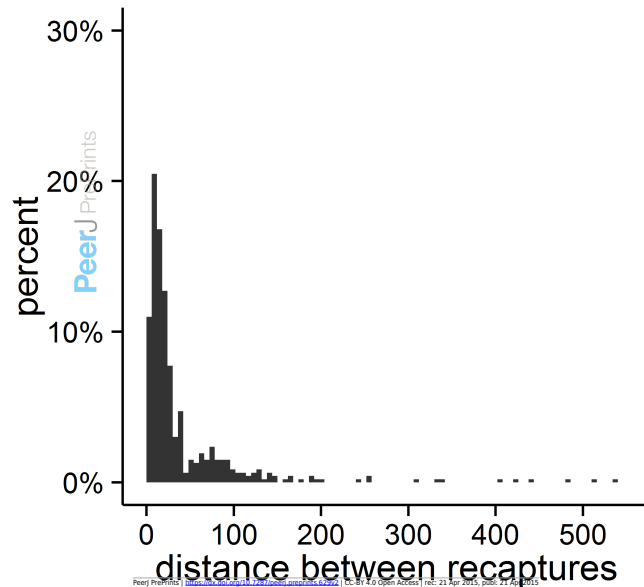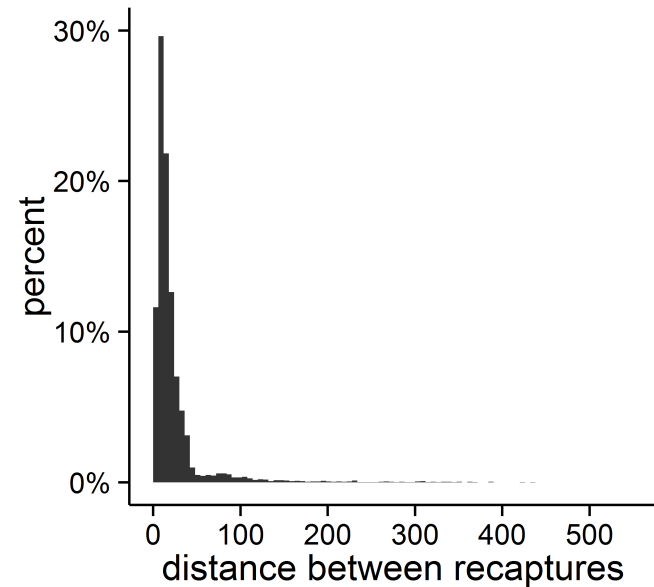
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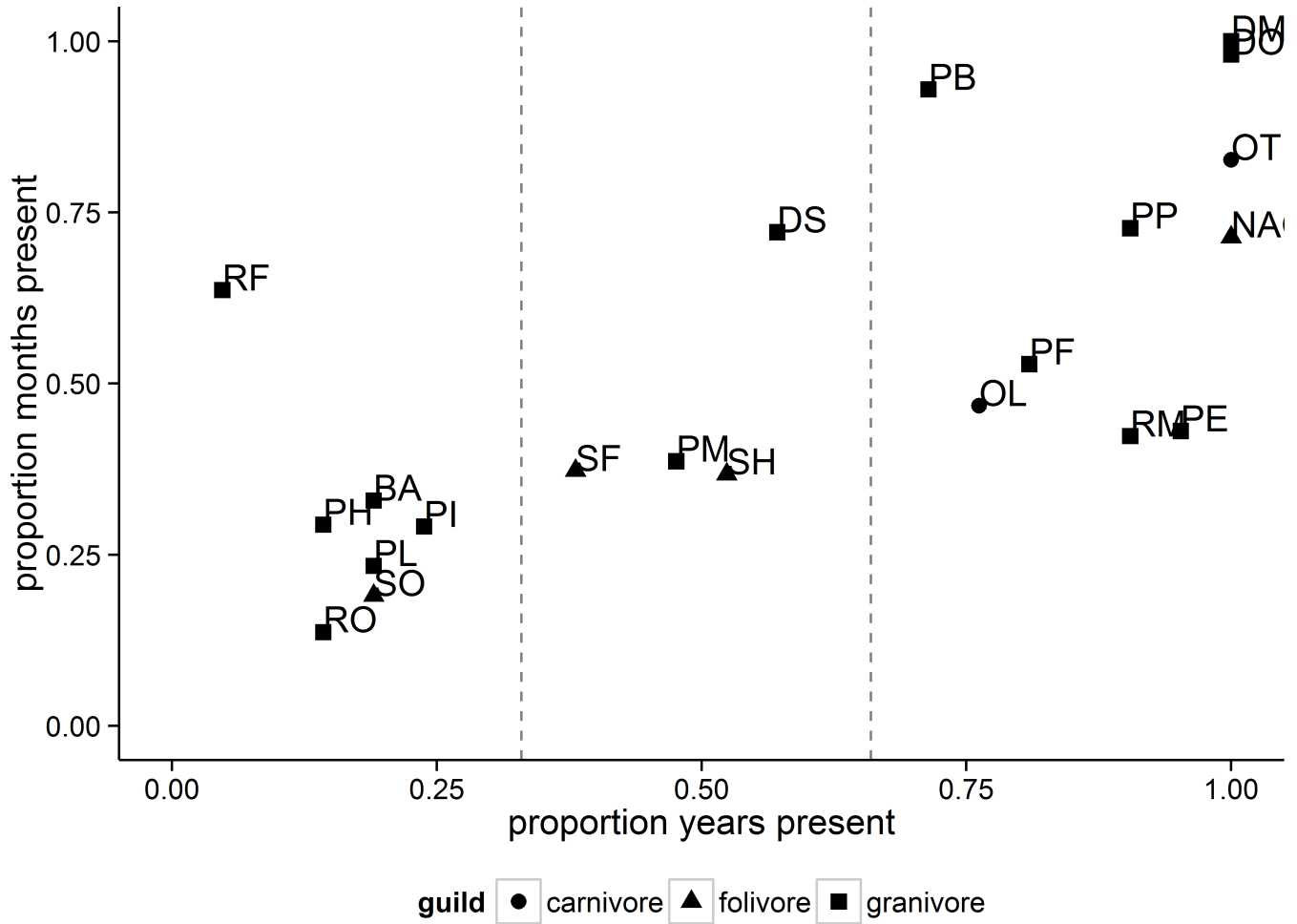
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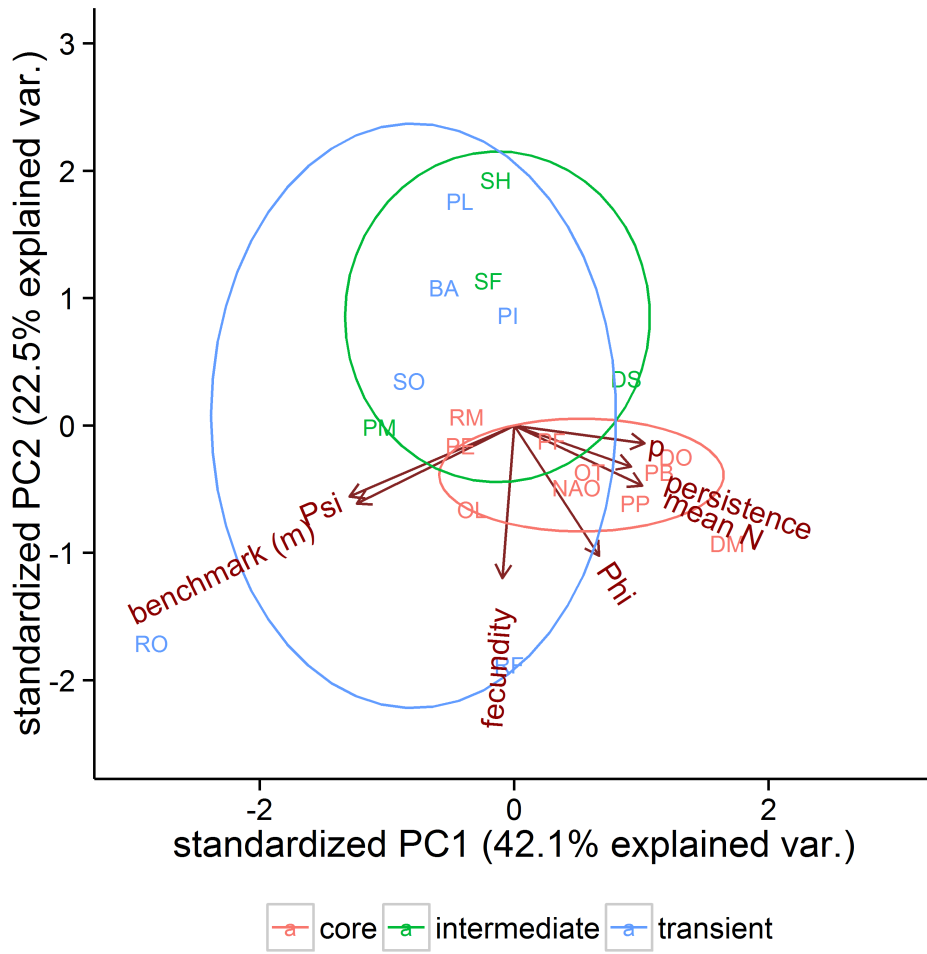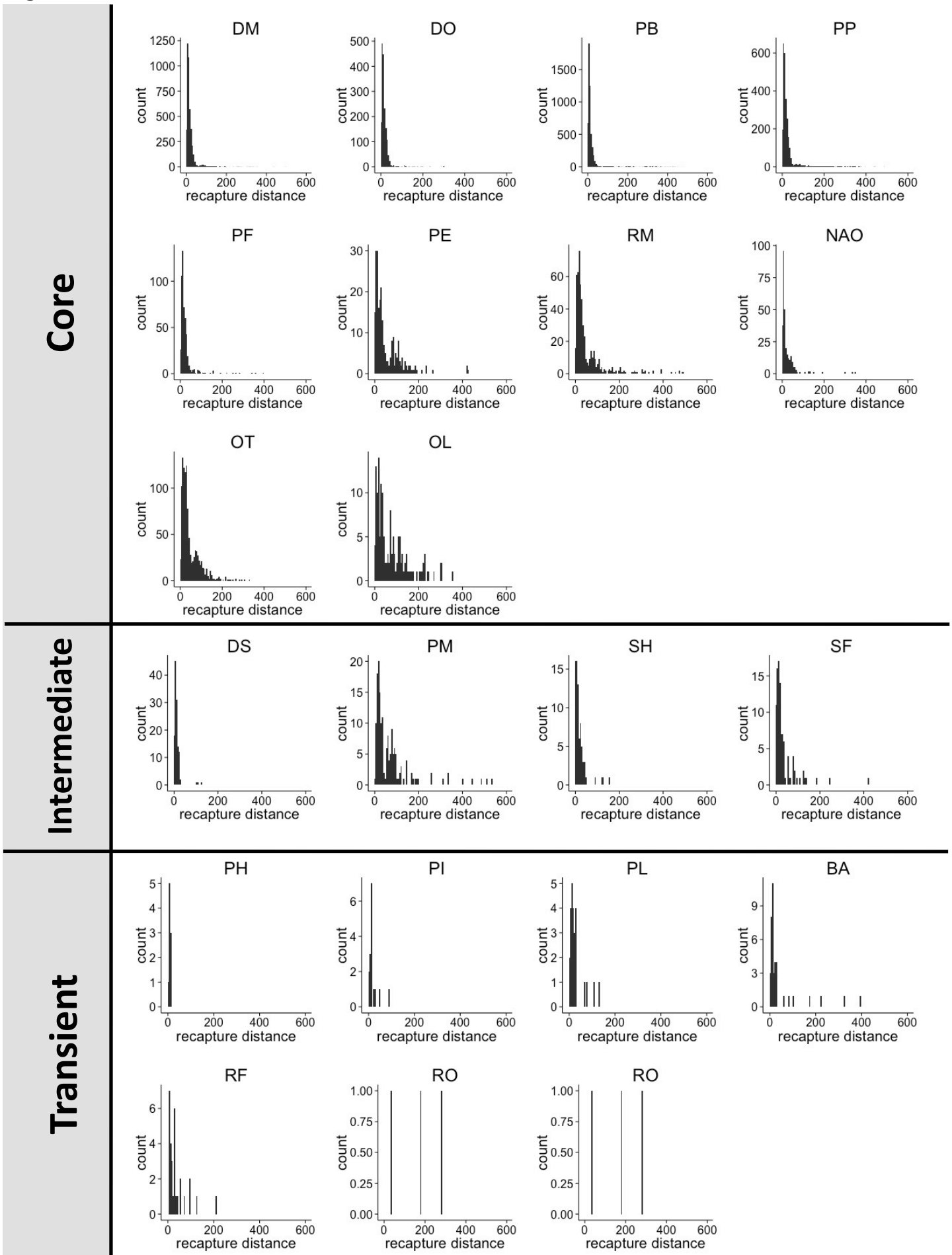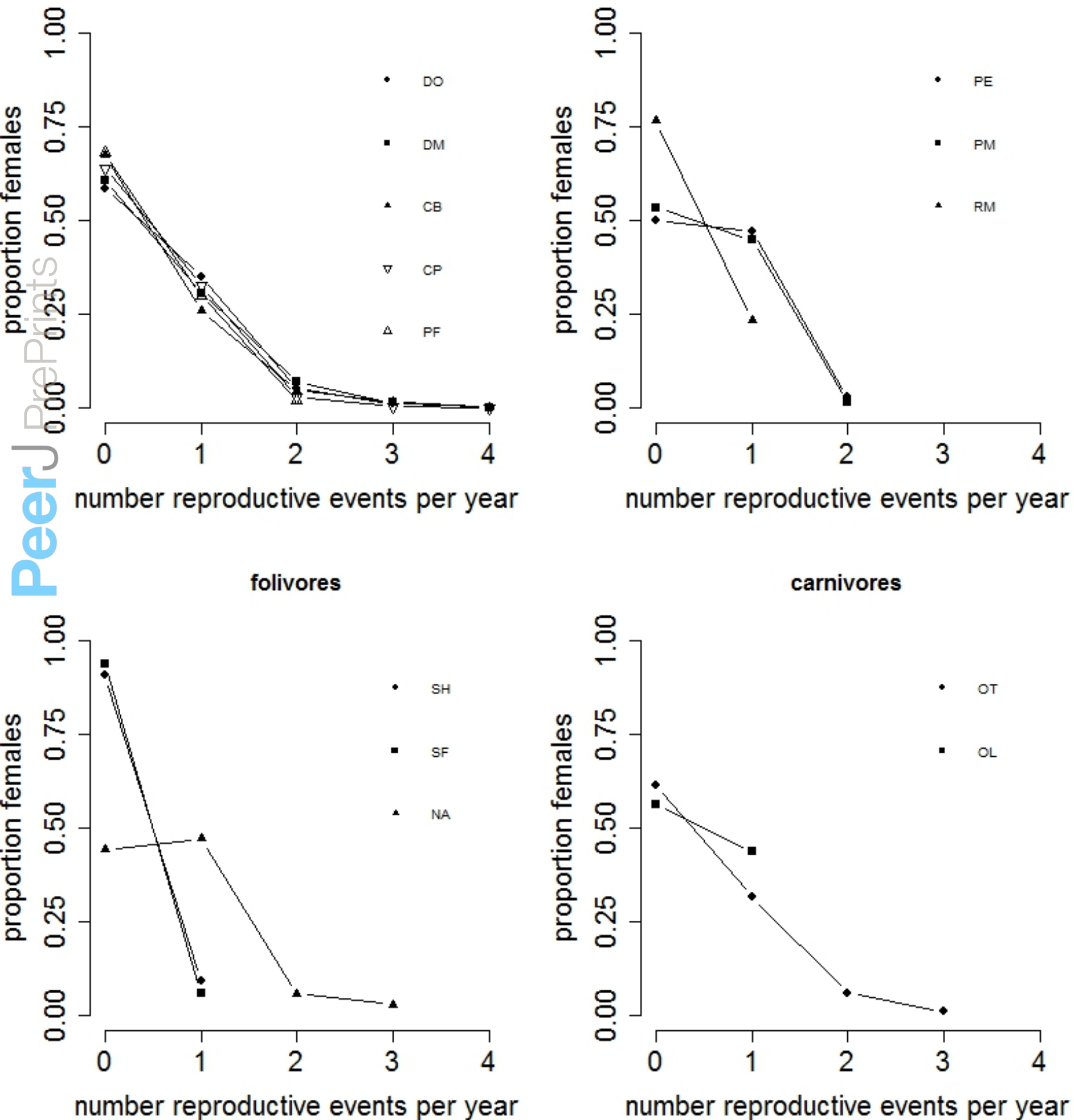
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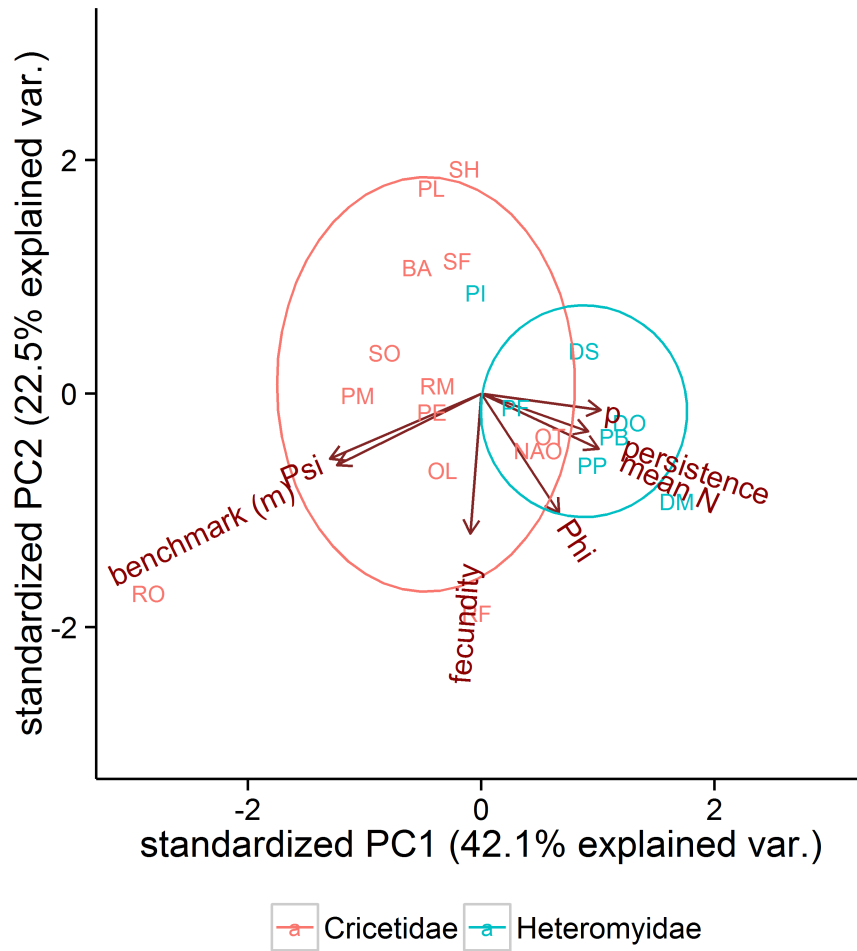
Figure A2

Figure A3

Figure A4

Figure A5

Figure A6