

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

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23 **Abstract**

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

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46 **Introduction**

47 A pervasive characteristic of ecological communities is that they tend to be comprised of a
48 few common species and many rare ones. Traditionally, ecology has attempted to use a single
49 model to explain patterns of abundance among all species in the community. An emerging
50 alternate view posits that communities actually consist of two different groups of species that
51 should be modeled differently (Magurran and Henderson 2003): core species that display high
52 temporal persistence (i.e. present most years) and transient species that exhibit low temporal
53 persistence (i.e. present only occasionally). Core species tend to account for most of the
54 abundance or biomass within a particular community. The richness of core species is better
55 predicted by local environmental conditions, presumably reflecting the need for strong local
56 adaptation to outcompete other species and maintain highly abundant, persistent populations in a
57 specific habitat (Ulrich and Ollik 2004; Belmaker 2009; Coyle et al 2013). In contrast, transient
58 species tend to be rare, and their richness in a local community is better predicted by regional
59 factors (e.g. spatial heterogeneity, regional species pool), presumably because dispersal is a
60 critical process allowing those species to immigrate into particular habitats. Because core species
61 require a strong match between their niche requirements and local environmental conditions to
62 maintain populations whereas immigration is the primary process governing the presence of
63 transient species, the core-transient framework suggests that the spatial and temporal scale of
64 processes influencing the two groups should differ.

65 Core-transient research has primarily focused on differences between these groups in how
66 they respond to the same environment. However, if core and transient species differ in the
67 importance of local and regional processes in maintaining populations, they may also differ in the
68 ecological and evolutionary drivers determining their presence, abundance and diversity

69 (Magurran and Henderson 2003; Dolan *et al.* 2009, Coyle *et al.* 2013). While little research has
70 focused on this question *per se*, a rich literature on metapopulations, metacommunities, and the
71 evolution of dispersal suggest that core and transient species could indeed experience different
72 pressures that would select for different ecologies or life history strategies. Core species must
73 successfully compete in, and adapt to, their local biotic and abiotic environment. As such, core
74 species that are strongly governed by local ecological processes experience strong local co-
75 evolutionary pressures with their biotic and abiotic environment (McCauley 2007). Species that
76 are highly adapted to a particular environment can evolve reduced dispersal tendencies in part
77 because of the cost of moving into a maladaptive environment (Kisdi 2002). Limited gene flow
78 through reduced dispersal among populations enhances the role of local natural selection and
79 adaptation for core species (Hanski 1982, McPeck and Holt 1992; Kisdi 2002; Urban *et al.* 2008).
80 By focusing on using local habitat and reducing the tendency to disperse, core species must also
81 be able to persist through acclimate environmental conditions. Core species without a dormancy
82 phase thus need a ‘survival’ strategy for adverse times. This likely involves specialized behaviors
83 or traits to allow persistence under poor conditions (Hanski 1982; Clutton-Brock 1991;
84 Ghalambor & Martin 2000; Kisdi 2002).

85 The ecological and evolutionary pressures on transient species are more complicated.
86 Although there is only one way to be core, there are two primary processes that may generate
87 transient species within a local community, each with different resulting expectations of the eco-
88 evolutionary pressures imposed. One process that can generate transients in a local community is
89 source-sink dynamics (e.g, Hanski 1982). Source-sink transients are species that are core
90 somewhere on the landscape, but not in the local habitat. Because they are well-adapted
91 elsewhere and immigration from the adapted source population should swamp local adaption to

92 the new environment (Holt and Gaines 1992; Lenormand 2002; Kawecki and Holt 2002; Kawecki
93 2008), we would expect source-sink transients to retain many of the same life history
94 characteristics as core species – except with low temporal occupancy.

95 In contrast to source-sink transients, some transients may form short-term reproducing
96 populations before disappearing and potentially reappearing later via immigration. Processes that
97 could generate this type of transient include opportunistic tracking of shifting resources across a
98 region (e.g. Jonzen et al. 2011) or competition-colonization tradeoffs (e.g., Kneitel and Chase
99 2004). Both cases create what we will call nomadic transients – species that have reproducing
100 populations for short periods of time in a local habitat before moving elsewhere on the landscape.
101 Nomadic transients are strongly governed by regional ecological processes with high levels of
102 dispersal across the landscape. Increased individual movement may impact the evolutionary
103 dynamics of nomadic transient species if: 1) high gene flow homogenizes gene pools and inhibits
104 local adaptation (Urban *et al.* 2008) or 2) intermediate gene flow increases the capacity for local
105 adaptation in unstable habitats via novel subsidies from the regional gene pool (Urban and Skelly
106 2006; Loeuille and Leibold 2008). Both the high gene flow and intermediate gene flow scenarios
107 suggest that on average transient species should be less adapted to local biotic and abiotic
108 conditions than core species. Because they are less well adapted to local conditions, they are
109 expected to be at a competitive disadvantage, except for their ability to exploit novel conditions in
110 unstable environments. If nomadic transient species depend on a regional life history strategy that
111 requires the ability to track suitable environmental conditions and use heterogeneous landscapes,
112 then they should be strongly associated with traits that enable them to traverse non-ideal habitat
113 patches and to colonize new suitable habitat patches as they arise (McCauley 2007). Increased
114 dispersal ability and movement rates come with costs that may include increased mortality risk

115 and increased time and energetic expenditure (Murray 1967; Hanski 1982; Waser 1985; Rousset
116 and Gandon 2002). To maximize fitness amidst such costs, it may be optimal for nomadic
117 transient species to trade-off survival investment toward increased reproductive allocation (*e.g.*,
118 Clutton-Brock 1991; Stearns 1992) and they may have thus evolved associations with life-history
119 traits such as low survival probability, high fecundity, early age of primiparity, and resource or
120 habitat generalism (Charlesworth 1980).

121 The core-transient framework can thus provide a key connection of the slow-fast theory of
122 life history evolution (Ricklefs and Wikelski 2002; Sibly and Brown 2007) with dispersal and
123 habitat use strategies. From theoretical and empirical studies on dispersal, metapopulations, and
124 metacommunities, we might expect a life history strategy for core species focused on local-scale
125 coexistence to include low dispersal rates, low mortality rates, high immune function, limited
126 gene flow among populations, high specialization for local conditions, and decreased fecundity.
127 Source-sink transients should show similar trait correlations as core species, except that they
128 should exhibit lower abundances and temporal persistence and little genetic differentiation
129 between source and sink populations (Gaggiotti 1996). For nomadic transients, we expect the
130 opposite set of characteristics from core species. Nomadic species should be expected to have
131 higher dispersal rates, be able to reproduce in a wider range of habitats, exhibit increased
132 fecundity, higher gene flow among populations, but lower survival (Mueller and Fagan 2008;
133 Baguette et al. 2013). While this possible link between the core-transient framework and life
134 history traits is intriguing, there has been no empirical evaluation, especially examining
135 correlations in traits across species within the same community.

136 We use 21-years of data from a diverse desert rodent community containing information
137 on movement, mark-recapture rates, and reproduction to test the hypothesis that core species have

138 fundamentally different life history strategies than transient species as expected from differences
139 in local vs. regional habitat use. We predict that core species will generally be associated with
140 relatively low movement rates, high survival rates, and low fecundity. We predict that non-core
141 species will display a mixture of traits, depending on whether they are source-sink or nomadic
142 transients, but generally have more incidence of high movement rates, low survival rates, high
143 fecundity, and resource or habitat generalism (Figure 1).

144

145 **Materials and Methods**

146 **Study site and data**

147 We evaluated the relationship between life history traits and core-transient status at our
148 site using 21 years (1989-2009) of capture-mark-recapture (CMR) data for rodents from a long-
149 term experimental site in the Chihuahuan desert in southeastern Arizona (the Portal Project field
150 site; Ernest *et al.* 2009). The study site consists of 24, 0.25 ha fenced plots (50 m X 50 m). Each
151 month, year-round, plots are trapped on a grid consisting of 49 evenly spaced permanent stakes
152 to survey the rodent community and to maintain experimental treatments. Four gates cut into
153 each side of the fenced plots allow free passage of rodents in and out of plots. Large-bodied and
154 behaviorally dominant kangaroo rats (*Dipodomys spp.*) have enlarged auditory bullae that make
155 it possible to selectively exclude them from plots that have a smaller gate size (n=8). Total
156 rodent removal plots have no gates (n=6), while control plots (n=10) have relatively large gates
157 that allow all species access (Brown 1998). Upon capture, each individual was marked by toe
158 clipping, ear tags or with a permanent, subcutaneous passive integrated transponder (PIT) tag
159 that allowed it to be uniquely identified upon capture. For each captured individual, we recorded

160 species, sex, reproductive status, hind foot length, weight, and individual PIT tag. For our
161 analysis, we right-censored data from individuals after the point that they were captured on total
162 rodent removal plots, or from kangaroo rat individuals captured on kangaroo rat removal plots
163 because these individuals were subsequently removed from the study site.

164 Since the small mammal community includes diverse species (n=21) representing a suite
165 of different feeding guilds and life history strategies (Table 1), our site is ideal for evaluating the
166 traits associated with core and transient species in 3 main feeding guilds: granivores (n=15),
167 folivores (n=4) and carnivores (n=2). At our site, species across the three guilds have a wide
168 range of body sizes (4-280 g) and divergent evolutionary histories (Bininda-Edmonds et al.
169 2007), leading to differing levels of adaptation to the arid environment, which results in them
170 being differently suited to local and regional habitat use strategies. We analyzed data for
171 individuals where there was no discrepancy in recorded species across captures. During 1989-
172 1999, individuals were marked using ear and toe tags, and during 2000-2009, individuals were
173 mainly marked with PIT tags. We conducted extensive data cleaning and error checking to
174 ensure that potential problems in the data (*e.g.*, duplicate tags, uncertainty in sex or species) were
175 resolved. In cases where the data with identical tags could be clearly partitioned into unique
176 individuals, we assigned new unique tag numbers to each individual. In cases where data could
177 not be clearly partitioned into individuals, or where species identity was questionable, the data
178 were excluded from analysis.

179 Core and transient species status was assigned based on temporal persistence, as defined
180 by the proportion of years that each species was present (1989-2009). Species that were present
181 in at least 2/3 of the years (≥ 0.66) were considered core (*sensu* Coyle *et al.* 2013). Species that

182 were present less than 1/3 of the years (≤ 0.33) were considered transient. All other species were
183 considered intermediate temporal status.

184 **Movement, Survival, and Fecundity**

185 Using individual-level recapture data, we assessed movement characteristics for each
186 species. Locations of the permanently marked trap stakes were recorded in 2010 using ProMark3
187 GPS Units with error < 2 cm. We recorded the distance in meters between trap stakes among
188 chronologically ordered capture histories for each individual. For each species, we binned the
189 individual movement data by 6-meter increments that roughly represent the distance between
190 stakes (with bin 1 representing distance 0-3 meters, or recapture at the same stake), and plotted
191 the data in histograms. For each species, we calculated the modal distance and the mean plus one
192 standard deviation of the log (Y+1) transformed data to determine a species-level benchmark at
193 which each movement distribution transitions into long-distance movements. We chose this
194 transformation to meet the assumptions of normality and because there are many 0 m movements
195 (Sokal and Rohlf 2012). For each species, these histograms provide insight into the frequency at
196 which individuals move short versus long distances. Using the combined individual movement
197 distances of the core species within each feeding guild (granivore, folivore, and carnivore), we
198 set the mean plus one standard deviation of log(Y+1) transformed data as our guild-level
199 benchmark defining a short versus a long distance movement to compare across all species. We
200 used this method because home range size likely differs based on trophic group (Mace and
201 Harvey 1983).

202 To more thoroughly evaluate life-history relationships between dispersal and apparent
203 survival, conditional on recapture probability, we used a multistate capture-mark-recapture
204 (CMR) modeling approach in Program Mark version 7.0 (White and Burnham 1999, White and

205 Cooch 2012) through the R programming environment 3.0.2 (R Core Development Team 2012)
206 and package RMark (Laake and Rexstad 2008; Laake *et al.* 2012). To address our questions of
207 whether core and transient species differ in apparent survival (Φ), recapture (p), and movement
208 probabilities (ψ), we used a two-state model where all species were first recorded in state 1, and
209 were switched to state 2 (or from state 2 back to state 1) conditional on the distance between
210 trapping stakes upon recapture being greater than the guild-level benchmark defining short
211 distance movements. In this two-state CMR model, transitioning between states indicates long
212 distance movement, and staying in the same state indicates short distance movement, conditional
213 on apparent survival and recapture probabilities. We defined apparent survival probability as the
214 probability that an individual alive in trapping period i survived and did not emigrate from the
215 entire study area by trapping period $i+1$. We defined recapture probability at trapping period $i+1$
216 as the probability that a live individual on the study area was recaptured in a trap. All
217 probabilities were measured over a time scale of approximately one month, the time between
218 trapping events. To address inconsistencies in the data, we controlled for omitted trap periods
219 (when trapping did not occur or the site was only partially trapped) by fixing recapture
220 probability to zero for those occasions. It should be noted that we could not differentiate between
221 permanent emigration and death, which may affect interpretation of our survival estimates. Thus,
222 low apparent survival probabilities may indicate low actual survival, high permanent emigration
223 from the study area, or both. We evaluated each species separately in RMark to estimate
224 apparent survival, recapture, and transition probabilities (White and Cooch 2012), except for
225 transient granivores, which we grouped together because there were not enough captures to
226 analyze species separately. Pooling data for all species into a single dataset, and designating
227 species or strategies with factors, led to an extremely large CMR dataset that prohibited

228 computational analysis using MARK and RMark. We thus used post hoc analyses to compare the
229 estimates for core versus intermediate and transient species. For further details on our RMark
230 analysis, please refer to our code, which is maintained online in a public GitHub repository along
231 with the data (<https://github.com/weecology/portal-rodent-dispersal>) and is available in the
232 online supplement.

233 To assess reproductive effort for each species, we tracked the reproductive history for
234 captured individual females within each calendar year. We considered females with enlarged
235 and/or red nipples or who were pregnant (researcher could feel embryos) to be actively
236 reproducing. If a female was marked in reproductive condition during consecutive trapping
237 periods, we assumed it to be a single reproductive event. Reproductive condition recorded across
238 non-consecutive trapping periods was considered as multiple reproductive events. We used data
239 from females because males display reproductive signals for a larger portion of the year, and
240 male reproductive status does not necessarily indicate recent copulation or reproductive success.
241 For each species, we also recorded litter size and number of litters per year from the literature
242 (Hoffmeister 1986).

243 To compare the life-history traits among groups, we standardized the data and results to
244 account for different units ($[(x - \text{mean}(x))/\text{sd}(x)]$) and controlled for the influence of
245 phylogenetic relatedness on our results (Felsenstein 1985). We used a generalized least squares
246 model to test for the correlation of traits and trait trade-offs with phylogenetic relatedness (APE,
247 Paradis et al. 2004; Geiger, Harmon et al. 2008; picante, Kembel et al. 2010) based on a
248 published mammalian phylogeny (Bininda-Emonds et al. 2007; PhyloOrchard, O'Meara et al.
249 2013) and using the assumption of linear decrease in trait covariance (bm gls; Brownian motion
250 model). We also compared species using a linear regression and PCA biplots to determine the

251 relative influences of temporal status, feeding guild, and phylogenetic relatedness on movement
252 patterns and life history traits.

253

254 **Results**

255 **Core-transient species designation**

256 During the 21-year study period, we captured 12,651 individuals from the 21 species
257 included in the analysis (Table 1). Based on the proportion of years that each species was
258 present, we placed species into three temporal persistence categories (Figure 2) consisting of 10
259 core (*Dipodomys ordii*, *D. merriami*, *Chaetodipus baileyi*, *C. penicillatus*, *Perognathus flavus*,
260 *Peromyscus eremicus*, *Reithrodontomys megalotis*, *Neotoma albigula*, *Onychomys torridus*, and
261 *O. leucogaster*), 7 transient species (*C. hispidus*, *C. intermedius*, *Peromyscus leucopus*, *R.*
262 *montanus*, *R. fulvescens*, *Baiomys taylori*, and *Sigmodon ochrognathus*), and 4 intermediate
263 species (*D. spectabilis*, *Peromyscus maniculatus*, *S. fulviventer*, and *S. hispidus*). Granivores and
264 folivores were represented across all three persistence categories, but both carnivorous species
265 were designated “core” (Table 1). We removed *Chaetodipus hispidus* from our main
266 comparisons because there were only 10 individuals with recaptures and we could not run
267 multistate CMR models on such a small sample. Since transient species were rarely captured at
268 the site and thus do not have enough data points for robust statistical analysis, we focus our
269 results on the comparison between core and non-core species, generally.

270 **Movement, Survival, and Fecundity**

271 For all the species, movement distances between recaptures were strongly unimodal and
272 left-skewed. Transient and intermediate species generally had a longer tail on their movement

273 distributions than core species and distributions for many non-core species had a secondary
 274 mode, suggesting more long-distance movements, larger home ranges, and possible emigration
 275 off-site (Table 1, Figure 3; Figure S1). Transient species that had few long-distance movements
 276 may be attributed to high mortality, low detectability on the site, low recapture due to rapid
 277 movement off the site, or a combination of these. Core species tended to move shorter distances
 278 (median species-level movement benchmark; core=42.91 meters [29.96-152.45]; non-core=65.24
 279 [24.70-365.01]). Among granivores, core species had a lower frequency of moving a relatively far
 280 distance away from the previous trap location (median benchmark=41.50 m) than intermediate
 281 (median benchmark=72.42 m) or transient granivore species (median benchmark=63.42 m;
 282 Table 1). Among folivores, the core species *N. albigula* generally moved shorter distances
 283 (benchmark=39.76 m) than the intermediate (benchmark=53.31 m) and transient species (mean
 284 benchmark=91.85 m; Table 1). Core guild-level movement benchmarks were used to
 285 parameterize the CMR model and differed across trophic groups (benchmark_{granivore}=36.70;
 286 benchmark_{folivore}=39.76; benchmark_{carnivore}=88.07).

287 When using the two-state CMR model in Mark to compare apparent survival, recapture,
 288 and dispersal probabilities among core and transient species, differences were most pronounced
 289 among core granivores versus transient and intermediate granivores (Table 1; Table S1). On
 290 average, core species had a lower probability of moving a long distance (mean $\psi_{\text{core}}=0.14$ [0.03-
 291 0.37]), but higher recapture ($p_{\text{core}}=0.39$ [0.21-0.63]) and apparent survival probabilities (mean
 292 $\Phi_{\text{core}}=0.76$ [0.63-0.84]) than non-core species (mean $\psi_{\text{non-core}}=0.25$ [0.02-0.86], mean $p_{\text{non-}}$
 293 $\text{core}=0.35$ [0.07-0.66], mean $\Phi_{\text{non-core}}=0.67$ [0.45-0.83]).

294 Reproductive results from the field data were best explained by phylogeny. For all
 295 species in *Heteromyidae* (5 core and 3 non-core), the majority of captured females were never

296 recorded in reproductive condition (Table 1; Figure S2). However, despite generally much lower
 297 abundance, species in *Cricetidae* were observed in reproductive condition more often. For
 298 example, nearly 50% of *Peromyscus eremicus* (core) and *P. maniculatus* (non-core) were
 299 recorded in reproductive condition at least once per year (Table 1) and *N. albigula* (core) females
 300 were often found in reproductive condition. However, *Sigmodon* (non-core) females were almost
 301 never recorded as reproductive (Table 1). The lack of observed reproduction may suggest that
 302 *Sigmodon* rarely reproduce at the site or that sampling error associated with the small number of
 303 captures affected our results. *Onychomys* (core) females were rarely captured when reproductive,
 304 but other data suggest that *O. torridus* may reproduce multiple times per year (Table 1, Table 2).

305 **Phylogeny and Trade-offs**

306 PCA results suggested that species can be grouped in multivariate space by their traits
 307 and core-transient status (Fig 4), and that traits appear to be strongly conserved within family
 308 (Fig A3). Phylogeny (family) was a significant predictor of ψ (linear model; $\text{lm}(\psi \sim \text{family})$,
 309 $p=0.016$, $r^2=0.28$), Φ ($\text{lm}(\Phi \sim \text{family})$, $p=0.006$, $r^2=0.35$), and mean abundance (lm
 310 ($\text{abundance} \sim \text{family}$), $p=0.004$, $r^2=0.37$), but not for the proportion of years a species was present.
 311 Mean abundance was positively related to the proportion of years a species was present in the
 312 study area when phylogeny was controlled for (bm gls, $p=0.005$). Body size was not a significant
 313 predictor for the proportion of years present, mean abundance, survival, reproduction, or
 314 movement (bm gls, $p \gg 0.05$). We did not detect strong movement-survival trade-offs or
 315 movement-reproduction trade-offs in this community using linear regression or phylogenetic
 316 methods (Figs A4, A5). There was a relationship between observed modal movement distance
 317 and temporal persistence ($\text{lm}(\text{distance mode} \sim \text{proportion years present})$, $p=0.03$, $r^2=0.23$; bm
 318 gls, $p=0.05$) where species that persisted longer moved shorter distances.

319

320 **Discussion**

321 Our study provides the first test, to our knowledge, of whether life history traits are
322 associated with the temporal persistence patterns of species in a community. Life-history traits
323 were generally conserved within evolutionary lineages, which in our system are also related to
324 higher or lower degrees of adaptation to desert environments. Our results provide some
325 indication that life history traits are also linked to the core-transient structure among species at
326 our site. Analysis of the movement, survival and reproduction data indicated that core species at
327 our site moved relatively short distances and had higher apparent survival rates than intermediate
328 and transient species, consistent with our predictions. Core species were generally more
329 abundant than transient or intermediate species, which may suggest greater competitive
330 dominance or ecological specialization. Transient species at our site exhibited lower apparent
331 survival and moved longer distances, on average, than core species, but the range of estimates
332 within this group varied widely. We interpret the high variation in survival and movement
333 estimates across species within the intermediate and transient groups as support for the idea that
334 this group includes both source-sink and nomadic transients. Among traits, we did not detect
335 strong movement-survival trade-offs, and too few reproductive events were observed to test for
336 survival-reproduction trade-offs.

337 Other research at our site also supports the idea that our core and transient species have
338 different effects on community structure and resource use. Core species that exhibit high self-
339 investment, strong competitive ability, and strong local adaptation are also expected to
340 successfully exploit most of the available resources at a local site (Kneitel and Chase 2004). The
341 most abundant core species at our site are indeed responsible for the majority of resource

342 consumption (Thibault et al. 2004), are behaviorally dominant (*Dipodomys* spp.; Reichmann and
343 Price 1993), and have cascading impacts on rodent and plant communities (Brown and Heske
344 1990; Heske *et al.* 1994; Valone and Schutzenhofer 2007). Pocket mice (*Chaetodipus* spp.),
345 another group of core species, become dominant in the absence of kangaroo rats (Ernest and
346 Brown 2001). Therefore, it is generally true that species with lower movement, higher
347 survivorship, and potentially lower reproductive rates are also the competitively dominant
348 species responsible for the majority of resource consumption (Thibault et al. 2004).

349 The life-history estimates for transient and intermediate species (n=11) generally
350 supported our hypotheses. We expected that results for this group of species would exhibit broad
351 interspecific variation because of the presence of both nomadic and source-sink transients.
352 Unfortunately, it is not possible to definitively distinguish between these groups using our data,
353 but using a combination of our results and the well-studied natural history of these species, we
354 can make some informed predictions. Species that exhibited trait correlations more similar to
355 core species could be source-sink transients (Lenormand 2002; Kawecki 2008), or could be
356 undergoing local extinction (Gibson et al. 1999). Because they are core somewhere else, source-
357 sink transients may generally be inferior competitors that temporarily colonize in response to
358 resource pulses and density dependent dispersal at other locations, both of which could create a
359 source-sink dynamic over time (Heske *et al.* 1994; Thibault *et al.* 2004). *Dipodomys* and
360 *Chaetodipus* species that were not core at our site are either undergoing local extinction due to
361 directional habitat change (*D. spectabilis*; Valone et al. 2002, Thibault et al. 2004) or are not
362 adapted to the habitat at our site (*C. intermedius* and *C. hispidus*; Hoffmeister 1986; Paulson
363 1988, Williams et al. 1993) and their occasional presence can likely be attributed to temporary
364 dispersal from nearby source populations (Wilson and Ruff 1999). At our site, *Sigmodon* and

365 *Reithrodontomys* are prairie-adapted species (Webster and Jones 1982; Hoffmeister 1986) that
366 usually arrive during years and seasons where climatic conditions lead to higher than normal
367 grass cover (Thibault *et al.* 2004). During our study period these species had relatively low
368 abundance and were rarely recorded in reproductive condition – strong evidence that our site
369 represents a habitat sink for these populations. Species that exhibited trait correlations different
370 from core species could be nomadic transients. *Peromyscus maniculatus* and *leucopus* at our site
371 were generally rare, moved longer distances more often, potentially reproduce multiple times per
372 year, and use a wider resource base than the core species (Hoffmeister 1986; Wilson and Ruff
373 1999), evidence that these species could readily colonize new locations. In addition, *Baiomys*
374 *taylori* seem to be dependent on high ground cover, and thus requiring populations to
375 nomadically track habitats receiving more than the usual amount of water (Wilson and Ruff
376 1999). Thus, through these two different processes, source-sink and nomadic transient species
377 maintain presence in the regional metacommunity and comprise a dynamic component of the
378 local community.

379 The core-transient framework, integrated with an eco-evolutionary viewpoint, suggests
380 that core and transient species may be responsible for maintaining different aspects of ecosystem
381 function. Because of their higher local adaptation and stronger ability to exploit resources under
382 local conditions, core species may be particularly important for maintaining ecosystem function
383 (Leibold *et al.*, *submitted*). In contrast, because of their higher dispersal rates, transient species
384 may be particularly important for maintaining local diversity through time and in response to
385 disturbance (Dornelas *et al.* 2014, Supp and Ernest 2014, Leibold *et al.* *submitted*). Our site
386 exhibits high annual composition turnover while generally maintaining species richness (Brown
387 *et al.* 2001, Goheen *et al.* 2005), which indicates a role for nomadic transients in the regional

388 metacommunity that can opportunistically fill empty niches and thus maintain community-level
389 species richness. Our results suggest that species with locally adapted traits well suited to
390 maximizing ecosystem functions related to resource use may also have lower dispersal rates. If
391 so, this relationship between traits and dispersal may be particularly important to explore in a
392 metacommunity context (Leibold et al *submitted*).

393 Assessing whether there are life history implications for species using local versus
394 regional scale processes for population maintenance is challenging. Long-term mark-recapture
395 data that provides information on movement, survival, and reproduction rates across an entire
396 community, including rare species, is very difficult data to obtain. Despite the shortcomings of
397 our data, our results suggest that core and transient species may differ not only in their temporal
398 persistence, but also in their use of landscapes, traits for resource use, and structure of their life
399 histories. If other studies support our findings, it suggests that core-transient species traits should
400 be modeled separately to understand how these groups might respond differently to
401 environmental change. Core and source-sink transient species generally associated with low
402 levels of gene flow or that are unable to track shifts in the location of suitable habitat across the
403 landscape, would be predicted to undergo catastrophic decline under environmental changes that
404 alter local conditions long-term (*e.g.* temperature, resource availability). Alternately, nomadic
405 transient species that emigrate readily and exhibit high levels of gene flow among populations
406 would be predicted to exhibit relatively small change in response to the same scenario. In the
407 drive to better understand the response of biodiversity to perturbations, a temporal perspective of
408 species demographics and persistence represents a critical link in identifying the linkages
409 between local and regional richness patterns and predicting community response to change.

410

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554

555 **Figure Legends**

556 **Figure 1. Hypothesized relationships between core-transient status and life history trade-**
557 **offs.** Temporal persistence is predicted to be correlated with life-history traits including survival,
558 reproduction, movement patterns, and resource use.

559

560 **Figure 2. The proportion of years and the mean proportion of months that a species was**
561 **present in the study period (1989-2009).** We designated core (≥ 0.66), intermediate (< 0.66 and
562 > 0.33) and transient (≤ 0.33) status based on the proportion of years only. Two-letter
563 abbreviations refer to the species names (*B. taylori*, BA; *C. baileyi*, PB; *C. hispidus*, PH; *C.*
564 *intermedius*, PI; *C. penicillatus*, PP; *D. merriami*, DM; *D. ordii*, DO; *D. spectabilis*, DS; *N.*
565 *albigula*, NA; *O. leucogaster*, OL; *O. torridus*, OT; *P. flavus*, PF; *Pe. eremicus*, PE; *Pe.*
566 *leucopus*, PL; *Pe. maniculatus*, PM; *R. flavescens*, RF; *R. megalotis*, RM; *R. montanus*, RO; *S.*
567 *fulviventer*, SF; *S. hispidus*, SH; *S. ochrognathus*, SO).

568

569 **Figure 3. Histograms grouped by temporal persistence for the distances at which**
570 **individuals were recaptured each month.** Note that the y-axes are the percent of observations
571 for each bin, but that there is a large difference in total number of individuals captured in each
572 group, that is not represented in the histograms (but see Table 1).

573
574 **Figure 4. PCA biplot with confidence ellipses for temporal persistence.** The relationship of
575 movement (Psi and benchmark), mean number of observed reproductive events for individuals of
576 each species per year (fecundity), apparent survival (Phi), recapture rates (p), mean abundance,
577 and the proportion of years a species was present (persistence). Two letter abbreviations refer to
578 species names as presented in Figure 2. PCA axes 1 and 2 explained a total 64.6% of the
579 variation.

580

581 **Supporting Information Legends**

582 **Figure S1. Panels showing the species-level movement distances calculated from the**
583 **recapture data.** Two-letter species name abbreviations are as follows from Figure 2.

584

585 **Figure S2. Observed yearly reproductive effort for individuals of each species from the**
586 **field study.** The y-axis represents the proportion females that we tracked that were recorded in
587 reproductive condition 0-4 times per calendar year (no individuals were recorded as having > 4
588 reproductive events within a calendar year). Two-letter species name abbreviations are as
589 follows from Figure 2.

590

591 **Figure S3. PCA biplot with confidence ellipses for phylogenetic relatedness at the family**
592 **level.** The relationship of movement (Ψ , benchmark), mean number of reproductive events
593 individuals of a species had per year (fecundity), apparent survival (Φ), recapture rates (p),
594 mean abundance, and the proportion of years a species was present (persistence). Two letter
595 abbreviations refer to species names as presented in Figure 2. PCA axes 1 and 2 explained a total
596 of 64.6% of the variation.

597
598 **Figure S4. Apparent survival estimates (Φ) shown against the $\log(Y+1)$ distance**
599 **(benchmark) moved for each species and probability of moving a relatively long distance**
600 **(ψ) as estimated using RMark.** The plotted variables have been standardized. Points represent
601 core (pink circles), intermediate (green triangles) and transient (blue squares) species.

602
603 **Figure S5. Movement estimates (benchmark, ψ) shown against fecundity for each species.**
604 Evidence for a reproduction-movement trade-off is not statistically significant. The plotted
605 variables have been standardized. Points represent core (pink circles), intermediate (green
606 triangles) and transient (blue squares) species.

607
608 **Figure S6. Relationship between the CMR estimates for apparent survival (Φ), movement**
609 **(Ψ) and recapture (p) probability from the CMR analysis for each species, plotted with**
610 **error bars representing standard error for each estimate.** Points represent core (pink),
611 intermediate (green) and transient (blue) species. Note that the transient species have the largest
612 error bars.

613

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

616

617 **Tables**

618

619

620

621 **Table 1. Summary of species traits from the field data.**

Species	Guild	Habitat Specialist	Status	N	Mean mass (g)	Mean num. reproduction events/year	Movement benchmark (m)	Φ	Std. Error Φ	p	Std. Error p	ψ	Std. Error ψ
<i>Dipodomys merriami</i>	Gran.	Yes	Core	1972	43.64	0.52	33.13	0.80	0.00	0.60	0.01	0.06	0.00
<i>D. ordii</i>	Gran.	Yes	Core	1030	48.32	0.47	30.35	0.75	0.01	0.63	0.01	0.03	0.00
<i>D. spectabilis</i>	Gran.	Yes	Intermed.	41	115.01	0.21	24.70	0.83	0.02	0.66	0.04	0.02	0.01
<i>Chaetodipus baileyi</i>	Gran.	Yes	Core	2063	31.77	0.40	29.96	0.84	0.00	0.56	0.01	0.04	0.00
<i>C. penicillatus</i>	Gran.	Yes	Core	2818	17.01	0.40	44.33	0.83	0.00	0.21	0.00	0.06	0.02
<i>C. hispidus</i>	Gran.	No	Transient	10	31.74	0.43	16.49	--	--	--	--	--	--
<i>C. intermedius</i>	Gran.	No	Transient	20	18.46	0.14	33.96	0.79	0.05	0.25	0.07	0.06	0.04
<i>Perognathus flavus</i>	Gran.	Yes	Core	648	8.12	0.54	41.50	0.78	0.01	0.23	0.01	0.06	0.01
<i>Peromyscus eremicus</i>	Gran.	Yes	Core	479	21.47	0.53	107.18	0.63	0.02	0.32	0.02	0.37	0.04
<i>Pe. maniculatus</i>	Gran.	No	Intermed.	398	21.41	0.46	120.13	0.62	0.02	0.28	0.03	0.53	0.05
<i>Pe. leucopus</i>	Gran.	No	Transient	77	22.41	0.24	56.05	0.46	0.06	0.44	0.11	0.12	0.06
<i>Reithrodontomys megalotis</i>	Gran.	No	Core	1180	10.71	0.23	95.17	0.63	0.01	0.27	0.01	0.33	0.2
<i>R. montanus</i>	Gran.	No	Transient	18	9.01	0.67	365.01	0.72	0.14	0.07	0.06	0.86	0.15
<i>R. fulvescens</i>	Gran.	No	Transient	11	13.90	1.50	63.42	0.81	0.05	0.63	0.08	0.22	0.08
<i>Baiomys taylori</i>	Gran.	No	Transient	106	8.76	0.26	70.65	0.63	0.05	0.22	0.05	0.12	0.05
<i>Sigmodon hispidus</i>	Foliv.	No	Intermed.	268	88.84	0.12	39.56	0.45	0.04	0.38	0.06	0.08	0.03
<i>S. fulviventer</i>	Foliv.	No	Intermed.	151	66.01	0.07	67.06	0.66	0.03	0.35	0.04	0.14	0.03
<i>S. ochrognathus</i>	Foliv.		Transient	27	55.55	0.37	91.85	0.70	0.07	0.21	0.07	0.31	0.14
<i>Neotoma albigula</i>	Foliv.	No	Core	255	167.05	0.66	39.76	0.79	0.01	0.33	0.02	0.10	0.02
<i>Onychomys torridus</i>	Carn.	No	Core	952	23.81	0.49	80.87	0.76	0.01	0.42	0.01	0.09	0.01
<i>O. leucogaster</i>	Carn.	No	Core	127	30.16	0.54	152.45	0.77	0.02	0.37	0.03	0.27	0.04

622

623 Species-level trait details summarizing feeding guild, core-transient status, ecological specialization, total number of individuals
624 tracked through the study (N), mean body mass across all recorded weights, mean yearly reproductive effort, and species-level
625 benchmarks defining where each movement distribution transitions into long-distance movements. Yearly reproductive effort was
626 estimated by taking weighted average of the number of individual females marked as reproductive 0-4 times per year. -- indicate that
627 we could not generate multistate CMR estimates due to small sample size (N < 10).

628 **Table 2. Summary of reproductive life-history traits.**

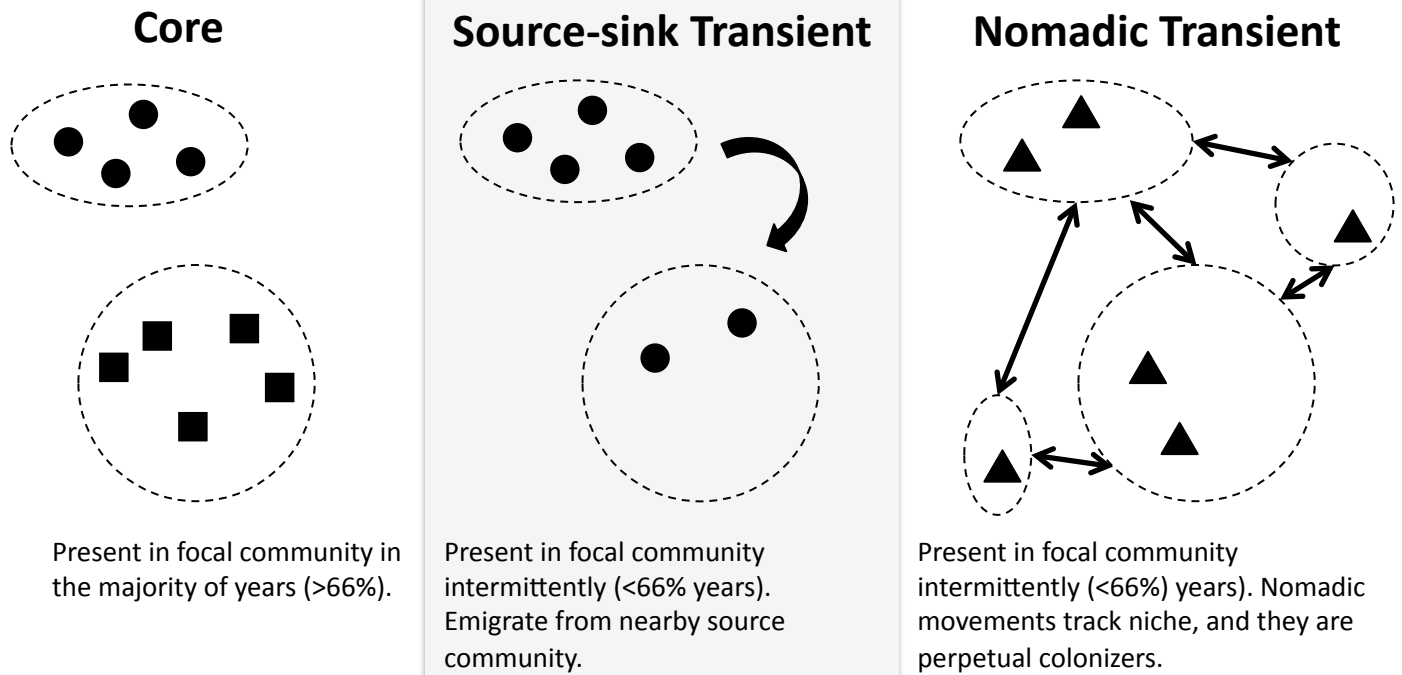
Species	Status	Litter size	Mean litter size	Number of litters per year	Typical breeding months
<i>Dipodomys ordii</i> *	Core	2-3	2.37	1-2	February-July ⁶³⁰
<i>D. merriami</i> *	Core	2-3	2	1-2	March-October ⁶³¹
<i>Chaetodipus baileyi</i> *	Core	1-6	3.6	--	April-August
<i>C. penicillatus</i> *	Core	2-8	4.72	1	April-August ⁶³²
<i>Perognathus flavus</i> *	Core	1-6	4	1	April-August
<i>Peromyscus eremicus</i> *	Core	1-4	2.53	1-4 [†]	Year-round ⁶³³
<i>Reithrodontomys megalotis</i> *	Core	3-7 [†]	3.6	1-10	Year-round
<i>Neotoma albigula</i>	Core	1-4	1.95	≥ 1	Year-round ⁶³⁴
<i>Onychomys torridus</i>	Core	2-5	3.45	--	March-October
<i>O. leucogaster</i>	Core	3-5	4	--	March-September
<i>D. spectabilis</i> *	Intermediate	1-3	2.1	1-2	January-August ⁶³⁵
<i>P. maniculatus</i>	Intermediate	1-6	4.29	2-4 [†]	Year-round ⁶³⁶
<i>Sigmodon hispidus</i>	Intermediate	2-10	5.6	1-9	Year-round ⁶³⁷
<i>S. fulviventris</i>	Intermediate	4-6 [†]	--	--	Year-round
<i>C. hispidus</i> *	Transient	4-7 [†]	--	1-2 [†]	-- ⁶³⁸
<i>C. intermedius</i> *	Transient	1-7	3.94	--	March-July
<i>P. leucopus</i> *	Transient	2-5	3.61	>1 [†]	February-October ⁶³⁹
<i>R. montanus</i> *	Transient	1-9 [†]	4 [†]	--	Year-round [†]
<i>R. fulvescens</i> *	Transient	2-4	--	--	Year-round ⁶⁴⁰
<i>Baiomys taylori</i> *	Transient	1-5 [†]	2.49	1-9	Year-round ⁶⁴¹
<i>S. ochrognathus</i>	Transient	2-6	--	--	Year-round [†]

642

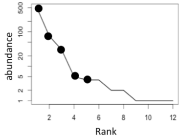
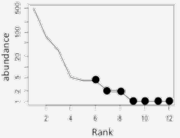
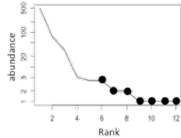
643 Data from Hoffmeister (1986), with missing data filled from Wilson and Ruff (1999)[†]. Dashes (--) indicate no data from either
 644 reference. Species marked with an asterisk (*) are directly competing for resources in the granivore feeding guild.

645

Figure 1

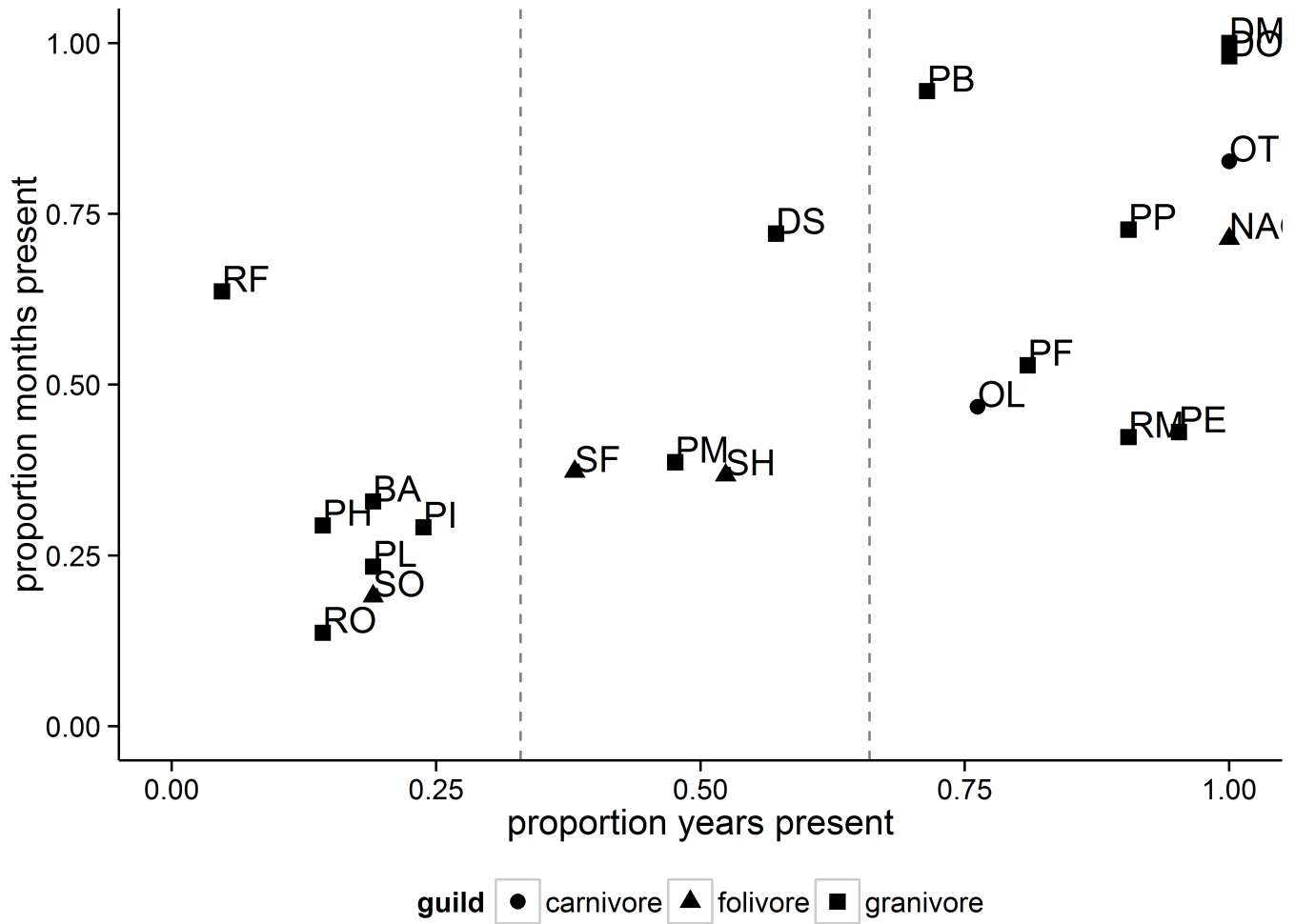


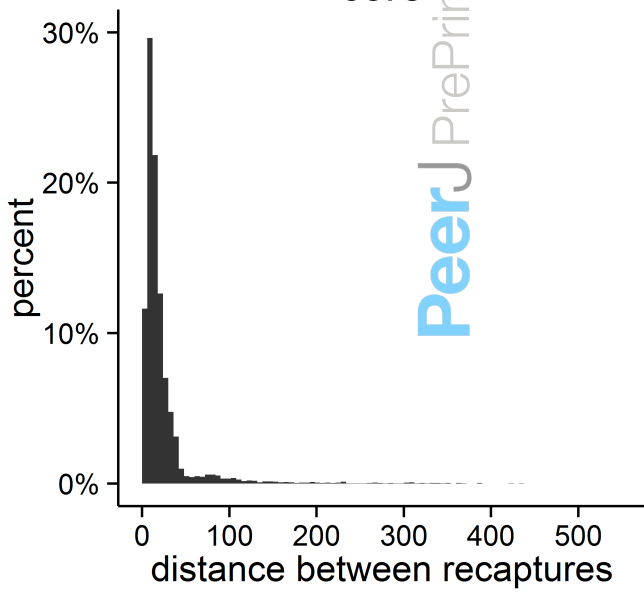
Species fall along a continuum of traits and temporal persistence

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

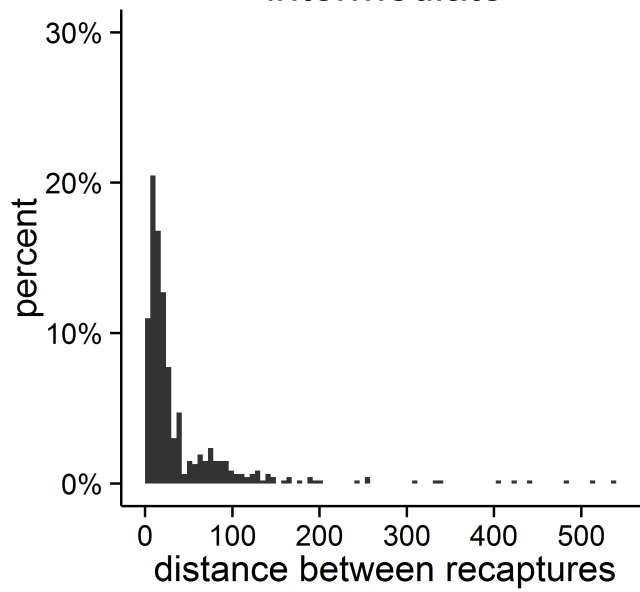
Circular habitat is "focal" community. Dashed lines represent that communities are open. Core-transient designation is a concept defined within a focal community, but we hypothesize that temporal persistence should be linked to traits.

Figure 2





intermediate



transient

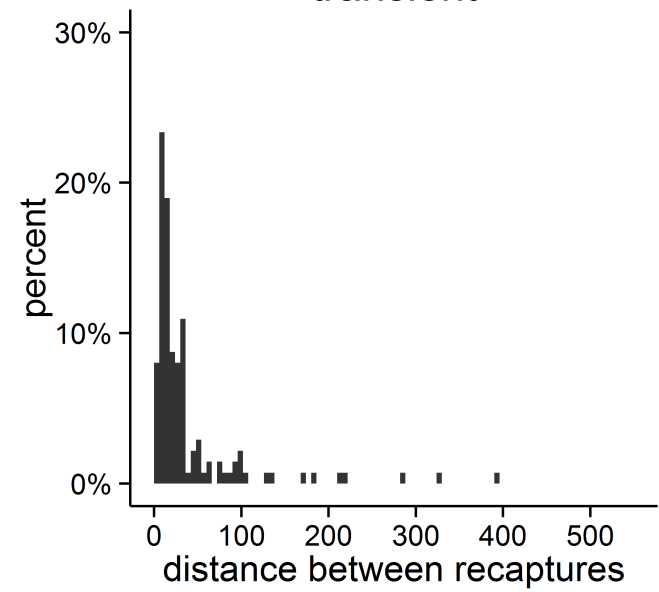


Figure 4

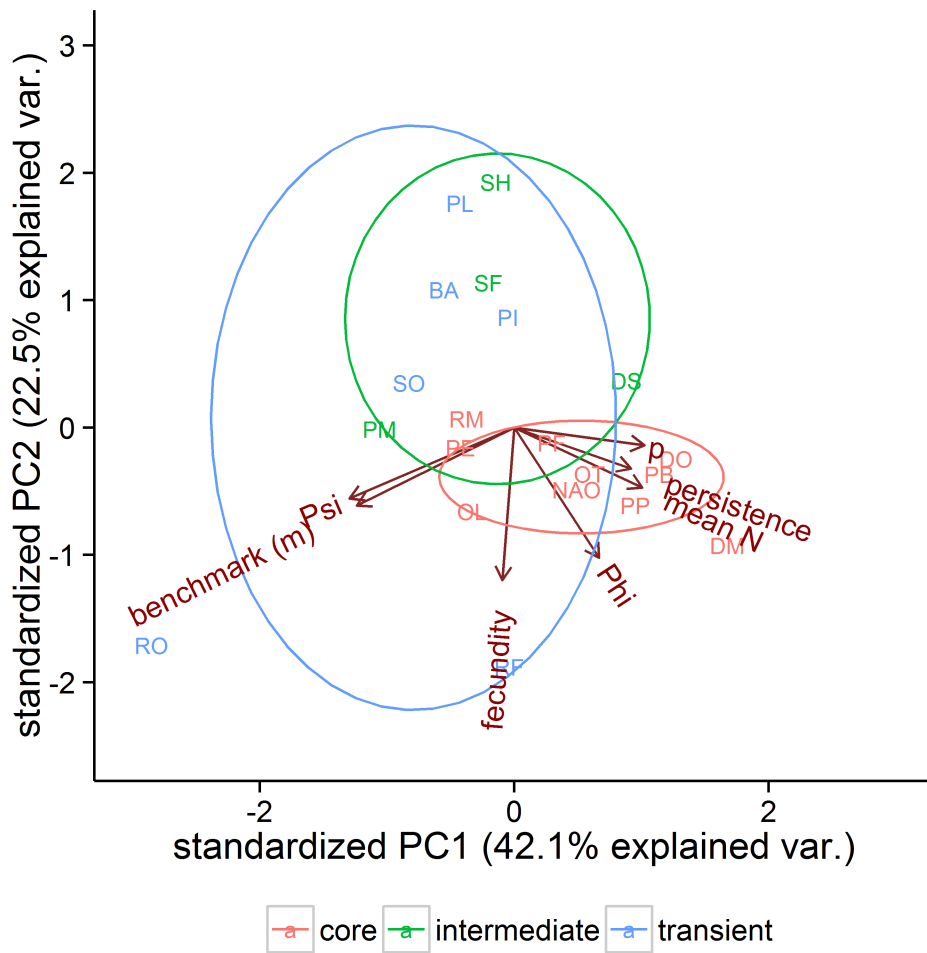
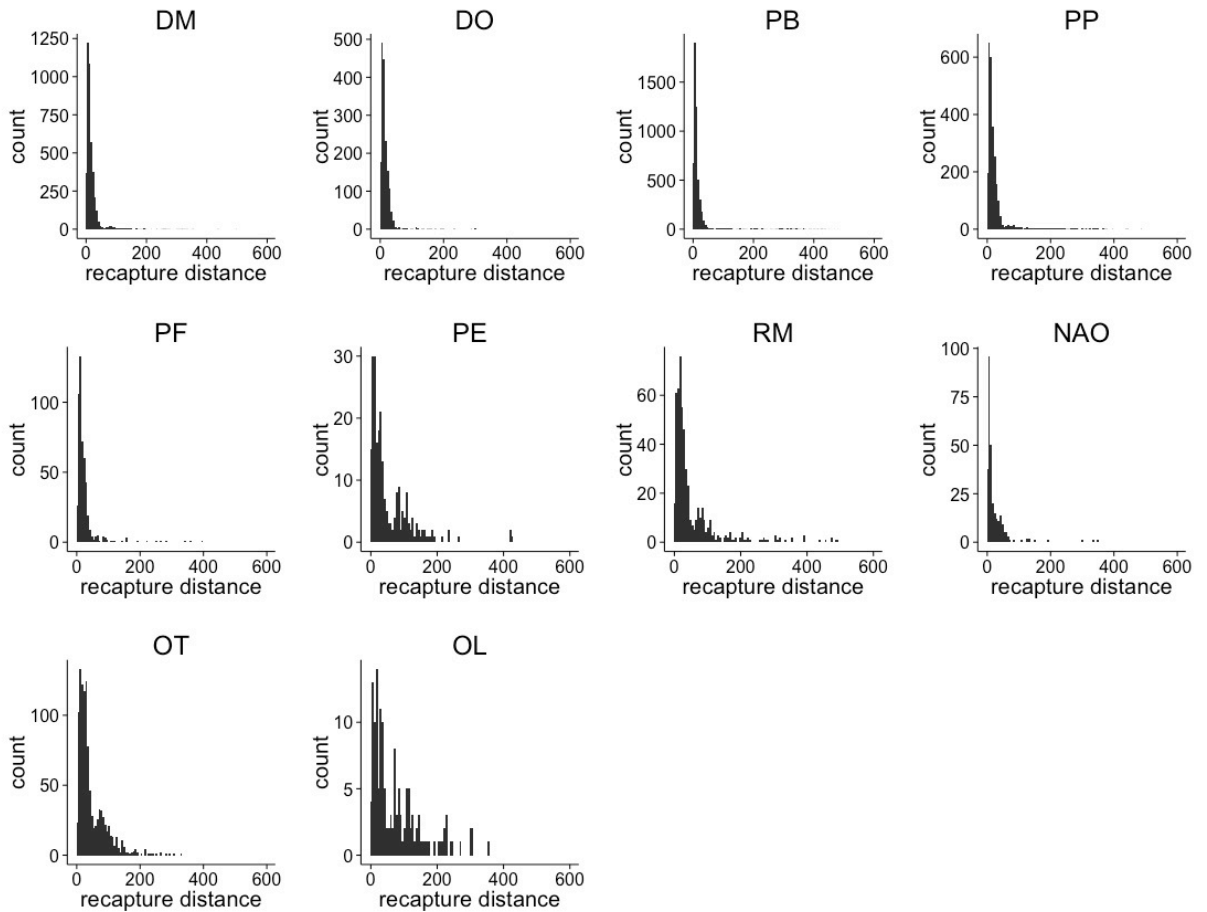
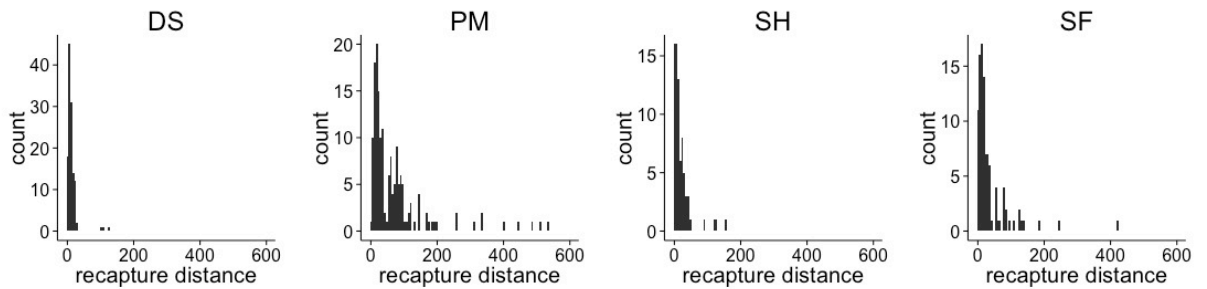


Figure S1

Core



Intermediate



Transient

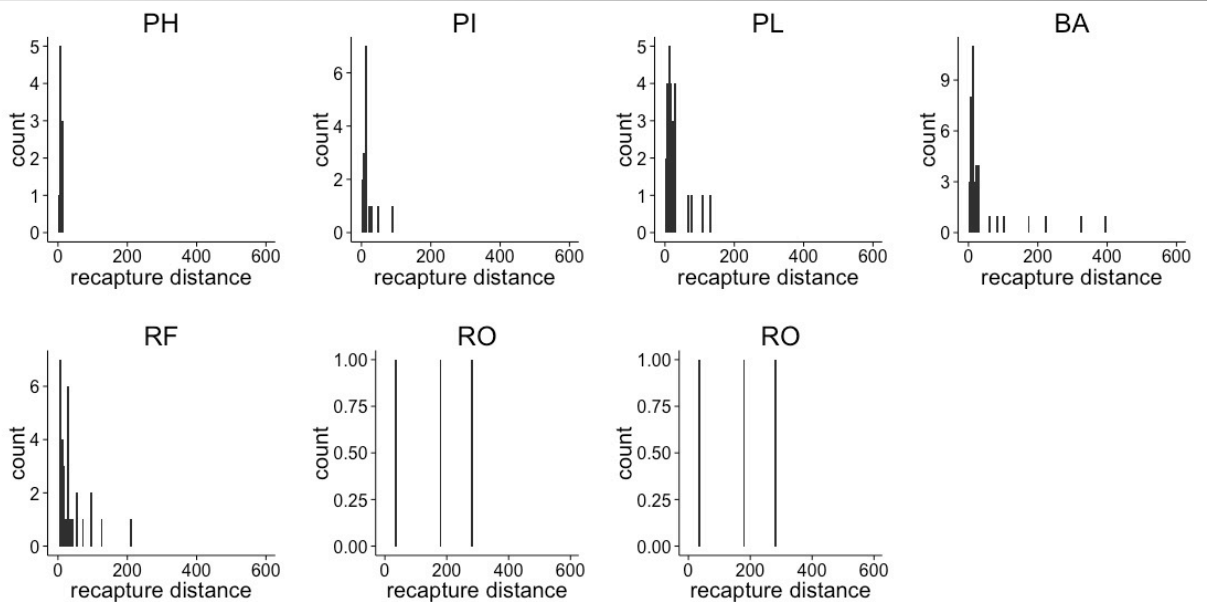


Figure S2

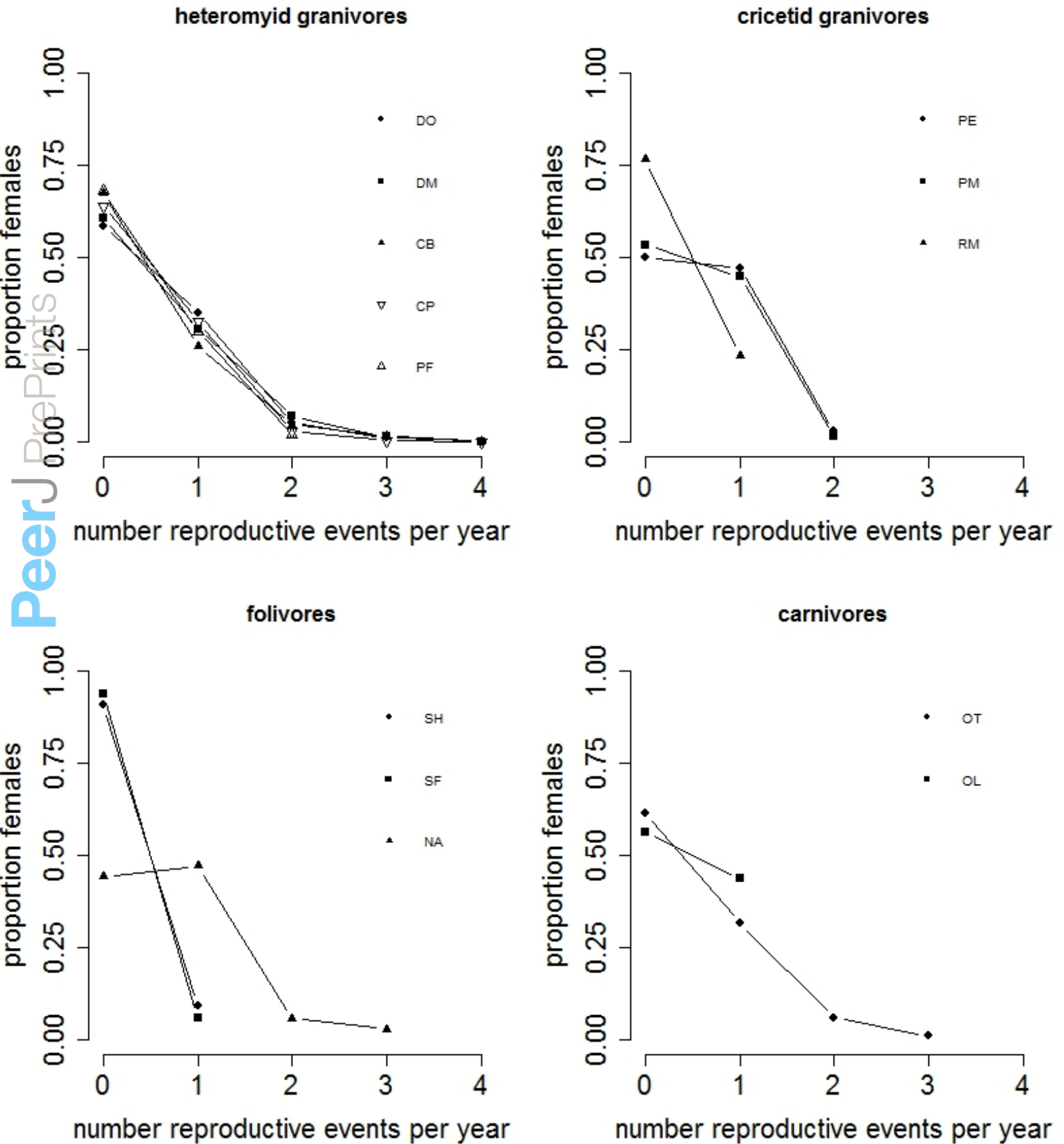


Figure S3

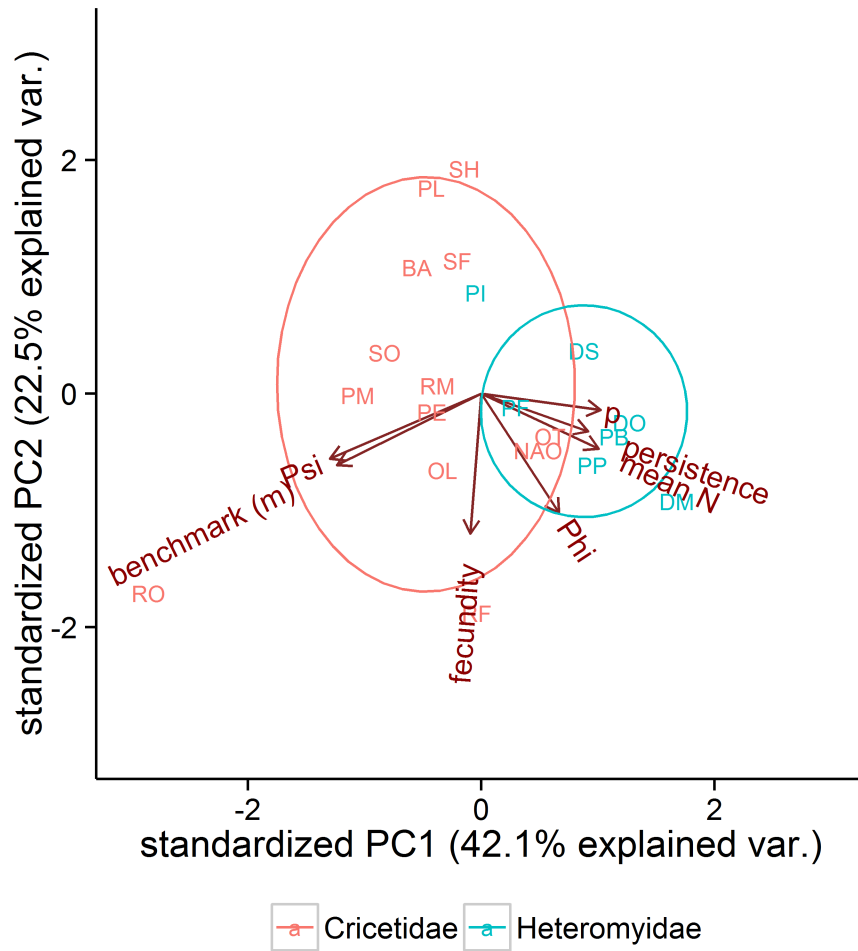


Figure S4

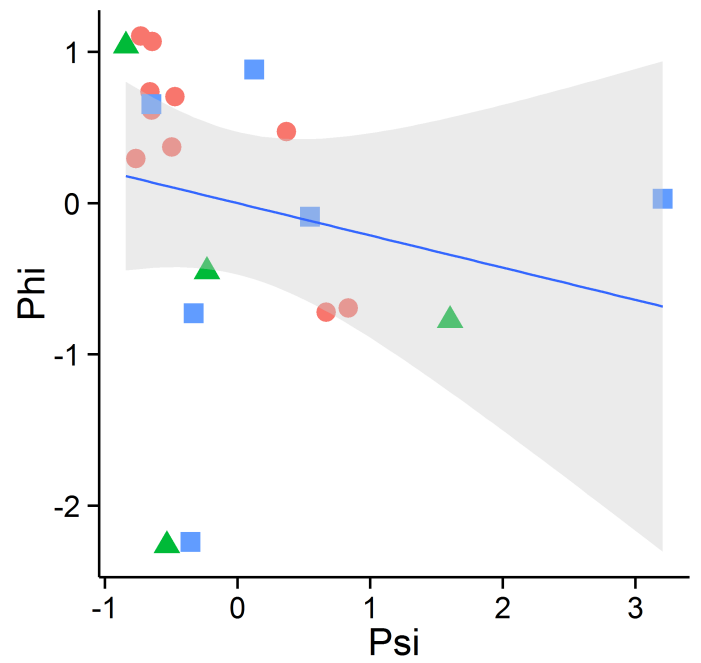
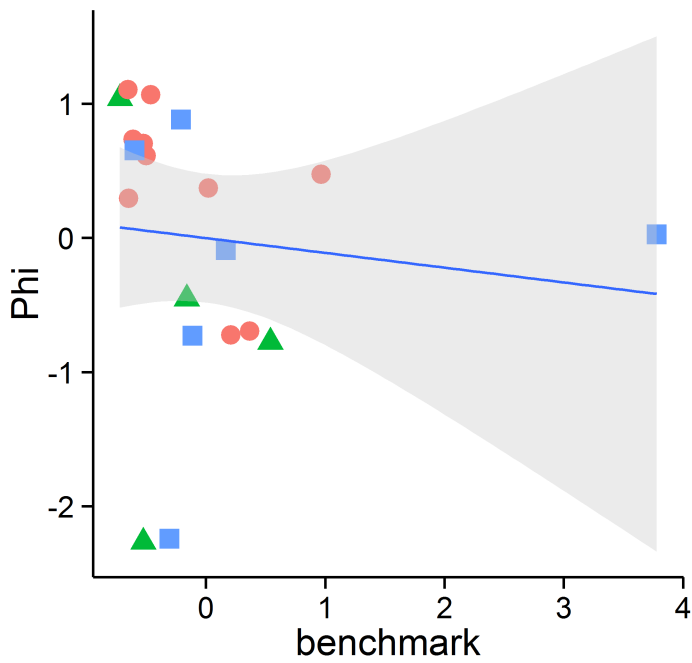


Figure S5

