Predicting changes in bee assemblages following state transitions in North American drylands

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Drylands worldwide are experiencing ecosystem state transitions: the expansion of some ecosystem types at the expense of others. Bees in drylands are particularly abundant and diverse, with potential for large compositional differences and seasonal turnover across ecotones. To better understand how future ecosystem state transitions may influence bees, we compared bee assemblages and their seasonality among three dryland ecosystem types of the southwestern U.S. (Plains grassland, Chihuahuan Desert grassland, and Chihuahuan Desert shrubland). Using passive funnel traps, we caught bees during two-week intervals from March through October during 2002 – 2014. The resulting dataset included 302 bee species and >70,500 individuals. Bee abundance, composition, and diversity differed among ecosystems, indicating the potential for future ecosystem state transitions to alter bee assemblage composition in drylands. We also found strong seasonal turnover in bee species, suggesting that bee phenological shifts may accompany ecosystem state transitions. Common rather than rare species drove the observed trends, and both specialist and generalist bee species were indicators of each ecosystem type or month; these species could be informative sentinels of community-wide responses to future shifts. Our work suggests that predicting the consequences of global change for bee assemblages will require accounting for both within-year and among-ecosystem variation.

Introduction

Drylands worldwide are experiencing ecosystem state transitions: the expansion of some ecosystem types at the expense of others[1,2]. These transitions include encroachment of C_3 shrubland into C_4 grassland[3] and conversion of woodland to savanna[4]. It is through these transitions that the largest changes in dryland ecosystem processes are occurring[5–7]. State transitions can produce dramatic changes in carbon fluxes[8,9], nutrient dynamics[10,11], spatial heterogeneity in vegetation[12], and consumer community composition[13,14]. Because drylands cover ~45% of land area on Earth[15] and support over 2 billion people[16], understanding how much dryland ecosystems currently differ in community composition can help to predict changes in future communities — and the ecosystem services they provide — under state transitions.

Bees may serve as important bio-indicators of state transitions and sentinels of altered ecosystem services[17,18]. In drylands, bees are important pollinators of both wild plants and agricultural

crops[19,20], and are particularly abundant and diverse. North America's highest bee diversity occurs in the southwestern U.S. and northwest Mexico, and 75% of the continent's bee species are found in the western U.S.[21,22]. Relative to mesic ecosystems, drylands can also host higher proportions of specialist bee species, which pollinate one or a few closely related plant species[23]. For example, creosote bush (*Larrea tridentata* (DC.) Coville), a widespread and abundant shrub in North American warm deserts[24], is visited by 22 documented specialist bee species[25]. Cacti also host many specialists[26]. Communities dominated by specialist bees may be less resilient to state changes or pollinator declines than communities dominated by generalist bees, which can buffer plants against crashes in other bee species[27,28]. Future ecosystem state transitions could therefore substantially influence bees in drylands, making it important to understand potential vulnerabilities of dryland bee assemblages to these shifts.

Understanding variation in bee composition among habitat types can shed light on how ecosystem state transitions will influence bee assemblages. Prior studies have largely focused on bee assemblage variation within agricultural environments, along urban-rural gradients, or with habitat fragmentation[29–31], while fewer studies have compared natural ecosystems. For instance, in Spain, shrub encroachment into grasslands corresponded with higher pollinator richness but fewer pollinator visits to forbs[32]. In xeric environments, some studies have documented bee species turnover across relatively small spatial scales[25,33,34]. For instance, during a single growing season, one study found lower bee abundance and richness in desert scrubland relative to riparian sites within a 4 km^2 area in the Sonoran Desert[33]. In contrast, abundances of insect pollinator functional groups did not differ between creosote bush-dominated and adjacent annual forb-dominated microsites in the Mojave Desert[35], although this study occurred on a smaller spatial scale with coarser taxonomic resolution. These contrasting results highlight the need for additional data to better predict the potential consequences for bee assemblages of specific state transitions in dryland ecosystems.

In addition, seasonal turnover in bee species composition suggests the potential for climate change to produce shifts in bee phenology[36]. Some bees may cue on climate variables for their emergence as adults, with temperature or precipitation conditions triggering the emergence of bee species at different times of year[37–39]. High temporal turnover in bee assemblage composition could thus indicate dominance of species with phenologies closely tied to climate, which may be particularly

susceptible to phenological shifts under climate change. Understanding bee assemblage seasonality in ecosystem types predicted to expand or contract under climate change could thus be important for predicting bee assemblage responses to state transitions. However, while bee composition is well documented to vary seasonally within a community[40–42], few studies have compared seasonal patterns among ecosystem types to discern how state transitions may shift bee phenology at the landscape scale. Seasonal trends in bee abundance and richness were found to differ between natural and human-altered landscape types during a single year in California, USA[43], and among agricultural land use classes during 3 years in New Hampshire, USA[44]. However, we lack studies that use long-term data to elucidate how general patterns of bee seasonality differ among natural ecosystem types that are expanding versus contracting.

This study compared bee assemblages and their seasonality among sites representing three dryland ecosystem types of the southwestern U.S.: Chihuahuan Desert shrubland, Chihuahuan Desert grassland, and Plains grassland. Our sites occurred within a relatively small area (within 2-10 km of one another) that encompassed ecotones between the types, and shared the same regional pool of bee species. We used 13 years of monthly bee trap data to address two questions: (1) How much do bee assemblage abundance, composition, and diversity differ among major southwestern U.S. ecosystem types? (2) Do dryland ecosystem types differ in their degree of seasonal variation in bee abundance, composition, or diversity? We examined patterns among ecosystem types and months of the year by averaging across the time series, enabling us to identify general trends. Whereas this analysis focused on intra-annual and among-habitat variation in bee composition, a companion study will report inter-annual change over the time series, providing substantial additional complexity to the analysis.

Methods

Ecosystem types

The Sevilleta National Wildlife Refuge (NWR; Socorro, NM) includes five ecosystem types that together represent ~80 million ha of the southwestern U.S. We focused on three major ecosystem types: Chihuahuan Desert shrubland, which is dominated by creosote bush (*Larrea tridentata*), Chihuahuan Desert grassland, which is dominated by black grama grass (*Bouteloua eriopoda* (Torr.) Torr.), and Plains

100 grassland, which is dominated by blue grama grass (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths)
101 (Table 1). Transitions among these ecosystem types are predicted to occur under climate change, with
102 Chihuahuan Desert shrubland encroaching upon Chihuahuan Desert grassland, which is predicted to
103 replace Plains grassland[45–47]. In our study, the two Chihuahuan Desert sites were separated by ~2 km;
104 the Plains grassland site was ~10 km from the Chihuahuan Desert sites (Table 1).

105 *Bee collection*

106 Bees were sampled along five transects located within each of the three focal ecosystem types.
107 To sample bees, we installed one passive funnel trap at each end of five 200 m transects/site. Each trap
108 consisted of a 946 mL paint can filled with ~275 mL of propylene glycol and topped with a plastic
109 automotive funnel with the narrow part of the funnel sawed off (funnel height = 10 cm, top diameter = 14
110 cm, bottom diameter = 2.5 cm; Supplementary Fig. S1). The funnels' interiors were painted with either
111 blue or yellow fluorescent paint (Krylon, Cleveland, OH or Ace Hardware, Oak Brook, IL). On each
112 transect, we randomly assigned one trap to be blue and the other to be yellow (total across the three
113 sites: N = 30 traps, with 15 traps/color). Because different bee taxa are known to be attracted to blue
114 versus yellow[48], we summed the samples collected in the two traps on a given transect. Each trap was
115 placed on a 45 cm high platform that was surrounded by a 60 cm high chicken wire cage to prevent
116 wildlife and wind disturbance (Supplementary Fig. S1). Funnel traps provide a measure of bee activity,
117 not a measure of presence, and may be biased by bee taxon and sociality[49,50]. From 2002 to 2014, bees
118 were sampled each month from March through October. Traps were opened each March as close as
119 possible to the first day of spring, and left open for 14 d, after which the bee specimens were collected.
120 The traps were then closed for 14 d. This two-week cycle was repeated through October. Bees were
121 rinsed and stored in 70% ethanol until processed.

122 *Bee identification*

123 Bees were identified to species by K.W.W. and T.L.G. Certain groups of bees could not be
124 identified to species, either because there are no practicing experts in the bee group and species are
125 unnamed for our study region, or because there are no revisions within the bee group to separate named
126 from unnamed species. In these cases, we separated females into morphotypes as best as possible. The
127 males of these groups could not be reliably linked to the females and were therefore excluded from the

128 dataset. The major groups treated in this manner were the genera *Sphecodes*, *Pseudopanurgus*, and
129 *Nomada*, the subgenera *Dialictus* and *Evylaeus* of the genus *Lasioglossum*, and the subgenus
130 *Micrandrena* of *Andrena*. We excluded *Nomada* from our analyses due to low abundance and lack of
131 ability to distinguish among species. New species of relatively well-known genera were recognized, and
132 the qualifiers nr. or aff. were used with uncertain identifications. Voucher specimens were deposited at
133 the University of New Mexico's Museum of Southwestern Biology and the USDA-ARS Pollinating Insects
134 Research Unit's U.S. National Pollinating Insects Collection. Information related to these specimens is
135 available via the Symbiota Collections of Arthropods Network (https://scan-bugs.org).

136 *Analysis*

137 Dataset. We created a species matrix in which cells contained the mean abundance of each bee
138 species for each month of collection, averaged over the years of collection (2002 – 2014). Each row was
139 a unique trapping transect, with five transects per ecosystem type per month (*N* = 120 observations).
140 Means were calculated using the <reshape2> package[51] in R version 3.4.2[52]. To examine whether
141 assemblage-level patterns were driven by common or rare species, we ran all abundance, composition,
142 and diversity analyses (described below) on the full dataset, on a dataset with singleton bee species
143 (those caught only on a single transect, in a single month) removed, and finally on a subset of the dataset
144 containing only the bee species that were present in >5% of the samples.

145 Overview. Analyses addressed our two key questions within one set of statistical models
146 (described below). First, (1) How much do bee assemblage abundance, composition, and diversity differ
147 among major southwestern U.S. ecosystem types? was determined by the statistical significance and
148 magnitude of the effect of ecosystem type in our models. We also compared the effect size of ecosystem
149 type against the effect size of month of sampling to estimate the relative importance of inter-ecosystem
150 versus seasonal variability. Then, to address (2) Do dryland ecosystem types differ in their degree of
151 seasonal variation in bee abundance, composition, or diversity? we evaluated whether the interaction
152 between ecosystem type and month of sampling was statistically significant, indicating that ecosystems
153 differed in the seasonality of bee abundance, composition, or diversity.

154 Bee assemblage composition and turnover. For bee composition, we calculated Bray-Curtis
155 similarities in Primer version 6.1.13[53]. We then tested for the influence of ecosystem type, month of

156 sampling, and the random effect of transect, which was nested within ecosystem type to account for the
157 repeated measures design, using perMANOVA (version 1.0.3) with 9999 permutations of residuals under
158 a reduced model. We additionally examined whether ecosystem types or months differed in bee
159 assemblage dispersion using permDISP in Primer[53]. We visualized assemblage composition with non-
160 metric multidimensional scaling analysis (NMDS) implemented with 500 restarts in Primer. For each
161 ecosystem type, we assessed bee species turnover among months, as well as the rate of community
162 change, using the <codyn> package in R[54]. Finally, to identify which taxa contributed most to bee
163 assemblage (i) divergence among ecosystem types and (ii) divergence among months within each
164 ecosystem type, we calculated Dufrene-Legendre indicator species values using the indval function in the
165 <labdsv> R package[55].

166 Bee diversity and abundance. For bee diversity, we calculated the Shannon diversity index (*H'*),
167 species richness, and evenness (Pielou's *J*) using the <vegan> package in R[56]. We then used linear
168 mixed effects models to examine the influences of ecosystem type, sampling month, and their interaction
169 (fixed effects), as well as transect identity (random effect nested within ecosystem type), on these three
170 responses, as well as on total bee abundance (function lmer, <lme4> package in R)[57]. When there was a
171 significant ecosystem type x sampling month interaction, we tested *a priori* contrasts for pairs of months
172 within each ecosystem type and for pairs of ecosystem types within each month using Tukey-Kramer
173 multiple comparisons in the <emmeans> package in R[58].

174

175 **Results**

176 *The dataset*

177 We captured a total of 70,951 individuals representing 302 species during the 13 years of
178 monthly trapping (see Supplementary Table S1 for a full species list). Species were distributed across 6
179 families and 56 genera (Supplementary Table S1 and Fig. S2). Our dataset was dominated by a small
180 number of abundant species and contained a large number of rare species (Supplementary Fig. S3). The
181 most commonly collected species were *Lasioglossum semicaeruleum* (36% of all collected specimens),
182 *Agapostemon angelicus* (21%), *Diadasia rinconis* (7%), *Melissodes tristis* (5%), *Anthophora affabilis* (5%),

183 and *Eucera lycii* (3%). Amongst the collected species, 30% were singletons, and 58% were found in <5%
184 of all samples.

185 *Bee assemblage composition: temporal variation surpassed differences among dryland ecosystem types*

186 Variation among ecosystems. All ecosystems significantly diverged in bee assemblage
187 composition, and this pattern was present during all months (Table 2, Fig. 1). The greatest difference
188 among ecosystems occurred in October, when the Plains grassland bee assemblage diverged most
189 strongly from the Chihuahuan Desert shrubland (mean similarity: 41.4, $P = 0.0089$) and also diverged
190 from the Chihuahuan Desert grassland (mean similarity: 51.6, $P = 0.0080$). The three ecosystem types
191 did not differ in assemblage dispersion ($F_{2,117} = 0.52$, $P = 0.71$), indicating similar levels of temporal beta-
192 diversity among ecosystem types (Fig. 1).

193 Indicators of variation among ecosystems. We identified 43 bee species as ecosystem indicators
194 according to their Dufrene-Legendre (DL) indicator species values (Table 3). Of these, 21 species were
195 indicators of Chihuahuan Desert shrubland, 14 species were indicators of Plains grassland, and 8 species
196 were indicators of Chihuahuan Desert grassland. All three ecosystems had indicator species within the
197 families Andrenidae, Apidae, Halictidae, and Megachilidae, and one Plains grassland indicator species
198 was in the family Colletidae (Table 3, Fig. 2). In all three ecosystems, *Lasioglossum semicaeruleum* (an
199 indicator of the Desert grassland), *Agapostemon angelicus* (an indicator of Plains grassland), *Diadasia*
200 *rinconis*, and *Melissodes tristis* were among the five most abundant bee species (Fig. 2). *Anthophora*
201 *affabilis* was also within the five most abundant species in the Plains and Chihuahuan Desert grasslands,
202 while *Perdita larreae* (a creosote bush specialist) was abundant in and an indicator of the Chihuahuan
203 Desert shrubland (Fig. 2).

204 Temporal variation. The month of sample collection explained an order of magnitude more
205 variation in bee assemblage composition than did ecosystem type (Table 2, Fig. 3). Generally,
206 assemblages diverged between the early and late months of the year and converged during the middle of
207 the summer. Across ecosystems, the pair of months most divergent in bee composition was March versus
208 October (mean similarity = 12.7, $P = 0.0001$). In contrast, June and July were most similar in bee
209 composition (mean similarity = 64.0, $P = 0.0001$).

Months additionally differed from one another in the magnitude of assemblage dispersion, a metric that captures the degree of beta-diversity across both sites and transects (Table 2, Fig. 3). The strongest differences in beta-diversity were between March or June, which had the smallest multivariate dispersions (mean ± s.e., March: 21.0 ± 1.5, June: 20.4 ± 0.8), against October, which had the largest average dispersion across ecosystems (29.8 ± 1.8).

Bee abundance and diversity: temporal variation exceeded variation among dryland ecosystems

Abundance. As with composition, across months, ecosystems diverged significantly from one another in total bee abundance (Table 4). Bee abundance was on average 43% lower in the Chihuahuan Desert shrubland relative to the two grassland sites from March through July (Fig. 4a). However, abundances within the ecosystems converged in August, and abundance differences disappeared in September and October (Fig. 4a), as indicated by a significant interaction between ecosystem type and month of collection (Table 4: Ecosystem x Month, $P < 0.0001$).

Diversity. Ecosystems also diverged in bee diversity as measured by the Shannon index and Pielou's evenness (Table 4). Differences in Shannon diversity (Fig. 4b) among ecosystems were more strongly driven by evenness (Fig. 4d) than by richness (Fig. 4c). On average across all months of sampling, the Chihuahuan Desert shrubland ecosystem had the highest bee Shannon diversity and evenness, with these diversity metrics 5% (Shannon diversity) and 2% (evenness) higher than in the Plains grassland. In turn, Plains grassland diversity metrics were 16% (Shannon diversity) and 12% (evenness) higher than the Chihuahuan Desert grassland. In contrast, on average across months, the ecosystems did not significantly differ in bee species richness (Table 4, Fig. 4c).

Importantly, differences among ecosystems in all diversity metrics varied by month of the year (Fig. 4, Table 4: Ecosystem x Month – Shannon diversity: $P < 0.0001$, richness: $P = 0.0137$, evenness: $P < 0.0001$), indicating that dryland ecosystem types differed in their degree of seasonal variation in bee diversity (Question 2). Specifically, Shannon diversity was greater in the Chihuahuan Desert shrubland than in the Desert grassland in all months except for March; differences in Shannon diversity were largest in May and September, when Shannon diversity respectively was 38% and 33% higher in the Chihuahuan Desert shrubland relative to grassland (Fig. 4b). Shannon diversity was also higher in the Chihuahuan Desert shrubland relative to Plains grassland in April, July, August, and October (Fig. 4b).

238 The largest difference occurred in October, in which Shannon diversity was 31% higher in the
239 Chihuahuan Desert shrubland than Plains grassland. However, this trend was reversed in both March
240 and September, when Shannon diversity was 19% and 16% higher, respectively, in Plains grassland than
241 in shrubland (Fig. 4b). The two grassland ecosystems differed in Shannon diversity in March, May, June,
242 and September, with greater Shannon diversity in the Plains relative to Chihuahuan Desert grassland in
243 all of these months (Fig. 4b).

244 *Dryland ecosystems diverged in the magnitude of seasonal variation in bee assemblage composition,*
245 *abundance, and diversity*

246 Assemblage composition. Bee assemblage composition varied strongly among months, with the
247 magnitude of seasonal change differing among ecosystems (Figs. 3,5; Table 2: Ecosystem X Month, P =
248 0.0001). The Chihuahuan Desert grassland had the greatest seasonal turnover in bee species
249 composition (Fig. 3b), and the highest rate of compositional change from month to month (Fig. 6). In
250 contrast, the Chihuahuan Desert shrubland had the lowest seasonal composition change (Figs. 3c,6),
251 with low turnover between July and August, and between August and September, compared to the other
252 ecosystems (Fig. 5). Among months, in all ecosystem types, bee species composition differed most
253 strongly between March and either September (Plains grassland: mean similarity = 16.4, P = 0.0077) or
254 October (Desert grassland: mean similarity = 9.2, P = 0.0091; shrubland: mean similarity = 11.7, P =
255 0.0070) (Fig. 3). In contrast, in all ecosystems, June and July were most compositionally similar to one
256 another, with low turnover between them (Figs. 3,5; Plains grassland: mean similarity = 76.2, P = 0.0091;
257 Desert grassland: mean = 72.42, P = 0.0077; Desert shrubland mean = 70.4, P = 0.0156). Seasonal
258 patterns in bee assemblage composition were largely driven by common rather than rare species, as
259 indicated by very few qualitative differences in analysis outcomes when excluding singletons or
260 moderately rare species (see Supplementary Fig. S4).

261 Abundance. Like species composition, total bee abundance also varied seasonally across the
262 three ecosystem types (Table 4), and ecosystem types exhibited differing trends in total abundance over
263 the course of the season (Fig. 4a). In the Chihuahuan Desert grassland, bee abundance increased from
264 March to April, then generally declined through the rest of the season (Fig. 4a). In contrast, the Plains
265 grassland had similar levels of bee abundance in March and April (df = 84, t = -1.13, P = 0.95), followed

266 by a ~50% decrease in abundance between April and May (*df* = 84, *t* = 11.12, *P* < 0.0001) and a 66%
267 increase in abundance between May and June (*df* = 84, *t* = -6.99, *P* < 0.0001). Between July and August,
268 while bee abundance decreased ~30% within both the Chihuahuan Desert grassland (*df* = 84, *t* = 4.62, *P*
269 = 0.0004) and Plains grassland ecosystems (*df* = 84, *t* = 5.93, *P* < 0.0001), it increased by 40% within the
270 Chihuahuan Desert shrubland (*df* = 84, *t* = -3.86, *P* = 0.0053) (Fig. 4a). Across ecosystem types, bee
271 abundances were generally lower in September and October relative to all other months (Fig. 4a).
272 Diversity. Within each ecosystem, most months had similar levels of species richness, with some
273 exceptions (Fig. 4c). Notably, there was a sharp decline in richness between August and October across
274 all three ecosystems (Fig. 4c). During this period, richness declined by 70% within the Chihuahuan Desert
275 grassland (*df* = 84, *t* = 11.18, *P* < 0.0001) and by 60% within both the Plains grassland (*df* = 84, *t* = 10.92,
276 *P* < 0.0001) and Desert shrubland (*df* = 84, *t* = 11.18, *P* < 0.0001). However, month-to-month trends in
277 Shannon diversity and evenness diverged among ecosystems (Fig. 4b,d). Patterns in total abundance,
278 Shannon diversity, richness, and evenness were all largely driven by common rather than rare species
279 (see Supplementary Fig. S5).
280 Indicators of temporal variation within ecosystem types. Certain bee taxa were indicators of
281 specific months across all three ecosystems according to their DL indicator values (Supplementary
282 Tables S3-S6). These included *Osmia* species, *Eucera lycii*, *Anthophora porterae,* and *Melecta pacifica*
283 (March), *Dioxys* and *Anthophora* species (April), *Diadasia australis* and *rinconis* (June), *Martinapis*
284 *lutericornis*, *Halictus ligatus*, and *Melissodes tristis* (July), and *Perdita semicaerulea* and *marcialis*
285 (August) (Supplementary Tables S3-S6). September and October lacked indicator species shared by all
286 ecosystems.
287 In contrast, certain bee taxa were only characteristic of a given month within one or two
288 ecosystems (Supplementary Tables S3-S6). For instance, in June, the shrubland site had 5 indicator
289 species in the genus *Lasioglossum*; one of these was also characteristic of the desert grassland site
290 (Supplementary Tables S3,S5,S6). In July, *Perdita* species (Andrenidae) were indicators of the
291 Chihuahuan Desert sites but not the Plains site, the grassland sites had indicator species in the Halictidae
292 (especially *Lasioglossum*), and differing members of the Apidae were characteristic of different
293 ecosystems (Supplementary Tables S3-S6). In September, *Perdita* species (Andrenidae) were

294 characteristic of the Plains grassland, *Macrotera* (Andrenidae) were characteristic of the desert sites, and
295 differing members of the Apidae were characteristic of each site (Supplementary Tables S3-S6). Finally,
296 25 species were indicators of a particular month in one or two ecosystem types, and were then indicators
297 of a different month, often the following one, in the other ecosystem(s) (Supplementary Table S3).
298
299 **Discussion**
300 We found large variation in bee assemblages and their seasonality among three dryland
301 ecosystem types of the southwestern U.S. These results indicate the potential for future ecosystem state
302 transitions to alter bee assemblage composition in drylands. Overall, ecosystem types in our study had
303 similar levels of bee species richness but differed from one another in species evenness and composition.
304 These results imply that state transitions could alter the presence/absence and relative abundances of
305 bee species in our system, bringing about substantial assemblage reordering.
306 Our data suggest that the most probable state transitions in our southwestern U.S. drylands –
307 shrub encroachment into Desert grassland and Desert grassland encroachment into Plains grassland [59,60]
308 – could substantially reshape bee communities. For the grass-to-shrub transition, our results suggest that,
309 on average over the season, total bee abundance will decrease while richness, Shannon diversity, and
310 Pielou's evenness will increase. In contrast, our findings predict that richness, Shannon diversity, and
311 evenness will decrease while total abundance will remain relatively unchanged if Desert grassland
312 replaces Plains grassland. The simultaneous occurrence of these state transitions could therefore
313 substantially alter the distribution of bees and their ecosystem services across the landscape.
314 A number of factors complicate accurately predicting the outcomes of ecosystem state transitions
315 for bees. First, bees may alter their foraging patterns based on floral resource availability[61], and could
316 respond to shifting vegetation composition by foraging for greater distances if floral resources are scarce
317 in a particular location[62]. However, foraging range can differ greatly among bee species based on body
318 size[63], and the energetic costs of longer foraging distances may be high[64]. These factors could mediate
319 the consequences of ecosystem state transitions for bee assemblage composition in ways that merit
320 further research, as they have been little-examined[61]. Our finding that particular bee species were
321 indicators of different months in different ecosystem types suggests that bees in our system may shift

322 their foraging locations based on floral availability (though they could alternatively be emerging at different
323 times of year in different ecosystems; see subsequent paragraphs) highlighting the importance of
324 examining foraging dynamics in the future.

325 Second, state transitions may create positive feedbacks that accelerate their pace and influence
326 bee responses[1]. Creosote bush expansion, which is limited by minimum nighttime temperature, is aided
327 by a feedback in which a creosote individual creates a warmer microclimate around itself, which can
328 buffer it from low temperatures, in turn creating conditions favorable to further creosote establishment[47,65].
329 This accelerated temperature increase could influence the relative dominances of bee species, which
330 may differ in their temperature responses. For instance, in one *Osmia* species, increased temperature
331 during larval development caused decreased prepupal weight and increased adult mortality[66], and in
332 another species it increased the frequency of 1-year rather than 2-year lifecycles[39]. If accelerated bee
333 assemblage shifts result in pollen limitation for plants already threatened by shrub encroachment, the
334 feedback could be enhanced, further increasing the pace of encroachment.

335 Our results contribute to a number of global studies suggesting how state transitions may
336 influence drylands arthropod communities. For instance, in the Chihuahuan Desert, ant species
337 composition varied with mesquite (*Prosopis glandulosa*) encroachment level, but richness and abundance
338 did not[67]. At the Sevilleta NWR, grasshopper assemblage similarity decreased with elevational variation in
339 shrub and *Bouteloua* sp. grass cover[68]. Similarly, at our study sites, the Desert grassland and shrubland
340 had distinct ground-dwelling arthropod assemblages, with higher abundance but similar richness in the
341 grassland relative to the shrubland, as we found[14]. These findings together suggest that Chihuahuan
342 Desert state transitions may similarly influence abundance and diversity patterns in several arthropod
343 groups. However, global evidence suggests that shrub encroachment can differentially affect arthropod
344 taxa[3]. For instance, shrub-encroached pastures in Spain had higher pollinator richness but fewer
345 pollinator visits to forbs relative to shrub-absent sites[32], contrasting with our finding of little difference in
346 bee richness between shrub- and grass-dominated sites. In the Kalahari Desert, shrub encroachment
347 corresponded with greater abundances of some ground-dwelling arthropod groups but declines in
348 others[69]. Our results thus add to understanding of how widely-occurring ecosystem transitions may affect
349 arthropods differentially across space.

350 Our work also bolsters evidence from human-altered landscapes about how bee assemblages
351 vary at a landscape scale. For instance, as in our study, bee abundance but not richness changed with
352 land use intensity in tropical agroecosystems for solitary bees, which comprised the majority of our
353 dataset[29]. In contrast, a different study found shifts in bee species composition but not abundance or
354 diversity among forest fragments[30]. Other studies have documented strong differences in both abundance
355 and richness of bees among habitat types[33,70,71]. These findings highlight the importance of separately
356 examining trends within particular ecosystem and land-use types to comprehensively predict future
357 patterns.
358 Month-to-month differences in bee species composition were an order of magnitude stronger than
359 ecosystem differences in our study. This finding suggests potential susceptibility of bees in all ecosystem
360 types to climate change-induced phenological shifts[36]. In particular, climate models for the southwestern
361 U.S. predict less precipitation in July and August, and more in September and October, resulting in an
362 extended period of aridity between spring rains and the start of the summer monsoon[72]. Evidence
363 suggests that desert bees, most of which nest underground, frequently cue on precipitation for their
364 emergence[37,38]. Under altered monsoon precipitation timing, bees that currently emerge in July or August
365 might shift emergence to September and October, leading to higher levels of bee abundance and
366 richness at all sites during these months. These differences could be particularly pronounced in the
367 Chihuahuan Desert shrubland ecosystem, for which bee abundance, Shannon *H'*, richness, and Pielou's
368 *J* (evenness) were all highest in July or August. The Chihuahuan Desert grassland could also be
369 particularly susceptible to altered dynamics, given that it had the strongest seasonal turnover. Substantial
370 assemblage reordering among months could occur if different bee species shift their phenological timing
371 to different degrees, which could have landscape-level consequences given that the Chihuahuan Desert
372 ecosystem types are expected to expand in the future[45–47]. In addition, for social bees that are active
373 throughout the growing season, such as those in the family Halictidae[73], loss of floral resources due to
374 midsummer aridity could cause abundance declines or colony death. Predicting the consequences of
375 ecosystem state transitions will thus require considering bee assemblage seasonality in ecosystem types
376 that are expanding versus contracting.

377 Regional climate predictions for the southwestern U.S. are dire – the probability of decadal
378 droughts is nearly 100% by the end of the century[74]. Such droughts could differentially affect bees with
379 differing phenologies and life history strategies, and could lead to bee assemblage reordering. For
380 instance, many desert bees can remain in diapause for one year or more, emerging when conditions are
381 favorable[37,38]. In one of the few studies on the topic, fewer bees emerged during a drought year compared
382 to the previous and following years in the northwestern Chihuahuan Desert[38]. A greater proportion of
383 specialist than generalist bees remained in diapause, and the specialists that emerged were those whose
384 host plants bloom under low precipitation conditions. For *Larrea tridentata*, which requires precipitation to
385 bloom[75], few specialist bees emerged during the drought, suggesting that these specialists time their
386 emergence with their host plant[38]. Differences among ecosystem types in their dominant flowering plant
387 species, their associated specialist versus generalist bee species, and their seasonality could therefore
388 lead to strong bee assemblage divergence among them as dominant bee species in each ecosystem
389 respond differentially to increased drought and shifted precipitation timing, with landscape-level bee
390 assemblage changes occurring as some ecosystems expand and others contract. Future analyses will
391 explore connections between bee abundance, diversity, and composition and individual aspects of
392 climate change over our time series.
393 Our findings of strong bee assemblage seasonality are consistent with work indicating high
394 temporal turnover in plant-pollinator interactions in subalpine and alpine communities over the course of
395 the growing season[41,76]. Seasonal variation in plant-pollinator networks has also been documented in
396 agricultural landscapes[44]. While our study was not designed to examine plant-pollinator interactions, our
397 results set the stage for considering how plant-pollinator networks could be altered by ecosystem state
398 transitions and climate-induced phenological shifts of bee species.
399 In our dataset, common rather than rare bee species drove the trends in abundance, diversity,
400 and composition that we observed over both space and time. Considering these species' ecologies may
401 thus be particularly important for predicting the consequences of ecosystem state transitions, and some
402 species may portend change in the bee assemblage as a whole[77]. Among the most abundant bees in our
403 dataset, three species (*Agapostemon angelicus, Lasioglossum semicaeruleum*, and *Melissodes tristis*)
404 were broad generalists that collect pollen from plants of many families[38,78], suggesting that plants visited

405 by these and other bees could be buffered to a certain extent if there are future bee declines. However,
406 specialist bees were also among the most abundant: *Diadasia rinconis* is a specialist on Cactaceae[79],
407 *Anthophora affabilis* is a generalist with a strong preference for *Astragalus*, and *Perdita larreae* is a
408 narrow specialist on *Larrea tridentata*[23,80]. The consequences of ecosystem state transitions for these bee
409 species may thus depend on shifts in their host plants. For instance, expansion of *Larrea tridentata* could
410 benefit populations of *P. larreae* and other creosote bush specialist bees, and possibly lead to stronger
411 competitive dynamics among creosote specialists and generalists under future conditions.
412 Our study identified bee species as indicators of each ecosystem type; monitoring these species
413 could help to illuminate the community-level consequences of ecosystem state transitions. The
414 Chihuahuan Desert shrubland had more indicator species than the other two ecosystem types,
415 suggesting that its future expansion could bring about distinctive assemblage shifts. The strongest
416 indicators of the shrubland included *Perdita larreae,* which specializes on *Larrea tridentata*, and *P.*
417 *diversa,* which specializes on *Tiquilia* spp., plants only found at the shrubland site. Abundance increases
418 of these bee species could thus signal effects of shrubland expansion on pollinator communities.
419 Similarly, in the Plains grassland, one indicator species (*Colletes scopiventer*) specializes on
420 *Chamaesaracha* spp., which are present in all three ecosystems but are most abundant in the Plains
421 grassland. Future decreases in the abundance of *C. scopiventer* could signal community-level shifts
422 accompanying the declining dominance of the Plains grassland. However, the remaining indicator species
423 of the two grassland ecosystems were broad generalists. Factors other than plant community
424 composition, such as nesting habitat preferences, may thus underlie their restriction to particular sites,
425 and they may be relatively less susceptible to climate-induced plant community shifts. This could also be
426 the case for *Macrotera portalis*, an indicator of the shrubland but a specialist on *Sphaeralcea* spp.[81],
427 which is common in all three ecosystem types, and for generalist bee species that were indicators of the
428 shrubland. The spatial distribution of suitable nesting habitat also merits future consideration in that
429 specialist bees could be negatively affected if their plant hosts shift their ranges away from potential
430 nesting sites.
431 In addition, cleptoparasitic bees were among our identified indicator species. These included one
432 indicator of the Chihuahuan Desert shrubland (*Neolarra vigilans*) and three of the Plains grassland

433 (*Melecta alexanderi* and two *Sphecodes* species). Not surprisingly, in the cases of *Neolarra* and *Melecta,*
434 their bee hosts, *Perdita* and *Anthophora,* were also among indicators of the same ecosystem types.
435 Cleptoparasitic bees may be particularly good indicators of environmental change, as they are relatively
436 diverse, and are known to be among the first bee functional groups to respond to disturbance[82].
437 Monitoring the abundances of these species could indicate shifts in bee assemblage dynamics as
438 ecosystem state transitions occur. Cleptoparasitc species were also amongst indicators of particular
439 months, frequently in tandem with possible hosts, and may thus be useful for tracking phenological
440 responses to environmental change[82]. For example, both *Melecta alexanderi* and *M. bohartorum* were
441 indicators of the shrubland site in March, but were indicators of the grassland sites in April, suggesting the
442 possibility of altered emergence timing under the warmer microclimate conditions of the shrubland[47,65],
443 and thus susceptibility to phenological shifts in response to increasing temperature.
444 We also identified bee species that were characteristic of particular times of year across
445 ecosystem types. Monitoring these species could enable the detection of broad, cross-site phenological
446 shifts that may occur in the future. For instance, *Osmia, Anthophora*, and *Diadasia* species may be
447 monitored to consider shifting pre-monsoon bee phenology, and *Perdita* species may be used to study
448 shifts in emergence timed with monsoon rains. Future publications using these data will investigate inter-
449 annual bee assemblage differences and relationships with climate variables.
450 Finally, we identified bee species that were characteristic of particular months only in specific
451 ecosystems. Among these, certain specialist bee species may be candidates for detecting important
452 phenological shifts within ecosystems, identifying phenological differences among ecosystems, and
453 tracking how specialists versus generalists respond to climate shifts. For instance, March in the
454 Chihuahuan Desert ecosystems had indicator species that likely specialize on Fabaceae (*Ashmeadiella*
455 *erema* and *A. rubrella*), and April in the grassland sites had a specialist on Brassicaceae (*Dufourea*
456 *pulchricornis*). In the Chihuahuan Desert ecosystem types, specialists of creosote bush were
457 characteristic of May, corresponding with creosote's spring bloom[75], June had Cactaceae specialists
458 (*Diadasia* sp.) timed with that family's bloom[79], and July had specialists on Asteraceae (*Perdita ignota*
459 *ignota, P. callicerata, P. fallax,* and *P. albovittata*) and *Tiquilia* sp. (*P. diversa*). In contrast, specialists on
460 Asteraceae (*Melissodes coreopsis*, *P. ignota ignota*, and *P. callicerata*) were indicators of August in the

Plains grassland, suggesting a shift in the importance of particular floral resources and/or differing phenological patterns among ecosystem types. In August, the Chihuahuan Desert sites were characterized by numerous creosote specialists, as documented in several studies[23,38], including *Hesperapis larreae*, *P. semicaerulea*, and *P. larreae.* These species may be candidates for examining how delayed monsoon influences bee phenology. The *Sphaeralcea* specialist *Macrotera portalis*[81] was an August indicator in the shrubland, but other *Sphaeralcea* specialists were characteristic of September in both Chihuahuan Desert ecotypes; perhaps competitive dynamics were responsible for this difference. These examples illustrate the suite of factors that could be important to consider to predict bee presence and seasonality across the landscape.

Our analysis of 13 years of bee assemblage data spanning 302 species suggests that future dryland ecosystem state transitions, by themselves, may alter bee species' relative abundances and presence/absence. Strong bee assemblage seasonal turnover, particularly in ecosystems predicted to expand, indicates the potential for bee phenological shifts to accompany state transitions, potentially reordering communities. Our results indicate that predicting the consequences of global change for bee assemblages will require accounting for both within-year and among-ecosystem variation.

Data availability

The data generated and analyzed during the current study will be available upon publication in the Environmental Data Initiative (EDI) Data Portal (https://portal.edirepository.org).

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665

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670

671 **Author contributions**

672 M.R.K. assisted with bee specimen collection, analyzed the data, and wrote the manuscript.
673 K.W.W. designed the study and completed the majority of specimen collection and identification. J.B.
674 assisted with specimen collection and identification. T.L.G. identified specimens and provided taxonomic
675 expertise. J.A.R. and K.D.W. contributed to manuscript conceptual framing, data analysis, and writing. All
676 authors contributed to revising the manuscript.
677

678 **Competing interests**

679 The authors declare no competing interests.

680

681 **Figure legends**

682 Figure 1. Non-metric multidimensional scaling (NMDS) plot depicting variation in bee species composition
683 among three dryland ecosystem types: Plains grassland (blue points), Chihuahuan Desert grassland
684 (black points), and Chihuahuan Desert shrubland (green points). NMDS was run with 500 randomized re-
685 starts and 2D stress = 0.13. On average, all ecosystem types significantly differed from one another
686 (Table 2): Plains grassland versus Chihuahuan Desert grassland (P = 0.0082), Plains grassland versus
687 Chihuahuan Desert shrubland (P = 0.0075), and Chihuahuan Desert grassland versus shrubland (P =
688 0.0084).

689

690 Figure 2. Mean yearly abundance + s.e. (darker, leftmost bar in each pair) and Dufrene-Legendre (DL)
691 indicator species value (lighter, rightmost bar in each pair) for important bee species within each
692 ecosystem type (Plains grassland, blue bars, B; Chihuahuan Desert grassland, black bars, G;
693 Chihuahuan Desert shrubland, green bars, C). Included bee species were within the 20 most abundant
694 species found across the study, and/or were top indicator species of particular ecosystem types
695 according to DL indicator value. Plots are arranged from left to right by mean yearly abundance across
696 ecosystem types.

697

698 Figure 3. Non-metric multidimensional scaling (NMDS) plots depicting variation in bee species
699 composition among months for three dryland ecosystems: (a) Plains grassland, (b) Chihuahuan Desert
700 grassland, and (c) Chihuahuan Desert shrubland. NMDS was run with all samples together, with 500
701 randomized re-starts and 2D stress = 0.13.

702

703 Figure 4. Variation across sampling months in per-transect bee abundance and diversity (± s.e.) as
704 measured by a) total bee abundance, b) Shannon diversity index (H'), c) richness, and d) evenness
705 (Pielou's J) for three dryland ecosystem types: Plains grassland (blue points), Chihuahuan Desert
706 grassland (black points), and Chihuahuan Desert shrubland (green points). Letters denote contrasts
707 between biomes within a given month; biomes labeled with different letters differed significantly from one

another in the relevant abundance/diversity metric. Points lacking letters did not differ significantly from any other biome in the given month. For total abundance, s.e. values were <0.1.

Figure 5. Total bee species turnover between pairs of months (indicated on the x-axis) for three dryland ecosystem types: Plains grassland (blue points), Chihuahuan Desert grassland (black points), and Chihuahuan Desert shrubland (green points).

Figure 6. Average rate of bee assemblage change during March through October in three ecosystem types: Plains grassland (slope = 9.34, s.e. = 4.99, t = 1.9, P = 0.0725), Chihuahuan Desert grassland (slope = 24.32, s.e. = 3.99, t = 6.1, P < 0.0001), and Chihuahuan Desert shrubland (slope = 7.81, s.e. = 2.92, t = 2.7, P = 0.0128). Intervals (x-axis) represent time lags between all pairwise combinations of months. Distances (y-axis) correspond with differences in bee assemblage composition between pairs of months, calculated as Euclidean distances. The slope of each line indicates the rate of bee assemblage change in each ecosystem.

723 Table 1. Latitude, longitude, and elevation of study sites representing three ecosystem types of the
724 southwestern U.S., along with current versus predicted future foundation species.
725

Ecosystem type	Latitude	Longitude	Elevation (m)	Current foundation species	Future foundation species
Desert shrubland	34.3431	-106.7417	1615	Creosote bush	Creosote bush
Desert grassland	34.3350	-106.7219	1616	Black grama	Creosote bush
Plains grassland	34.3325	-106.6328	1670	Blue grama	Black grama

726

727 Table 2. Results of 1) perMANOVA with 9999 permutations to test for the influence of ecosystem type
728 and month of sample collection on bee assemblage composition, using a Bray-Curtis similarity metric,
729 and 2) permDISP examining differences among ecosystem types and months in bee assemblage
730 dispersion.
731

		perMANOVA				permDISP		
	num. df	*SS*	*MS*	pseudo-*F*	*P*	*denom. df*	*F*	*P*
Ecosystem	2	23252.00	11626.00	34.54	0.0001	117	0.52	0.7074
Month	7	139860.00	19981.00	94.02	0.0001	112	5.92	0.0002
Ecosystem x month	14	34139.00	2438.50	11.48	0.0001			
Transect (ecosystem)	12	4039.70	336.64	1.58	0.0003			
Residuals	84	17851.00	212.51					

732

Table 3. Indicator species for each ecosystem (Plains grassland, Chihuahuan Desert grassland, and Chihuahuan Desert shrubland) according to Dufrene-Legendre indicator species value. Species are listed from highest to lowest indicator value within each ecosystem.

Species	Family	Indicator value	*P*-value
Plains grassland			
Colletes scopiventer	Colletidae	0.64	0.0010
Halictus ligatus	Halictidae	0.62	0.0010
Anthophora montana	Apidae	0.52	0.0010
Agapostemon angelicus	Halictidae	0.50	0.0010
Halictus tripartitus	Halictidae	0.41	0.0010
Anthidium porterae	Megachilidae	0.27	0.0280
Sphecodes sp. 1	Halictidae	0.27	0.0010
Anthophora urbana	Apidae	0.26	0.0190
Melecta alexanderi	Apidae	0.20	0.0390
Sphecodes sp. 5	Halictidae	0.18	0.0250
Melissodes thelypodii thelypodii	Apidae	0.17	0.0090
Sphecodes sp. 6	Halictidae	0.15	0.0090
Megachile policaris	Megachilidae	0.14	0.0110
Pseudopanurgus sp. 2	Andrenidae	0.10	0.0210
Chihuahuan Desert grassland			
Lasioglossum (*Dialictus*) sp. 2	Halictidae	0.66	0.0010
Lasioglossum semicaeruleum	Halictidae	0.51	0.0010
Diadasia megamorpha	Apidae	0.20	0.0250
Perdita sphaeralceae alticola	Andrenidae	0.18	0.0020
Megachile sublaurita	Megachilidae	0.16	0.0240
Perdita cara	Andrenidae	0.15	0.0160
Atoposmia aff. *daleae*	Megachilidae	0.10	0.0330
Atoposmia aff. *daleae* 2	Megachilidae	0.10	0.0420
Chihuahuan Desert shrubland			
Agapostemon melliventris	Halictidae	0.56	0.0010
Perdita larreae	Andrenidae	0.50	0.0010
Neolarra vigilans	Apidae	0.45	0.0010
Perdita marcialis	Andrenidae	0.42	0.0010
Perdita diversa	Andrenidae	0.40	0.0010
Lasioglossum aff. *pervarum*	Halictidae	0.40	0.0080
Lasioglossum (*Dialictus*) sp. 8	Halictidae	0.39	0.0010
Ashmeadiella meliloti	Megachilidae	0.35	0.0440
Anthophorula completa	Apidae	0.33	0.0010
Lasioglossum morrilli	Halictidae	0.32	0.0240
Lasioglossum (*Dialictus*) sp. 7	Halictidae	0.31	0.0050
Ashmeadiella bigeloveae	Megachilidae	0.27	0.0160
Ashmeadiella cactorum	Megachilidae	0.25	0.0060
Macrotera portalis	Andrenidae	0.22	0.0090
Dianthidium implicatum	Megachilidae	0.20	0.0010
Anthophora cinerula	Apidae	0.19	0.0110
Anthidium cockerelli	Megachilidae	0.17	0.0070
Perdita austini	Andrenidae	0.16	0.0040
Apis mellifera	Apidae	0.16	0.0410
Megachile lobatifrons	Megachilidae	0.14	0.0140
Megachile spinotulata	Megachilidae	0.11	0.0370

Table 4. Results of linear mixed effects models testing the influences of ecosystem type and month of sample collection on total bee abundance, as well as bee assemblage Shannon diversity index (*H'*), richness, and evenness (Pielou's *J*).

		Total abundance		Shannon *H'*		Richness		Evenness	
	df	X^2	*P*	X^2	*P*	X^2	*P*	X^2	*P*
Ecosystem	2	45.19	< 0.0001	34.72	< 0.0001	1.38	0.50044	47.28	< 0.0001
Month	7	796.09	< 0.0001	105.64	< 0.0001	221.14	< 0.0001	85.33	< 0.0001
Ecosystem x month	14	359.31	< 0.0001	142.78	< 0.0001	28.13	0.01368	320.07	< 0.0001

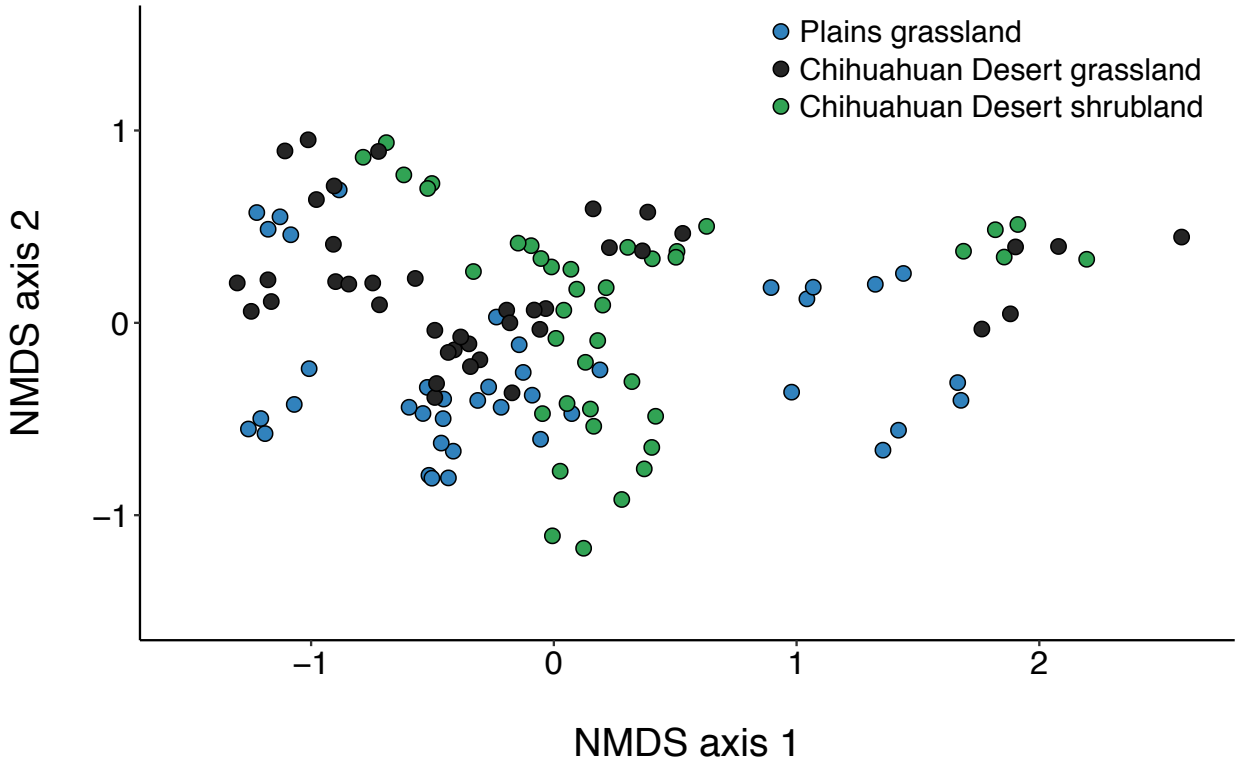
Plains grassland
Chihuahuan Desert grassland
Chihuahuan Desert shrubland
NMDS axis 2
NMDS axis 1
1
0
−1
−1
0
1
2

Figure 1

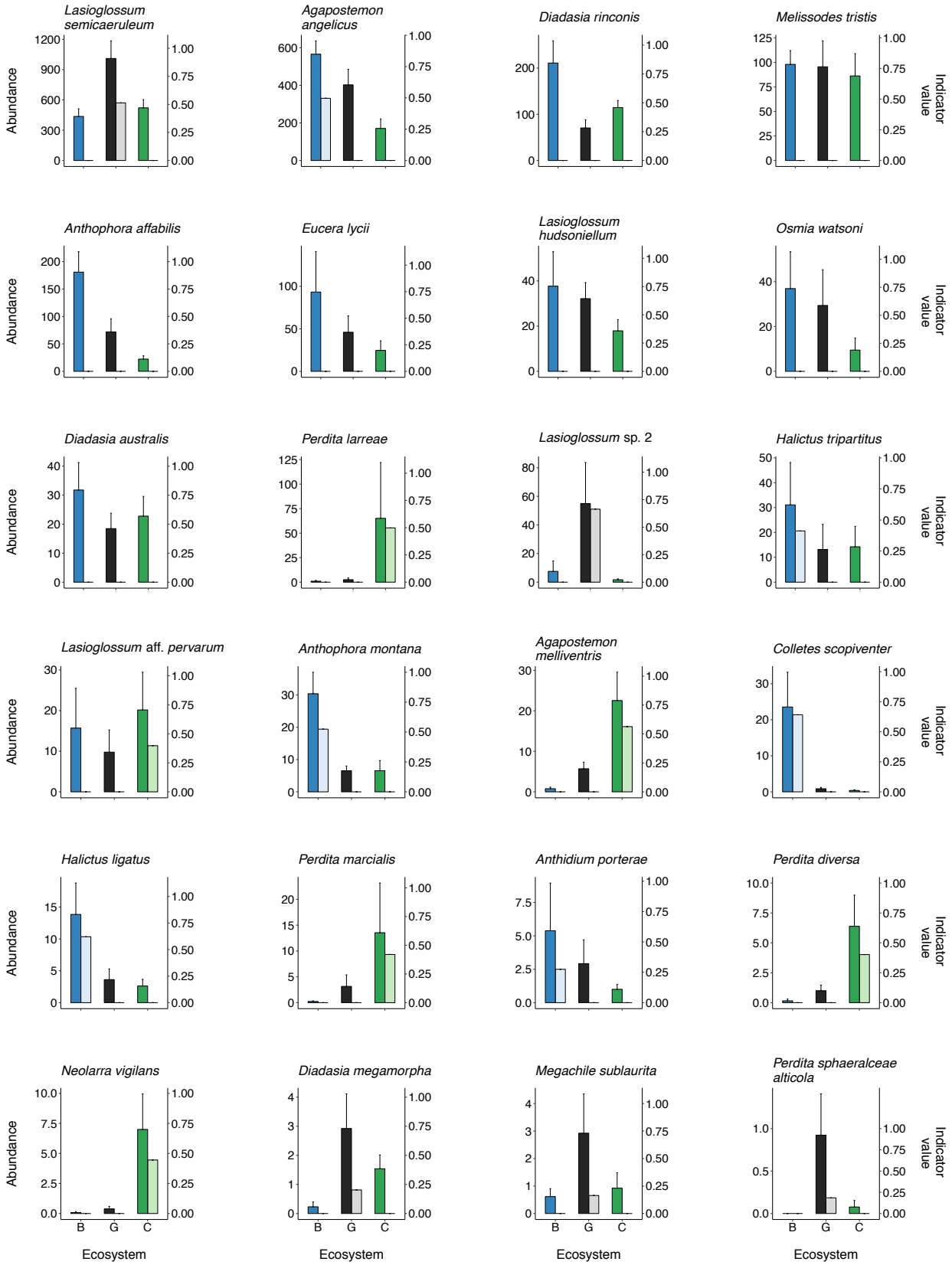
Lasioglossum semicaeruleum
Agapostemon angelicus
Diadasia rinconis
Melissodes tristis
Anthophora affabilis
Eucera lycii
Lasioglossum hudsoniellum
Osmia watsoni
Diadasia australis
Perdita larreae
Lasioglossum sp. 2
Halictus tripartitus
Lasioglossum aff. pervarum
Anthophora montana
Agapostemon melliventris
Colletes scopiventer
Halictus ligatus
Perdita marcialis
Anthidium porterae
Perdita diversa
Neolarra vigilans
Diadasia megamorpha
Megachile sublaurita
Perdita sphaeralceae alticola
Abundance
Indicator value
B
G
C
Ecosystem

Figure 2

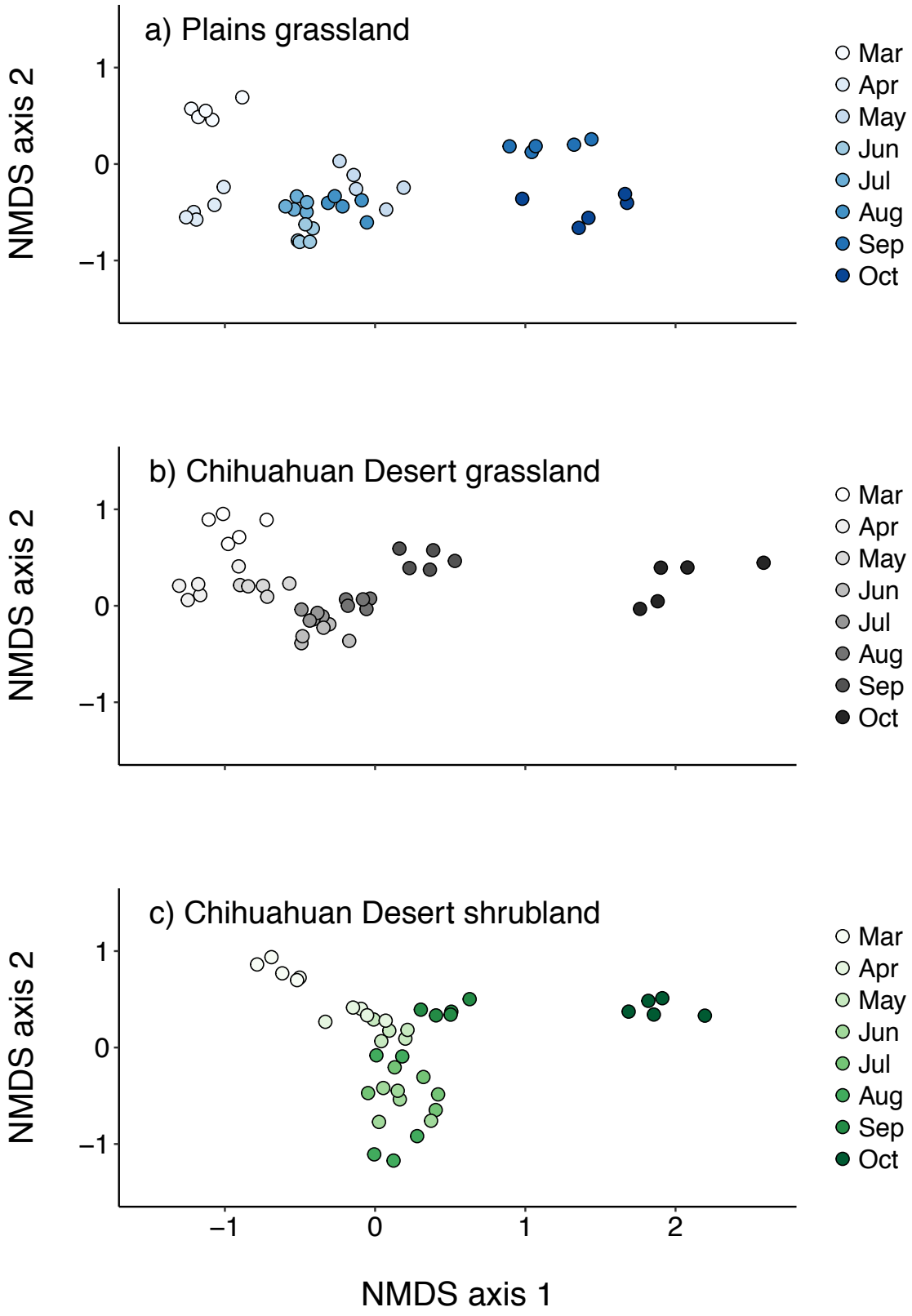
a) Plains grassland
b) Chihuahuan Desert grassland
c) Chihuahuan Desert shrubland
NMDS axis 2
NMDS axis 1
1
0
−1
−1
0
1
2
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct

Figure 3

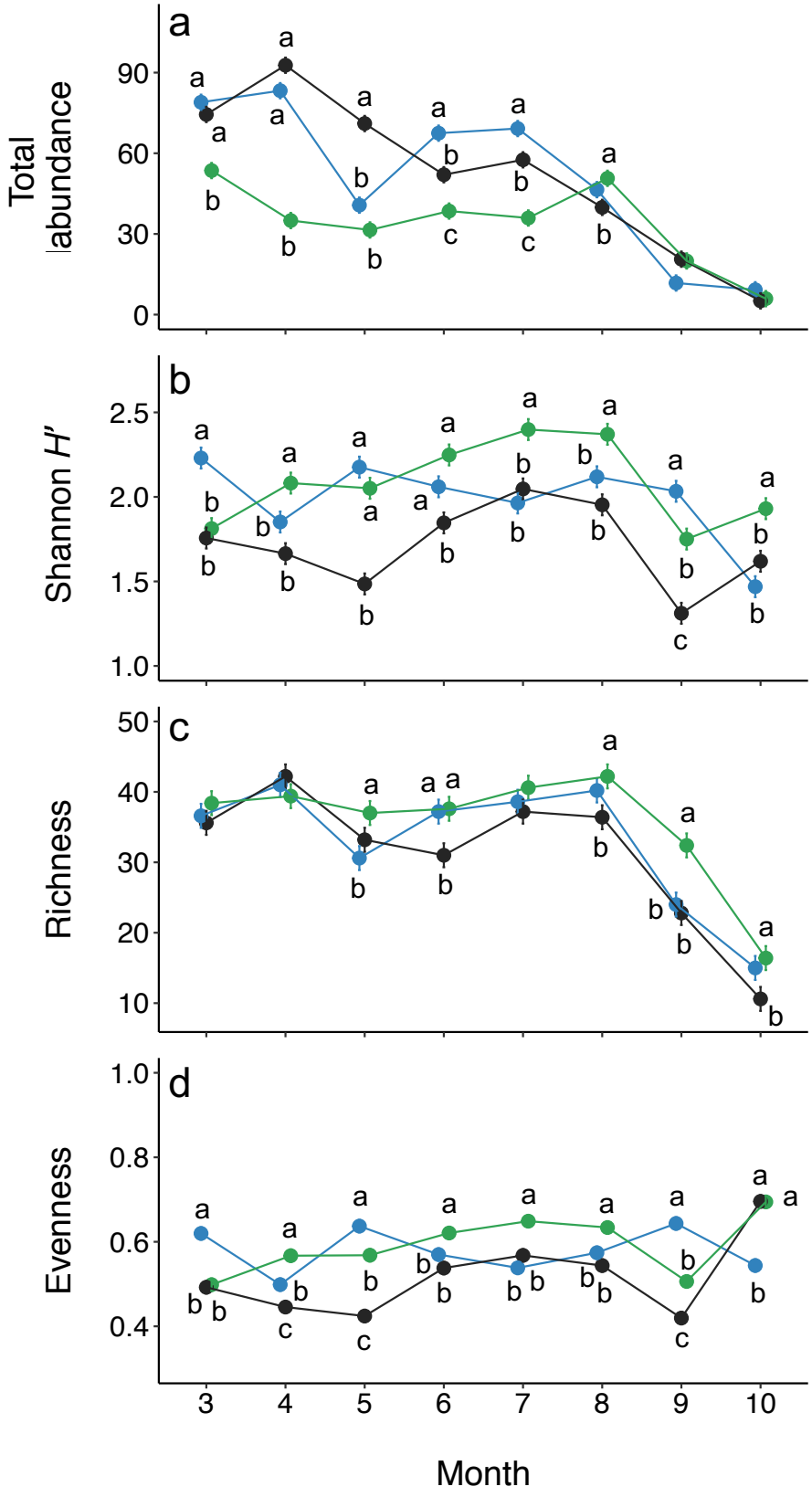
a
Total abundance
0
30
60
90
b
Shannon H'
1.0
1.5
2.0
2.5
c
Richness
10
20
30
40
50
d
Evenness
0.4
0.6
0.8
1.0
3
4
5
6
7
8
9
10
Month

Figure 4

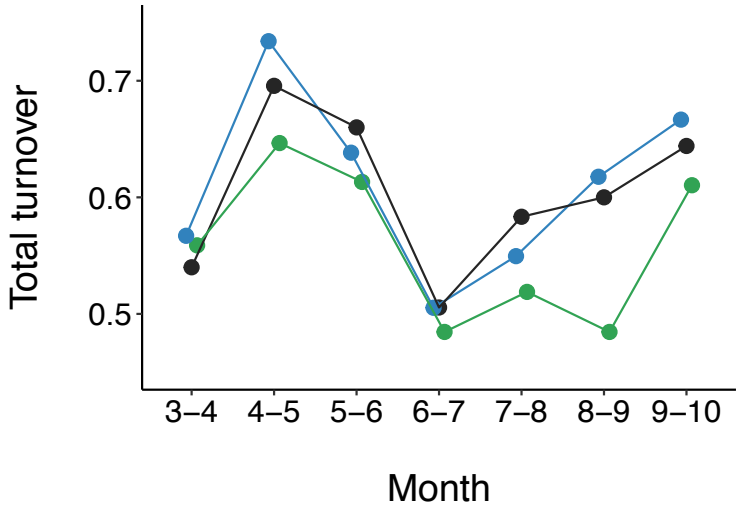

Figure 5

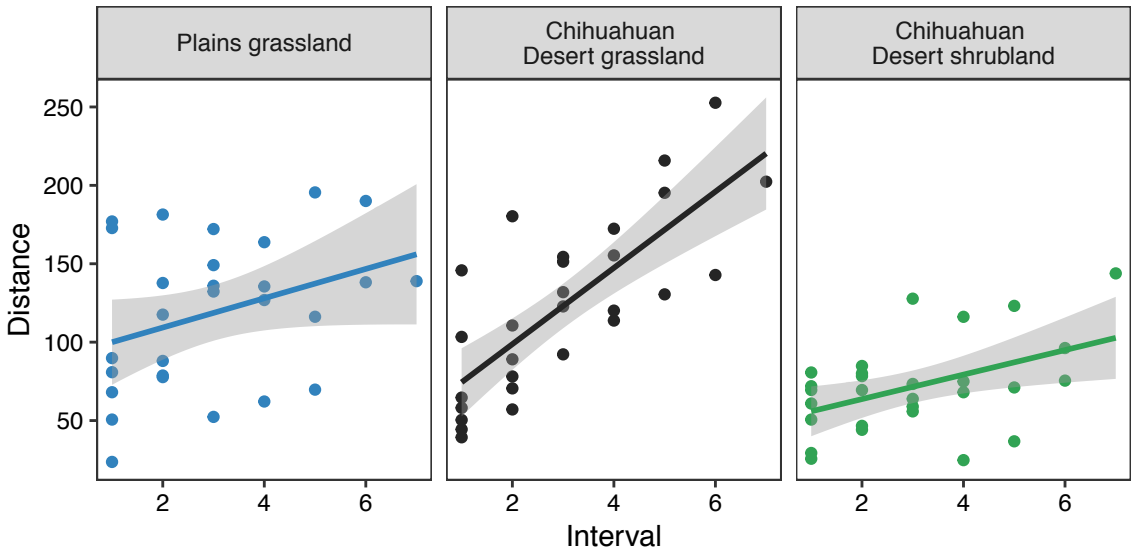
Plains grassland
Chihuahuan Desert grassland
Chihuahuan Desert shrubland
Distance
250
200
150
100
50
2
4
6
Interval

Figure 6