

2 **Evolutionary consequences of dispersal ability in cactus-feeding insects**3
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10 *Key words:* cerambycidae, coenopoeus, flightlessness, gene flow, habitat patchiness, moneilema
1112 **Abstract**13 Although gene flow is an important determinant of evolutionary change, the role of ecological factors such
14 as specialization in determining migration and gene flow has rarely been explored empirically. To examine
15 the consequences of dispersal ability and habitat patchiness on gene flow, migration rates were compared in
16 three cactophagous Longhorn beetles using coalescent analyses of mtDNA sequences. Analyses of
17 covariance were used to identify the roles of dispersal ability and habitat distribution in determining
18 migration patterns. Dispersal ability was a highly significant predictor of gene flow ($p < 0.001$), and was
19 more important than any other factor. These findings predict that dispersal ability may be an import factor
20 shaping both microevolutionary and macroevolutionary patterns; this prediction is borne out by
21 comparisons of species diversity in cactus-feeding groups.
2223 **Introduction**25 Gene flow is a fundamental determinant of the rate
26 and trajectory of genetic diversification in sexual
27 organisms. Levels of gene flow between popula-
28 tions influence the degree to which isolated demes
29 will either share a common evolutionary trajectory,
30 or will diverge over time through genetic drift and
31 natural selection (Wright, 1943; Wright, 1978;
32 Slatkin, 1985; Slatkin, 1987). Cessation of gene
33 flow is therefore necessary for speciation to proceed
34 (Mayr, 1942), and many biologists consider genetic
35 isolation to be diagnostic of species status (Mayr,
36 1942; Mayr, 1963; Templeton, 2001). Conversely,
37 sustained gene flow between demes may either
38 allow beneficial mutations to spread, or may pre-
39 vent peripheral populations from adapting to local
40 environments at the edge of a species' range (Do-
41 bzhansky, 1937; Futuyama, 1987; Thompson &
42 Cunningham, 2002).43 Elucidating the mechanisms that either pro-
44 mote or impede gene flow between demes istherefore essential to explaining both the evolu- 45
tionary process and the diversification of sexual 46
organisms. The distribution of populations 47
(Roderick, 1996; Young, Boyle & Brown, 1996), 48
dispersal ability (Peterson & Denno, 1998), and 49
geographic barriers to dispersal (Avice, 1994) 50
represent some of the most obvious factors that 51
may determine rates of gene exchange between 52
populations, but other ecological factors such as 53
host specificity, mutualistic relationships, and 54
competition may also play equally important 55
roles. However, despite the importance of migra- 56
tion and gene flow in the evolutionary process, the 57
role of ecological factors in governing rates of 58
gene flow between populations has received little 59
empirical study. Although there has been 60
increasing interest in how the distribution of ge- 61
netic variation may influence ecological phenom- 62
ena (Antonovics, 1992; Collins, 2003; Morin, 63
2003), very little attention has been paid to how 64
ecological processes shape population genetic 65
patterns. 66

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67 Phytophagous insects present an appropriate
68 venue in which to explore how ecological factors
69 affect levels of gene exchange and population
70 structure. Within a group as species rich and
71 diverse in their natural history as the Insecta, it
72 may be possible to identify multiple, evolution-
73 arily distinct groups that share common ecolog-
74 ical characteristics and to examine the
75 consequences of those characteristics for popu-
76 lation structure. Also, because the vast majority
77 of phytophagous insects feed on a limited num-
78 ber of plant species (Strong et al., 1984), they
79 have discreet, and easily definable potential
80 habitats.

81 Much previous work has focused on the pivotal
82 role that specialization may play in determining
83 population structure and migration rates in phy-
84 tophagous insects. It has been suggested, for
85 example, that insects specialized on one or a few
86 hosts may have smaller, and more patchily dis-
87 tributed populations with inherently lower rates of
88 gene flow between populations, and that this may
89 in turn have promoted the diversification of spe-
90 cialist lineages (Farrell & Mitter, 1994; Futuyama &
91 Moreno, 1988; Farrell, 1998).

92 However, the current empirical evidence
93 regarding the effect of specialization on gene flow
94 and population structure is equivocal. A study of
95 carabid ground beetles found that populations of
96 montane species, with consequently patchy distri-
97 butions, were generally isolated from one another,
98 and had lower levels of migration between popu-
99 lations than lowland species in more continuous
100 habitats (Liebherr, 1988). However a review of 43
101 previous studies of gene flow in phytophagous
102 insects found no significant differences in the de-
103 gree of isolation by distance between monophag-
104 ous, oligophagous, and polyphagous insects
105 (Peterson & Denno, 1998). Additionally, whereas
106 Liebherr's (1988) study found no significant cor-
107 relation between flight wing development and gene
108 flow, the latter study found that dispersal ability,
109 rather than specialization, or distribution, was a
110 much more important determinant of population
111 structure (Peterson & Denno, 1998). Finally, al-
112 though a comparison of a comparison of two sister
113 species of bark beetles that differed in diet breadth
114 (Kelley et al., 2000) found that the specialist had
115 lower levels of gene flow between populations, this
116 study did not consider whether the species differed
117 in dispersal ability.

118 The ambiguity of the existing empirical evi-
119 dence is heightened by the fact that many previous
120 studies have relied on F_{st} statistics inferred from
121 allozyme data, which may be an unreliable esti-
122 mator of actual gene flow (Whitlock & McCauley,
123 1999; Wilkinson-Herbots & Ettridge, 2004).
124 Additionally, a lack of phylogenetic control makes
125 it difficult to draw firm conclusions from the
126 existing evidence. Although Kelley et al's study
127 explicitly contrasted sister species, Peterson and
128 Denno underscored that the heterogeneity of
129 individual studies grouped into the three diet-
130 breadth classes in their study made it difficult to
131 control for confounding variables, such as differ-
132 ences in the organisms' ecology, and phylogenetic
133 and biogeographic histories.

134 The ideal way to resolve the existing ambiguity
135 surrounding this issue would be to specifically
136 estimate gene flow using coalescent-based meth-
137 ods, rather than relying on F_{st} statistics, and to
138 more closely control for variation in habitat
139 patchiness (or predictors thereof) and dispersal
140 ability. Towards that end, we examined popula-
141 tion structure in three species of cactus-feeding
142 longhorn beetles. There are two major genera of
143 cactus-specialists within the longhorn beetles
144 (Cerambycidae), the flightless beetles in the genus
145 *Moneilema* (Say) and the fully volant *Coenopoeus*
146 (Horn). Previous research on the genus *Moneilema*
147 indicated significant phylogeographic structure
148 within and between species and indicated that
149 topographic barriers were a significant determi-
150 nant of migration rates in these flightless animals
151 (Smith, 2003; Smith & Farrell, 2005; Smith &
152 Farrell, In Press-a; Smith & Farrell, In Press-b).
153 Here we examine genetic diversity in the longhorn
154 cactus beetle *Coenopoeus palmeri* LeConte using
155 coalescent-based estimates of migration rates, and
156 compare these results with two previous studies of
157 population structure in the flightless *Moneilema*
158 cactus beetles *M. gigas* LeConte and *M. appressum*
159 LeConte.

160 Because of their exceedingly similar host and
161 habitat use, these three species provide a uniquely
162 well-controlled natural experiment in which to
163 examine the ecological factors that determine lev-
164 els of gene flow. *M. appressum* and *C. palmeri*
165 occur in sympatry in semidesert grasslands and
166 mixed forest in the border regions of the south-
167 western United States and northwestern Mexico,
168 and are nearly identical in their natural history and

169 ecology. Both species feed on *Opuntia* cacti as
 170 adults, and the larvae burrow inside the stems of
 171 these cacti until they pupate and later emerge as
 172 adults during the mid-summer monsoon rains.
 173 Additionally, both *M. appressum* and *C. palmeri*
 174 occur primarily in fragmented habitats in mid-
 175 elevation grassland and mixed-forest communities,
 176 feeding on two sister species of cacti, *O. spinosior*
 177 and *O. imbricata* (but see Lingafelter (2003) for
 178 noteworthy exceptions). In contrast, *M. gigas*, al-
 179 though also a cactus specialist, feeds on a wide
 180 variety of prickly pear and cholla cacti, has been
 181 reported from a number of other non-*Opuntia*
 182 cacti (Crosswhite & Crosswhite, 1985), and has a
 183 continuous range that includes a variety of low
 184 and mid-elevation habitats from tropical decidu-
 185 ous forests through desert scrub and semi-desert
 186 grasslands (Raske, 1966).

187 Here, we examine population structure in these
 188 three species using mitochondrial DNA (mtDNA)
 189 sequence data and coalescent-based methods to
 190 infer migration rates. We then use analyses of
 191 covariance to evaluate the relative contributions of
 192 dispersal ability, diet breadth, and habitat
 193 distribution in determining population structure.

194 Materials and methods

195 Insect collections

196 Specimens of *Moneilema* and *Coenopoeus* were
 197 collected in Arizona, New Mexico, and Sonora,
 198 Mexico, during the summers of 1998–2000 (See
 199 Table 1). Collection localities were identified by
 200 referring to published records (Linsley & Chem-
 201 sak, 1984), museum collections, and biotic com-
 202 munities maps (Brown, 1994; Brown,
 203 Reichenbacher & Franson, 1998). Specimens were
 204 collected by hand and preserved in 100% ethanol.

205 Genetic data

206 Specimens were selected for sequencing to obtain
 207 representative samples from across the species'
 208 range. Whole genomic DNA was extracted using
 209 the salting-out procedure described by Sunnucks
 210 and Hales (1996). PCR and thermal cycle
 211 sequencing were used to amplify and sequence *ca.*
 212 790 bp of the mitochondrial Cytochrome Oxidase
 213 One (COI) gene, corresponding to positions 2183

Table 1. Collection localities for *C. palmeri*

Population	Location	Coordinates	Number of individuals sequenced
Skeleton canyon	Peloncillo Mts. Skeleton Canyon Road off AZ Rte 80, Cochise County, Arizona	31°35'25" N 109°03'47" W	3
Peppersauce canyon	Mt Lemmon Backroad, Southeast of Oracle, Pinal Cty., AZ	32°31'26" N 110°42'18" W	2
KM 100	Mexico Hwy 15, 100 KM north of Hermosillo, Sonora, Mexico	30°00'00" N 111°08'00" W	4
Tollhouse canyon	Peloncillo Mts. Hwy 191 west of Clifton, Greenlee Cty, Arizona	33°46'25" N 109°18'40" W	4
Box canyon	Box Canyon Road between Greaterville and the Santa Rita Experimental Range Station, Santa Cruz County, Arizona	31°47'00" N 110°50'18" W	5
Willowsprings	Off Az Hwy 77, South West of Oracle, Arizona.	32°44'54" N 110°53'50" W	3
San Simon	Pinaleno Mts. Hwy 191 South of Safford, Graham Cty, NM.	25°48'21" N 104°46'40" W	2
Cochise Stronghold	Dragoon Mts. Ironwood Rd, East of Cochise Ranger Station, Cochise Cty, AZ	31°56'56" N 109°55'59" W	2
Willcox Playa	Railroad Avenue, Southwest of Willcox, Cochise Cty, Arizona	32°12'05" N 109°52'02" W	2
Globe	Pinal Mts. Forest Service Rd 55 South of Claypool, Gila Cty, Arizona	33°21'36" N 110°48'56" W	3
College peak	AZ Rte 80, Northeast of Douglas, Cochise County, Arizona	31°28'56" N 109°25'24" W	7



214	to 2963 of the <i>Drosophila yakuba</i> mitochondrial	262
215	genome. PCR conditions and DNA sequencing	263
216	protocols are described in Smith (2003), Smith and	264
217	Farrell (2005), and Smith and Farrell (In Press-b).	265
218	Primer sequences used for PCR and sequencing	266
219	are described in Farrell (2001)	267
220	DNA sequence data were assembled in	268
221	Sequencher version 4.1 (Gene Codes Corporation,	269
222	Ann Arbor Michigan), and easily aligned by eye	270
223	using MacClade vers. 4.03 (Maddison &	271
224	Maddison, 2001).	
225	<i>Coalescent analyses</i>	
226	Per generation migration rates in <i>C. palmeri</i> were	273
227	estimated using the same procedures described by	274
228	Smith and Farrell (2005) and Smith and Farrell (In	275
229	Press-b) to estimate migration rates in <i>M.</i>	276
230	<i>appressum</i> and <i>M. gigas</i> . That is, symmetric, per-	277
231	generation rates of migration between all pairs of	278
232	populations were estimated using the MDIV pro-	279
233	gram developed by Rasmus Nielsen to implement	280
234	models of the coalescent process described by	281
235	Nielsen and Wakeley (2001). Migration rates were	282
236	expressed as the parameter ' <i>M</i> ', equal to the	283
237	average number of migrants moving between two	284
238	populations per generation. In order that esti-	285
239	mated migration rates would be maximally com-	286
240	parable to those previously estimated for <i>M.</i>	287
241	<i>appressum</i> and <i>M. gigas</i> , <i>a priori</i> maximum	288
242	migration rates and divergence times were the	289
243	same as those described in the previous studies	290
244	($M_{\max} = 3$, $T_{\max} = 10$) and the solution space was	291
245	explored using a three million generation Markov	292
246	Chain Monte Carlo (MCMC) with a five hundred	293
247	thousand generation burn-in using a finite sites	294
248	model of evolution.	295
249	In order to explore aspects of demographic	296
250	history in this species that could potentially influ-	297
251	ence estimates of gene flow, divergence times be-	298
252	tween demes were also calculated using MDIV,	299
253	and the coalescent-scaled parameter ' <i>T</i> ' was	300
254	converted to years as follows:	301
	$T_{\text{div}} = T\Theta / (2\mu)$	302
256	where μ is equal to the expected number of	303
257	mutations that will occur in a sample of <i>n</i> base	
258	pairs per generation. In this case we assumed one	
259	generation per year (Linsley & Chemsak, 1984),	
260	and used the maximum likelihood estimate of P	
261	($=2Ne\mu$) calculated from MDIV. The neutral	
	mutation rate was assumed to be 1.5% per million	262
	years, based on a calibration for the closely related	263
	<i>Tetraopes</i> milkweed beetles (Farrell, 2001).	264
	Likewise, in order to test for deviations from a	265
	standard coalescent model that might bias esti-	266
	mates of migration rates, such as exponential	267
	population growth or natural selection, Tajima's	268
	<i>D</i> was calculated in Arlequin (Schneider, Rosselli	269
	& Excoffier, 2000), and compared to <i>D</i> computed	270
	from 1000 simulated data sets.	271
	<i>Biogeographic variables</i>	272
	In order to examine the effects of distance and	273
	habitat distribution on migration rates, the distance	274
	between collection localities and the relative	275
	'patchiness' of available habitat were calculated.	276
	Great circle distances between collection localities	277
	were calculated from GPS coordinates using the	278
	program EarthDistances (Byers, 1999), and were	279
	compiled into a distance matrix. Habitat patchi-	280
	ness was quantified by identifying biotic commu-	281
	nities in which each insect species is known to	282
	occur, and a biotic communities map (Brown,	283
	1994) was used to determine whether two collec-	284
	tion localities were connected by contiguous areas	285
	of suitable habitat for a given species. If a partic-	286
	ular species could pass between two localities,	287
	traveling in a straight line, without having to tra-	288
	verse habitat where no suitable hosts occur, then	289
	these localities were considered contiguous. Con-	290
	versely, if a particular species, traveling in a	291
	straight line between two particular localities,	292
	would have to pass areas communities without	293
	suitable hosts, these two populations were con-	294
	sidered to be non-contiguous. On this basis, a	295
	matrix of pair-wise contrasts between collection	296
	localities was created for each species, corre-	297
	sponding to the level of connectivity between each	298
	pair of localities; contrasts between contiguous	299
	localities were assigned a score of one (1), con-	300
	trasts between non-contiguous localities were	301
	assigned a score of zero (0). This matrix is avail-	302
	able from the authors upon request.	303
	<i>Statistical analyses</i>	304
	Correlations of migration rates with geographic	305
	distance between populations within species were	306
	calculated using a Mantel test implemented in	307
	FSTAT version 2.9.3.2 (Goudet, 2002) using	308

309 20,000 permutations each. The effect of habitat
310 patchiness on migration rates within species was
311 examined using a partial Mantel test to examine
312 residual variation in migration rates after the effect
313 of distance had been removed.

314 Following Peterson and Denno (1998) analyses
315 of covariance were used to examine the effects of
316 dispersal ability and habitat patchiness on gene
317 flow, while controlling for the confounding effect
318 of distance. Dispersal ability was coded as a cate-
319 gorical variable, with each species coded as either
320 flightless (0) or flight-capable (1); migration rates
321 and biogeographic variables were calculated as
322 described above. Analyses of covariance were
323 executed in Statistica version 6.0 (Stat Soft, Inc.
324 Tulsa OK), and the distance-corrected, mean val-
325 ues of the parameter 'M' for each category were
326 computed using a least-squares method.

327 Results

328 About 730 bp of mtDNA sequence data were
329 obtained from 38 individuals sampled from
330 populations across southeastern Arizona and
331 northern Sonora, Mexico (GenBank accession #'s
332 AY763352–AY763388). There were 61 variable
333 sites within the ingroup, of which 34 were non-
334 synonymous substitutions.

335 Coalescent analyses using MDIV revealed that
336 per generation migration rates between popula-
337 tions of *C. palmeri* varied from 0.21 to 3 migrants
338 per generation, with an average of 1.15 +/- 0.97
339 (See Table 2). Divergence times varied between
340 739 and 670,000 years, with an average diver-
341 gence time of 174,000 +/- 165,000 years, and

342 with the highest divergence times being between
343 populations separated by the largest geographic
344 distance. However, examination of the posterior
345 distributions suggests that for most contrasts the
346 divergence times were not statistically different
347 from zero. Tajima's *D* statistic was equal to
348 -0.06956 ; based on 1000 simulated data sets, this
349 value is not significantly different from zero
350 ($p=0.5390$).

351 Mantel and partial Mantel tests of migration
352 rates within species were significantly correlated
353 with the distance between populations across all
354 three species ($p<0.01$) (See Figure 1), but there
355 was no evidence that habitat patchiness signifi-
356 cantly decreased migration rates when correcting
357 for distance using a partial Mantel test. For *C.*
358 *palmeri* and *M. gigas* the effects of habitat patch-
359 iness were non-significant ($p=0.4135$ $n=55$ and
360 $p=0.0815$ $n=231$, respectively), and for *M.*
361 *appressum* there was marginally significant, nega-
362 tive correlation between habitat patchiness and
363 distance-corrected migration rates ($p=0.0227$
364 $n=91$). That is, demes connected by areas of po-
365 tential habitat had lower (distance corrected)
366 migration rates than demes separated by inhospit-
367 able habitats.

368 In the interspecific comparisons using analysis
369 of covariance, although migration rates were sig-
370 nificantly influenced by flight ability ($p<0.001$,
371 $n=377$) (see Figure 2 and Table 3), there was no
372 significant difference in migration rates based on
373 habitat patchiness ($p=0.395$) Neither did the two
374 species of flightless beetles differ in average
375 migration rates ($p=0.214$, $n=322$) (see Table 4)
376 despite the differences in habitat connectivity
377 between populations in these two species.

Table 2. Migration rates between populations in *C. palmeri*

KM 100	/	129973	159269	340917	455979	199558	369090	553014	242812	130696	672914
Box canyon	2.76	/	23300	86253	96980	80723	83966	97957	246481	73603	216539
Willowsprings	1.026	2.922	/	123507	77929	80723	56893	158060	175409	21107	53333
Peppersauce	0.438	1.098	1.428	/	8160	35375	2666	24806	1076	363262	298307
Globe	0.168	1.896	2.262	2.79	/	139122	92777	73315	120317	450626	516539
Cochise stronghold	0.894	2.64	1.662	1.602	2.028	/	164075	65691	54817	5880	173904
Willcox	0.456	1.068	1.278	2.988	1.572	0.834	/	739	2211	396430	509460
San Simon	0.21	1.092	0.708	1.35	1.626	1.35	1.782	/	3215	415580	311578
Tollhouse	0.198	0.246	0.522	2.88	0.498	0.654	1.182	2.868	/	292019	92207
Skeleton canyon	0.546	1.098	0.48	0.042	0.186	3	0.09	0.06	0.054	/	2479
College peak	0.048	0.606	1.5	0.3	0.252	0.81	0.348	0.3	0.246	2.928	/



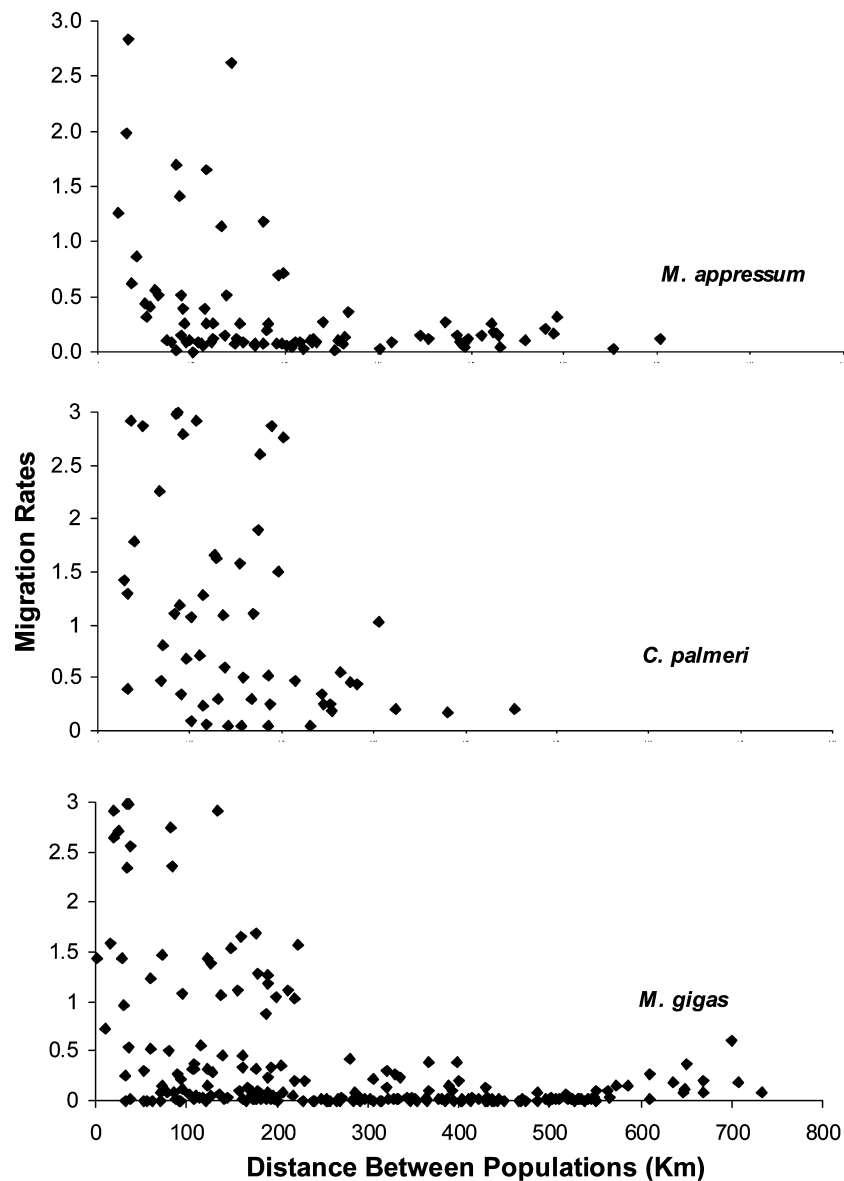


Figure 1. Effect of distance between localities on symmetric, per generation migration rates (M) in *M. appressum*, *C. palmeri*, and *M. gigas*.

378 Discussion

379 These results suggest that the populations of *C.*
 380 *palmeri* sampled in this study are experiencing high
 381 rates of ongoing gene flow, and that, despite an
 382 isolation-by-distance effect, the data did not differ
 383 significantly from expectations under a simple
 384 coalescent model. These results differ markedly
 385 from biogeographic patterns found in the symp-
 386 atrically distributed *M. appressum* (Smith and

Farrell, In Press-b), where there was evidence that
 topographic variation presented a significant bar-
 rier to dispersal, and that populations separated by
 major river valleys were genetically isolated.

Across species, statistical comparisons reveal
 highly significant difference in migration rates be-
 tween the flight-capable *Coenopoeus palmeri*, and
 the two flightless *Moneilema* species. Although it
 would be ideal to be able to compare sister species,
 as in the Kelley et al. (2000) study, it is rarely

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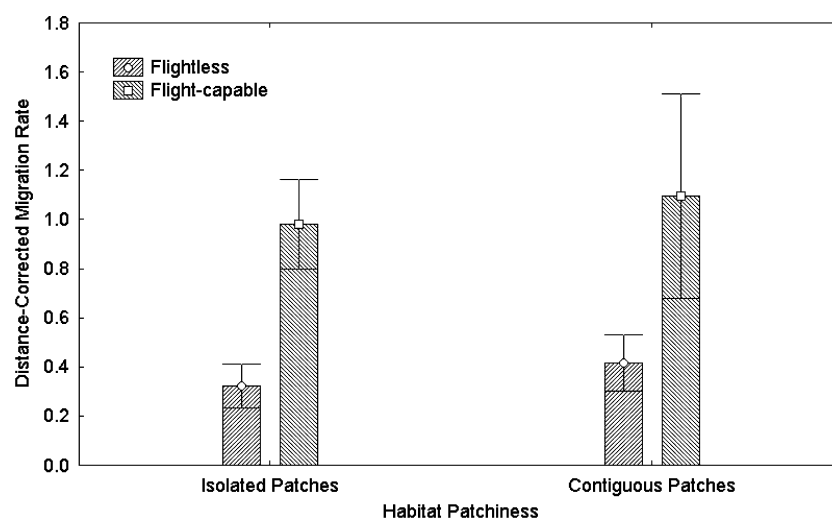


Figure 2. Distance-corrected migration rates between isolated and contiguous habitat patches in flightless ($n=322$ pair wise contrasts) and flight-capable species ($n=55$ pair wise contrasts). Migration rates are shown as least-squares means; error bars show the 95% confidence intervals. The effect of flight ability on migration rates is highly significant ($p<0.001$), the effect of habitat patchiness is not ($p=0.395$).

397 possible in natural systems to find contrasts that
 398 control for all variables, particularly because sister
 399 taxa almost always differ in distribution or host
 400 preference. In this case, the remarkable similarity
 401 in the ecology of *M. appressum* and *C. palmeri*

Table 3. Analysis of covariance across all taxa $n=377$

Effect	Sum of squares	Mean squares	F	P
Distance	23.01	23.01	58.85	<0.001*
Flight	11.56	11.56	29.57	<0.001*
Habitat patchiness	0.28	0.28	0.73	0.395
Flight×Habitat Patchiness	0.00	0.00	0.01	0.925

Table 4. Analysis of covariance within *Moneilema* $n=322$

Effect	Sum of squares	Mean squares	F	P
Distance	15.72	15.72	50.38	<0.001*
Species	0.48	0.48	1.55	0.214
Habitat Patchiness	0.01	0.01	0.04	0.838
Species*Habitat Patchiness	0.88	0.88	2.83	0.093

allows us to examine dispersal ability directly with
 a precision that is not generally possible in
 sister-group comparisons.

In contrast, there was almost no difference
 attributable to the relative patchiness of habitats.
 Whereas the strong effect of dispersal ability on
 migration rates was expected, it is noteworthy that
 there was almost no reduction in migration rates
 due to the patchiness of habitat distributions,
 neither across taxa nor within species. These data
 suggest that, contrary to other recent studies
 (Dobler & Farrell, 1999; Kelley et al., 2000) the
 changes in population structure that accompany
 specialization may have only minor effects on the
 rate of genetic divergence between populations,
 at least in these desert insects. Instead, extrinsic factors
 such as barriers to dispersal and demographic
 history may be more important in determining
 genetic variation within and between populations
 in these groups.

It is unclear, however, to what extent this
 finding would hold true for other groups of phy-
 topagous insects. Whereas migration rates in the
 two flightless species may be inherently low, and
 hence the additional reductions in gene flow due to
 habitat patchiness may be insignificant, within
Coenopoeus palmeri the absence of an effect of
 habitat patchiness on migration rates may reflect
 the spatial scale of the study.



431 It is also worth considering what effect sample
432 size may have had on estimates of migration rates.
433 Unfortunately, local population density is highly
434 variable in cactus beetles, and consequently for
435 some demes only a very small number of individ-
436 uals were collected. It is unlikely, however, that the
437 small sample sizes for these populations biased the
438 overall results. Although it is possible that migra-
439 tion rates may not be estimated accurately for
440 populations that included only a few individuals,
441 and that this in turn may have introduced some
442 noise into the analysis, small sample sizes should
443 not have biased the study towards rejecting the
444 null hypothesis of no difference in migration rates
445 between flightless and volant species. Indeed, using
446 simulations to examine deviations from the stan-
447 **1** dard coalescent, Sjodin et al. (2005) showed that
448 for extremely small sample sizes population
449 structure is overestimated, suggesting that if small
450 sample sizes had biased this study we would have
451 been unable to reject the null hypothesis. The
452 highly significant difference in migration rates be-
453 tween flightless and winged species is therefore a
454 strong indication that sample sizes did not
455 introduce statistical bias.

456 Finally, it seems reasonable to explore the
457 consequences of the microevolutionary phenom-
458 ena seen here on macroevolutionary patterns in
459 general. Habitat patchiness due to host special-
460 ization is often identified as one factor that may
461 have occasioned the startling diversity of phy-
462 tophagous insects (Futuyma & Moreno, 1988;
463 Farrell, 1998). Given that the data presented here
464 suggest that dispersal ability may be much more
465 important in determining population structure and
466 the potential for local demes to diverge through
467 genetic drift, it seems fair to consider whether
468 lineages with inherently low capacity for dispersal
469 might be more prone to speciation and hence more
470 diverse. Alternatively, groups with low intrinsic
471 rates of dispersal might be more prone to extinc-
472 tion; the infrequency of immigration makes it
473 more likely that small populations will die out, and
474 low levels of gene flow could make it more difficult
475 for beneficial mutations to spread throughout a
476 metapopulation.

477 Although hypotheses about the relative diver-
478 sity of different groups are best addressed using a
479 phylogenetic approach that control differences in
480 the age of groups, such as contrasts between sister
481 groups (Mitter, Farrell & Wiegmann, 1988),

comprehensive phylogenetic information is rarely
available for studies that would consider an entire
fauna. An approach that has been used for this
purpose in the past is the comparison of species/
genus ratios (Carlquist, 1974; Peck, Wigfull &
Nishida, 1999). As a preliminary investigation of
the consequences of dispersal ability for diversifi-
cation rates, we surveyed the literature to quantify
the diversity of cactus-feeding insects in North
America and then compared the average number
of species per genus in groups that were either
primarily, or entirely flightless with those where
flight was well-developed. We excluded species
that were primarily associated with necrotic tissue
– host fidelity in these might not be comparable to
that of true herbivores (Mann, 1969), – species
that occurred exclusively in South America – this
fauna is not as well known, and likely omits many
undescribed species (Mann, 1969; Zimmerman &
Granata, 2002), – and species where host records
were doubtful. This comparison suggests that
among the 30 genera of cactus feeding insects
found in North America, the three sedentary
groups are significantly more diverse ($p < 0.001$),
comprising 42% of the 118 described species (see
Table 5 and Figure 3).

This comparison does not take into account the
relative age of the different groups, so time cannot
be ruled out as an alternative explanation, but the
fact that all of these taxa are cactus specialists
obviously imposes a natural upper limit on their
ages of origin, and there is no reason to think that
flightless groups should be older than the other
genera included in this contrast. Indeed, given that
flightless species may be more prone to extinction,
we should expect that flightless groups should be
generally younger. However, as with any retro-
spective study, the correlation between dispersal
ability and species does not necessarily imply
causation. It is therefore possible that some com-
mon cause may underlie the observed pattern. For
example, if flightlessness represents an adaptation
to cactus feeding, then older groups, that have a
longer history of cactus association over macro-
evolutionary time, might be more likely to have
become flightless and might also have had greater
opportunity to diversify.

Nevertheless, together these findings do seem to
suggest that dispersal ability may play an impor-
tant, and as yet under-appreciated role in shaping
evolutionary patterns on a variety of time scales.

Table 5. Taxonomic distribution, diversity, and dispersal ability of North American, cactus-feeding insects

Order	Family	Genus	Dispersal	# Cactophagus species in NA	References
Coleoptera	Anobiidae	<i>Tricorynus</i>	Vagile	1	(Mann, 1969)
Coleoptera	Cerambycidae	<i>Archlagocheirus</i>	Vagile	1	(Mann, 1969)
Coleoptera	Cerambycidae	<i>Coenopoeus</i>	Vagile	2	(Mann, 1969; Blackwelder, 1982)
Coleoptera	Cerambycidae	<i>Moneilema</i>	Sedentary	16	(Raske, 1966; Linsley & Chemsak, 1984)
Coleoptera	Chrysomelidae	<i>Diabrotica</i>	Vagile	1	(Badii & Flores, 2001)
Coleoptera	Chrysomelidae	<i>Disonycha</i>	Vagile	1	(Mann, 1969)
Coleoptera	Curculionidae	<i>Cactophagus</i>	Vagile	3	(Mann, 1969; Badii & Flores, 2001)
Coleoptera	Curculionidae	<i>Cylindrocopturus</i>	Vagile	2	(Mann, 1969; Badii & Flores, 2001; Zimmerman & Granata, 2002)
Coleoptera	Curculionidae	<i>Gerstaeckeria</i>	Sedentary	28	(Mann, 1969; O'Brien, 1969; Blackwelder, 1982)
Coleoptera	Curculionidae	<i>Onychobaris</i>	Vagile	1	(Mann, 1969)
Coleoptera	Scarabaeidae	<i>Phyllophaga</i>	Vagile	1	(Badii & Flores, 2001)
Diptera	Cecidomyiidae	<i>Asphondylia</i>	Vagile	3	(Mann, 1969; Zimmerman & Granata, 2002)
Diptera	Cecidomyiidae	<i>Mayetolia</i>	Vagile	3	(Mann, 1969)
Diptera	Cecidomyiidae	<i>Neolasioptera</i>	Vagile	1	(Mann, 1969)
Diptera	Lonchaeidae	<i>Dasiops</i>	Vagile	1	(Mann, 1969)
Hemiptera	Capsidae	<i>Hesperolabops</i>	Vagile	1	(Mann, 1969; Oliveira et al., 1999; Badii & Flores, 2001)
Hemiptera	Coreidae	<i>Chelinidea</i>	Vagile	5	(Mann, 1969; Herring, 1980; Badii & Flores, 2001; Zimmerman and Granata, 2002)
Hemiptera	Coreidae	<i>Leptoglossus</i>	Vagile	2	(Mann, 1969; Mendez et al., 2004)
Hemiptera	Coreidae	<i>Narnia</i>	Vagile	3	(Mann, 1969; Zimmerman & Granata, 2002)
Homoptera	Dactylopiidae	<i>Dactylopius</i>	Sedentary	5	(Mann, 1969; Perez Guerra & Kosztarab, 1992; Badii & Flores, 2001; Zimmerman & Granata, 2002)
Homoptera	Diaspididae	<i>Diaspidae</i>	Sedentary	1	(Mann, 1969; Zimmerman and Granata, 2002)
Lepidoptera	Gelechiidae	<i>Aerotypia</i>	Vagile	1	(Mann, 1969)
Lepidoptera	Gelechiidae	<i>Metapleura</i>	Vagile	1	(Mann, 1969)
Lepidoptera	Gracilariidae	<i>Marmara</i>	Vagile	1	(Mann, 1969)
Lepidoptera	Phycitidae	<i>Alberada</i>	Vagile	2	(Mann, 1969)
Lepidoptera	Phycitidae	<i>Cactobrosis</i>	Vagile	5	(Mann, 1969; Fleming & Holland, 1998)
Lepidoptera	Phycitidae	<i>Cahela</i>	Vagile	1	(Mann, 1969)
Lepidoptera	Phycitidae	<i>Eremberga</i>	Vagile	3	(Mann, 1969)
Lepidoptera	Phycitidae	<i>Melitara</i>	Vagile	4	(Mann, 1969; Wangberg & Parker, 1981; Burger & Louda, 1994; Carlton & Kring, 1994; Solis, Hight & Gordon, 2004)
Lepidoptera	Phycitidae	<i>Olycella</i>	Vagile	3	(Mann, 1969; Badii & Flores, 2001; Zimmerman and Granata, 2002)
Lepidoptera	Phycitidae	<i>Ozamia</i>	Vagile	4	(Mann, 1969; Solis, Hight & Gordon, 2004)
Lepidoptera	Phycitidae	<i>Rumatha</i>	Vagile	2	(Mann, 1969; Solis, Hight & Gordon, 2004)
Lepidoptera	Phycitidae	<i>Yosemitea</i>	Vagile	4	(Mann, 1969; USFWS, 1993)
Lepidoptera	Pyalidae	<i>Laniifera</i>	Vagile	1	(Badii & Flores, 2001)
Lepidoptera	Pyalidae	<i>Upiga</i>	Vagile	1	(Fleming & Holland, 1998)
Lepidoptera	Pyraustidae	<i>Megastes</i>	Vagile	1	(Mann, 1969; Zimmerman & Granata, 2002)
Lepidoptera	Pyraustidae	<i>Mimorista</i>	Vagile	2	(Mann, 1969; Nieman, 1991)
Lepidoptera	Pyraustidae	<i>Noctuelia</i>	Vagile	1	(Mann, 1969)
Lepidoptera	Tineidae	<i>Dyotopasta</i>	Vagile	1	(Mann, 1969)
Thysanoptera	Thripidae	<i>Sericothrips</i>	Vagile	1	(Badii & Flores, 2001; Zimmerman and Granata, 2002)



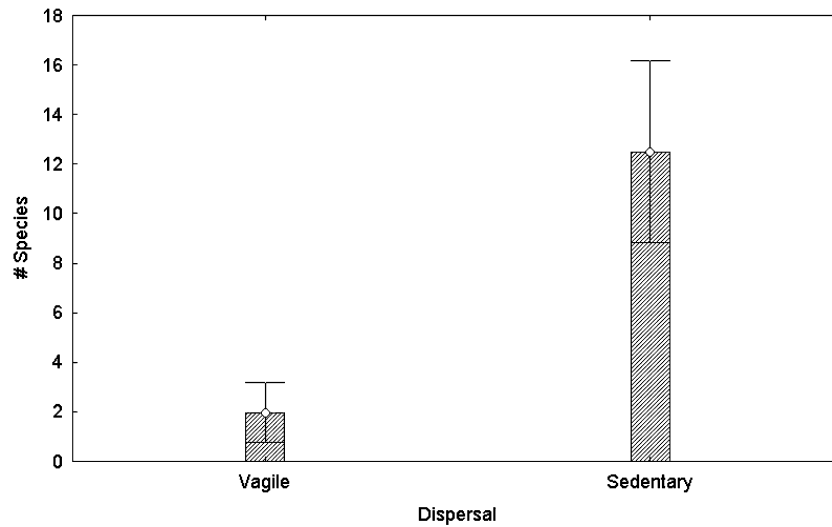


Figure 3. Least squares mean number of species per genus in sedentary and highly vagile groups of North American, cactus-feeding insects. Error bars represent 95% confidence intervals. The effect of dispersal ability on species diversity is highly significant ($p < 0.001$).

533 Dispersal ability has a significant impact on local
 534 population structure and gene flow over micro-
 535 evolutionary time, and this impact ultimately
 536 shapes macroevolutionary patterns. These results
 537 suggest, therefore, that extrinsic barriers to dis-
 538 persal and gene flow be more important than
 539 ecological factors, such as diet breadth, in
 540 promoting divergence and speciation.

541

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