

## Evolutionary consequences of dispersal ability in cactus-feeding insects

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Received 2 April 2005 Accepted 7 July 2005

*Key words:* Cerambycidae, *Coenopoeus*, flightlessness, gene flow, habitat patchiness, *Moneilema*

### Abstract

Although gene flow is an important determinant of evolutionary change, the role of ecological factors such as specialization in determining migration and gene flow has rarely been explored empirically. To examine the consequences of dispersal ability and habitat patchiness on gene flow, migration rates were compared in three cactophagous longhorn beetles using coalescent analyses of mtDNA sequences. Analyses of covariance were used to identify the roles of dispersal ability and habitat distribution in determining migration patterns. Dispersal ability was a highly significant predictor of gene flow ( $p < 0.001$ ), and was more important than any other factor. These findings predict that dispersal ability may be an important factor shaping both microevolutionary and macroevolutionary patterns; this prediction is borne out by comparisons of species diversity in cactus-feeding groups.

### Introduction

Gene flow is a fundamental determinant of the rate and trajectory of genetic diversification in sexual organisms. Levels of gene flow between populations influence the degree to which isolated demes will either share a common evolutionary trajectory, or will diverge over time through genetic drift and natural selection (Wright, 1943; Wright, 1978; Slatkin, 1985; Slatkin, 1987). Cessation of gene flow is therefore necessary for speciation to proceed (Mayr, 1942), and many biologists consider genetic isolation to be diagnostic of species status (Mayr, 1942; Mayr, 1963; Templeton, 2001). Conversely, sustained gene flow between demes may either allow beneficial mutations to spread, or may prevent peripheral populations from adapting to local environments at the edge of a species' range (Dobzhansky, 1937; Futuyama, 1987; Thompson & Cunningham, 2002).

Elucidating the mechanisms that either promote or impede gene flow between demes is

therefore essential to explaining both the evolutionary process and the diversification of sexual organisms. The distribution of populations (Roderick, 1996; Young, Boyle & Brown, 1996), dispersal ability (Peterson & Denno, 1998), and geographic barriers to dispersal (Avice, 1994) represent some of the most obvious factors that may determine rates of gene exchange between populations, but other ecological factors such as host specificity, mutualistic relationships, and competition may also play equally important roles. However, despite the importance of migration and gene flow in the evolutionary process, the role of ecological factors in governing rates of gene flow between populations has received little empirical study. Although there has been increasing interest in how the distribution of genetic variation may influence ecological phenomena (Antonovics, 1992; Collins, 2003; Morin, 2003), very little attention has been paid to how ecological processes shape population genetic patterns.

Phytophagous insects present an appropriate venue in which to explore how ecological factors affect levels of gene exchange and population structure. Within a group as species rich and diverse in their natural history as the Insecta, it may be possible to identify multiple, evolutionarily distinct groups that share common ecological characteristics and to examine the consequences of those characteristics for population structure. Also, because the vast majority of phytophagous insects feed on a limited number of plant species (Strong et al., 1984), they have discrete, and easily definable potential habitats.

Much previous work has focused on the pivotal role that specialization may play in determining population structure and migration rates in phytophagous insects. It has been suggested, for example, that insects specialized on one or a few hosts may have smaller, and more patchily distributed populations with inherently lower rates of gene flow between populations, and that this may in turn have promoted the diversification of specialist lineages (Farrell & Mitter, 1994; Futuyma & Moreno, 1988; Farrell, 1998).

However, the current empirical evidence regarding the effect of specialization on gene flow and population structure is equivocal. A study of carabid ground beetles found that populations of montane species, with consequently patchy distributions, were generally isolated from one another, and had lower levels of migration between populations than lowland species in more continuous habitats (Liebherr, 1988). However a review of 43 previous studies of gene flow in phytophagous insects found no significant differences in the degree of isolation by distance between monophagous, oligophagous, and polyphagous insects (Peterson & Denno, 1998). Additionally, whereas Liebherr's (1988) study found no significant correlation between flight wing development and gene flow, the latter study found that dispersal ability, rather than specialization, or distribution, was a much more important determinant of population structure (Peterson & Denno, 1998). Finally, although a comparison of a comparison of two sister species of bark beetles that differed in diet breadth (Kelley et al., 2000) found that the specialist had lower levels of gene flow between populations, this study did not consider whether the species differed in dispersal ability.

The ambiguity of the existing empirical evidence is heightened by the fact that many previous studies have relied on  $F_{st}$  statistics inferred from allozyme data, which may be an unreliable estimator of actual gene flow (Whitlock & McCauley, 1999; Wilkinson-Herbots & Ettridge, 2004). Additionally, a lack of phylogenetic control makes it difficult to draw firm conclusions from the existing evidence. Although Kelley et al's study explicitly contrasted sister species, Peterson and Denno underscored that the heterogeneity of individual studies grouped into the three diet-breadth classes in their study made it difficult to control for confounding variables, such as differences in the organisms' ecology, and phylogenetic and biogeographic histories.

The ideal way to resolve the existing ambiguity surrounding this issue would be to specifically estimate gene flow using coalescent-based methods, rather than relying on  $F_{st}$  statistics, and to more closely control for variation in habitat patchiness (or predictors thereof) and dispersal ability. Towards that end, we examined population structure in three species of cactus-feeding longhorn beetles. There are two major genera of cactus-specialists within the longhorn beetles (Cerambycidae), the flightless beetles in the genus *Moneilema* (Say) and the fully volant *Coenopoeus* (Horn). Previous research on the genus *Moneilema* indicated significant phylogeographic structure within and between species and indicated that topographic barriers were a significant determinant of migration rates in these flightless animals (Smith, 2003; Smith & Farrell, 2005; Smith & Farrell, In Press-a; Smith & Farrell, In Press-b). Here we examine genetic diversity in the longhorn cactus beetle *Coenopoeus palmeri* LeConte using coalescent-based estimates of migration rates, and compare these results with two previous studies of population structure in the flightless *Moneilema* cactus beetles *M. gigas* LeConte and *M. appressum* LeConte.

Because of their exceedingly similar host and habitat use, these three species provide a uniquely well-controlled natural experiment in which to examine the ecological factors that determine levels of gene flow. *M. appressum* and *C. palmeri* occur in sympatry in semidesert grasslands and mixed forest in the border regions of the southwestern United States and northwestern Mexico, and are nearly identical in their natural history and

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

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

## Materials and methods

### *Insect collections*

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

### *Genetic data*

Specimens were selected for sequencing to obtain representative samples from across the species' range. Whole genomic DNA was extracted using the salting-out procedure described by Sunnucks and Hales (1996). PCR and thermal cycle sequencing were used to amplify and sequence *ca.* 790 bp of the mitochondrial Cytochrome Oxidase 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

to 2963 of the *Drosophila yakuba* mitochondrial genome. PCR conditions and DNA sequencing protocols are described in Smith (2003), Smith and Farrell (2005), and Smith and Farrell (In Press-b). Primer sequences used for PCR and sequencing are described in Farrell (2001)

DNA sequence data were assembled in Sequencher version 4.1 (Gene Codes Corporation, Ann Arbor Michigan), and easily aligned by eye using MacClade vers. 4.03 (Maddison & Maddison, 2001).

#### *Coalescent analyses*

Per generation migration rates in *C. palmeri* were estimated using the same procedures described by Smith and Farrell (2005) and Smith and Farrell (In Press-b) to estimate migration rates in *M. appressum* and *M. gigas*. That is, symmetric, per-generation rates of migration between all pairs of populations were estimated using the MDIV program developed by Rasmus Nielsen to implement models of the coalescent process described by Nielsen and Wakeley (2001). Migration rates were expressed as the parameter ' $M$ ', equal to the average number of migrants moving between two populations per generation. In order that estimated migration rates would be maximally comparable to those previously estimated for *M. appressum* and *M. gigas*, *a priori* maximum migration rates and divergence times were the same as those described in the previous studies ( $M_{\max}=3$ ,  $T_{\max}=10$ ) and the solution space was explored using a three million generation Markov Chain Monte Carlo (MCMC) with a five hundred thousand generation burn-in, using a finite sites model of evolution.

In order to explore aspects of demographic history in this species that could potentially influence estimates of gene flow, divergence times between demes were also calculated using MDIV, and the coalescent-scaled parameter ' $T$ ' was converted to years as follows:

$$T_{\text{div}} = T\Theta / (2\mu)$$

where  $\mu$  is equal to the expected number of mutations that will occur in a sample of  $n$  base pairs per generation. In this case we assumed one generation per year (Linsley & Chemsak, 1984), and used the maximum likelihood estimate of  $\Theta (=2Ne\mu)$  calculated from MDIV. The neutral

mutation rate was assumed to be 1.5% per million years, based on a calibration for the closely related *Tetraopes* milkweed beetles (Farrell, 2001).

Likewise, in order to test for deviations from a standard coalescent model that might bias estimates of migration rates, such as exponential population growth or natural selection, Tajima's  $D$  was calculated in Arlequin (Schneider, Rosselli & Excoffier, 2000), and compared to  $D$  computed from 1000 simulated data sets.

#### *Biogeographic variables*

In order to examine the effects of distance and habitat distribution on migration rates, the distance between collection localities and the relative 'patchiness' of available habitat were calculated. Great circle distances between collection localities were calculated from GPS coordinates using the program EarthDistances (Byers, 1999), and were compiled into a distance matrix. Habitat patchiness was quantified by identifying biotic communities in which each insect species is known to occur, and a biotic communities map (Brown, 1994) was used to determine whether two collection localities were connected by contiguous areas of suitable habitat for a given species. If a particular species could pass between two localities, traveling in a straight line, without having to traverse habitat where no suitable hosts occur, then these localities were considered contiguous. Conversely, if a particular species, traveling in a straight line between two particular localities, would have to pass areas without suitable hosts, these two populations were considered to be non-contiguous. On this basis, a matrix of pair-wise contrasts between collection localities was created for each species, corresponding to the level of connectivity between each pair of localities; contrasts between contiguous localities were assigned a score of one (1), contrasts between non-contiguous localities were assigned a score of zero (0). This matrix is available from the authors upon request.

#### *Statistical analyses*

Correlations of migration rates with geographic distance between populations within species were calculated using a Mantel test implemented in FSTAT version 2.9.3.2 (Goudet, 2002) using

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

Following Peterson and Denno (1998) analyses of covariance were used to examine the effects of dispersal ability and habitat patchiness on gene flow, while controlling for the confounding effect of distance. Dispersal ability was coded as a categorical variable, with each species coded as either flightless (0) or flight-capable (1); migration rates and biogeographic variables were calculated as described above. Analyses of covariance were executed in Statistica version 6.0 (Stat Soft, Inc. Tulsa OK), and the distance-corrected, mean values of the parameter ' $M$ ' for each category were computed using a least-squares method.

## Results

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

Coalescent analyses using MDIV revealed that per generation migration rates between populations of *C. palmeri* varied from 0.21 to 3 migrants per generation, with an average of 1.15  $\pm$  0.97 (See Table 2). Divergence times varied between 739 and 670,000 years, with an average divergence time of 174,000  $\pm$  165,000 years, and

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

Mantel and partial Mantel tests showed that migration rates within species were significantly correlated with the distance between populations across all three species ( $p < 0.01$ ) (See Figure 1), but there was no evidence that habitat patchiness significantly decreased migration rates when correcting for distance using a partial Mantel test. For *C. palmeri* and *M. gigas* the effects of habitat patchiness were non-significant ( $p=0.4135$   $n=55$  and  $p=0.0815$   $n=231$ , respectively), and for *M. appressum* there was marginally significant, negative correlation between habitat patchiness and distance-corrected migration rates ( $p=0.0227$   $n=91$ ). That is, demes connected by areas of potential habitat had lower (distance corrected) migration rates than demes separated by inhospitable habitats.

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

Table 2. Migration rates between populations in *C. palmeri* (lower triangle), Divergence times (upper triangle)

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	/

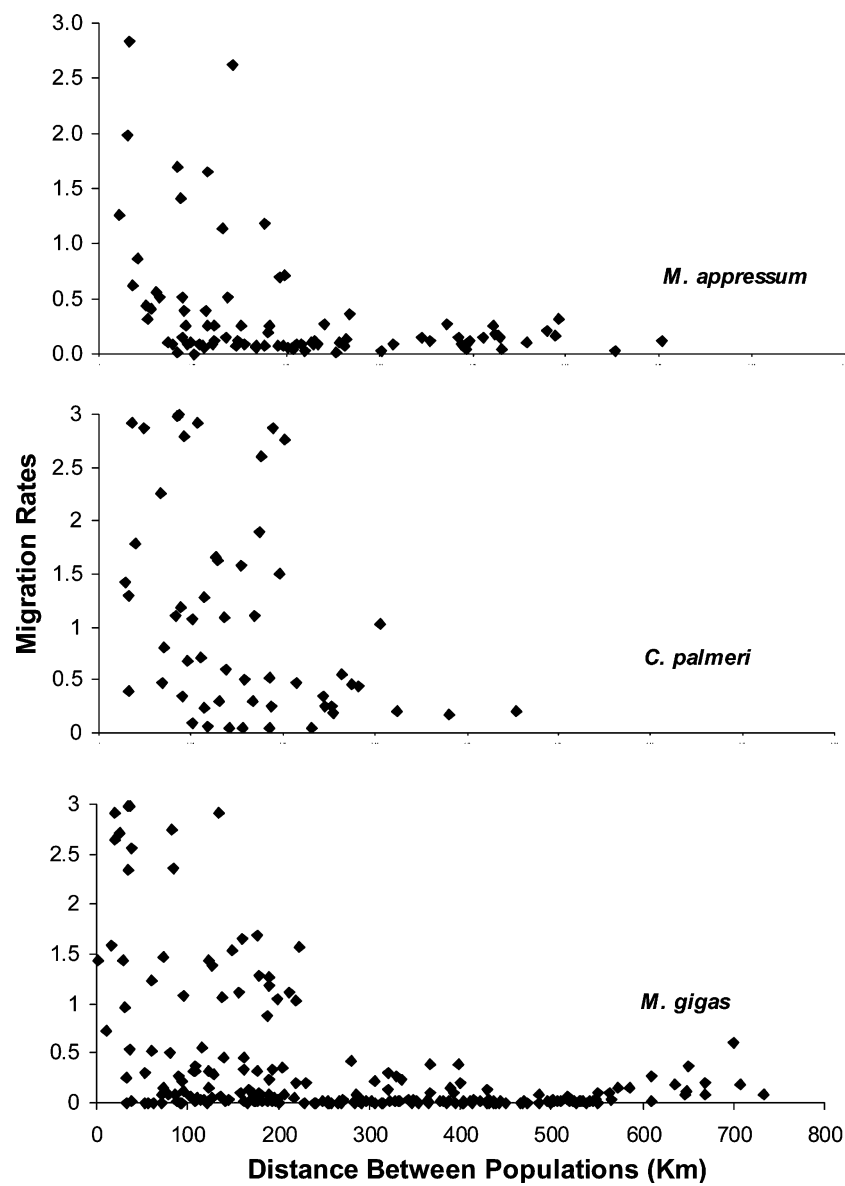


Figure 1. Effect of distance between localities on symmetric, per generation migration rates ( $M$ ) in *M. appressum*, *C. palmeri*, and *M. gigas*.

### Discussion

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

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

Across species, statistical comparisons reveal highly significant difference in migration rates between 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

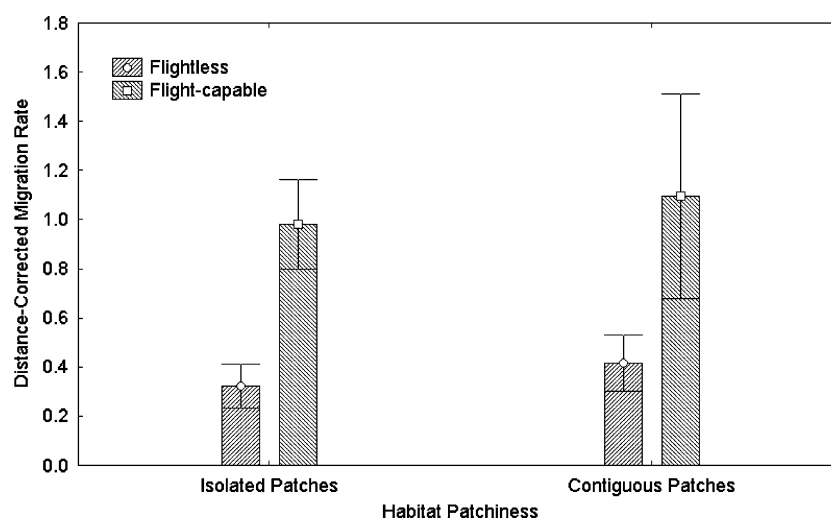


Figure 2. Distance-corrected migration rates between isolated and contiguous habitat patches in flightless ( $n=322$  pair wise contrasts) and flight-capable species ( $n=55$  pair wise contrasts). Migration rates are shown as least-squares means; error bars show the 95% confidence intervals. The effect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

possible in natural systems to find contrasts that control for all variables, particularly because sister taxa almost always differ in distribution or host preference. In this case, the remarkable similarity 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 phytophagous 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.

It is also worth considering what effect sample size may have had on estimates of migration rates. Unfortunately, local population density is highly variable in cactus beetles, and consequently for some demes only a very small number of individuals were collected. It is unlikely, however, that the small sample sizes for these populations biased the overall results. Although it is possible that migration rates may not be estimated accurately for populations that included only a few individuals, and that this in turn may have introduced some noise into the analysis, small sample sizes should not have biased the study towards rejecting the null hypothesis of no difference in migration rates between flightless and volant species. Indeed, using simulations to examine deviations from the standard coalescent, Sjodin et al. (2005) showed that for extremely small sample sizes population structure is overestimated, suggesting that if small sample sizes had biased this study we would have been unable to reject the null hypothesis. The highly significant difference in migration rates between flightless and winged species is therefore a strong indication that sample sizes did not introduce statistical bias.

Finally, it seems reasonable to explore the consequences of the microevolutionary phenomena seen here on macroevolutionary patterns in general. Habitat patchiness due to host specialization is often identified as one factor that may have occasioned the startling diversity of phytophagous insects (Futuyma & Moreno, 1988; Farrell, 1998). Given that the data presented here suggest that dispersal ability may be much more important in determining population structure and the potential for local demes to diverge through genetic drift, it seems fair to consider whether lineages with inherently low capacity for dispersal might be more prone to speciation and hence more diverse. Alternatively, groups with low intrinsic rates of dispersal might be more prone to extinction; the infrequency of immigration makes it more likely that small populations will die out, and low levels of gene flow could make it more difficult for beneficial mutations to spread throughout a metapopulation.

Although hypotheses about the relative diversity of different groups are best addressed using a phylogenetic approach that control differences in the age of groups, such as contrasts between sister 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 diversification 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 retrospective study, the correlation between dispersal ability and species does not necessarily imply causation. It is therefore possible that some common 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 macroevolutionary 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 important, 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>Cactobrosia</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>Yosemitia</i>	Vagile	4	(Mann, 1969; USFWS, 1993)
Lepidoptera	Pyralidae	<i>Laniifera</i>	Vagile	1	(Badii & Flores, 2001)
Lepidoptera	Pyralidae	<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>Noctuella</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)

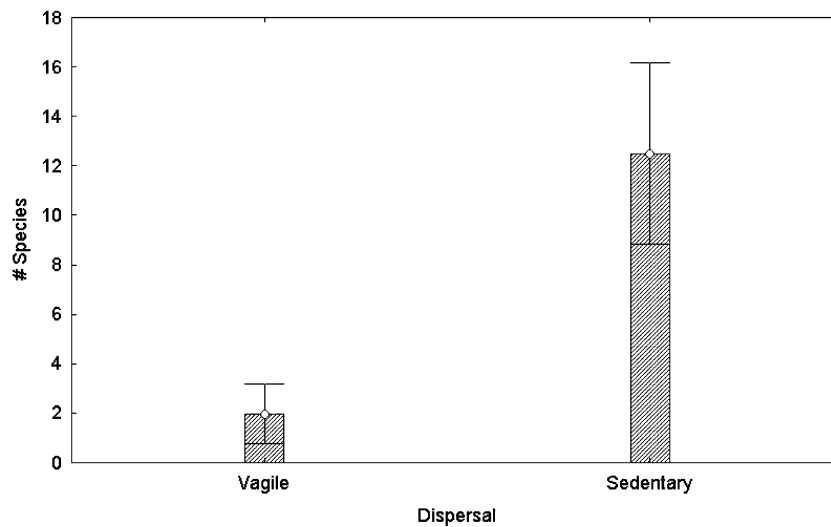


Figure 3. Least squares mean number of species per genus in sedentary and highly vagile groups of North American, cactus-feeding insects. Error bars represent 95% confidence intervals. The effect of dispersal ability on species diversity is highly significant ( $p < 0.001$ ).

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

### Acknowledgements

We wish to thank the Coronado National Forest and the Mexican Secretary of the Environment and Natural Resources for granting permission to collect insects and conduct research within their jurisdictions (USDA Permit # 2075-01; Mexico SRE Permit # DAN-03200; Mexico SEMARNAT Permit # DOO 02-2916). Dr. Rick Brusca, Wendy Moore, Nelia Padilla, John-Migue and Dylan Wilmsen, and Dr. Derrick Zwickl assisted during field collections. Molly Moore assisted with PCR and DNA sequencing for this project. Funding for this project was provided by the Putnam Expedition fund to the MCZ and the NSF doctoral dissertation improvement grant to C. I. Smith (Award # 0073291). We

are indebted to Professor Olle Pellmyr and two anonymous reviewers who provided thoughtful and constructive comments about this manuscript.

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