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NICHE BREADTH AND ABUNDANCE AS DETERMINANTS OF GENETIC VARIATION IN POPULATIONS OF MYCOPHAGOUS DROSOPHILID FLIES (DIPTERA:DROSOPHILIDAE)

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More than a decade before the selectionist-neutralist controversy began, Ludwig (1950), Levene (1953), Dempster (1955) and others had pointed out that polymorphism can be maintained if different alleles are selectively favored in different habitats. About the same time, Dobzhansky and DaCunha (DaCunha et al., 1950; Dobzhansky et al., 1950; DaCunha and Dobzhansky, 1954) proposed that the amount of adaptive chromosomal polymorphism would show a positive association with the variety of habitats exploited by populations. Van Valen (1965) later advanced essentially the same arguments as had Dobzhansky and DaCunha, citing the theoretical treatments of "multiple niche polymorphism" for support. His "niche-variation hypothesis" asserted that populations utilizing a variety of resources would have more genetic, and thus more phenotypic, variation than would populations of more specialized species.

Early studies of correlates of genetic variation supported the niche-variation concept. DaCunha and Dobzhansky (1954) showed that the mean number of heterozygous chromosome inversions in *Drosophila willistoni* individuals was larger in regions of greater environmental heterogeneity, while Beardmore and Levine (1963) measured greater additive genetic variance for abdominal chaeta number in *Drosophila pseudoobscura* that had been maintained in a variable thermal environment than in populations kept at a constant temperature. Numerous recent tests of the theory have assessed the genetic variation revealed by electrophoretic techniques. Powell (1971; Powell and Wistrand, 1978) and McDonald and Ayala (1974) demonstrated that environmental heterogeneity can preserve genic heterogeneity in some laboratory populations of *Drosophila*. Steiner (1977) did, and yet Sabath (1974) did not, find the predicted correlation between niche breadth and genetic variation in natural populations of *Drosophila*. Comparisons among putatively broad-niched and narrow-niched populations of many other organisms have also been offered both in support (e.g., Avise and Selander, 1972; Levinton, 1973; Bryant, 1974; Nevo, 1976) and in refutation (e.g., Schopf and Gooch, 1971; Somero and Soulé, 1974; Ayala and Valentine, 1979; Mitter and Futuyma, 1979; Smith, 1981) of the belief that electrophoretically detectable variation is maintained by heterogeneous selection pressures. After reviewing electrophoretic studies of 243 species of plants and animals, Nevo (1978) concluded that while overall trends supported the niche-variation hypothesis, there was a need for well designed tests of the theory.

To test the niche-variation hypothesis one needs to study populations in which both the ecological niche breadths and the levels of variation are comparable. To assure that levels of genetic variability are comparable, the sampled populations must be sufficiently close phylogenetically to avoid other causes of different characteristic levels of genetic variation among taxa (Van Valen and Grant, 1970; Rothstein, 1973; Somero and Soulé, 1974). Ideally,

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conspecific populations should be used, although this necessitates using allopatric populations, perhaps making valid comparisons of ecological niches impossible. Reasonable comparisons of ecological niche breadths can only be made among populations within an ecological guild that utilize very similar resources in sympatric habitats. A comparison of allopatric populations, occupying different roles in very different communities, confounds so many habitat differences that it is impossible to judge which is exploiting the broader niche.

One must insure also that a rescaling of arbitrary niche metrics cannot lead to a reversal in the apparent niche widths. This problem can be overcome, however, by restricting claims of relative niche widths to "included niches," those in which the range of resource use by the population with the broader niche contains that of the narrow-niched population. Among previous studies, perhaps only Mitter and Futuyma (1979) and Richardson et al. (1977) have focused on guilds of sympatric organisms known to exploit similar resources in similar ways. No published studies, to my knowledge, have investigated populations occupying "included niches."

The fungus-feeding guild of Drosophilidae are well-suited for tests of the niche-variation hypothesis. The flies of these species mate, oviposit and feed both as larvae and adults on mushrooms, and often require mushrooms in diet. While some of the fly species have been collected from decaying vegetation (*D. testacea*: Kimura et al., 1977), sap fluxes, and rotting fruit (*D. putrida, D. tripunctata* and *D. "transversa"* [probably *D. falleni* or *D. recens*]: Sturtevant, 1921; Carson and Stalker, 1951), the more specialized of the fungus-feeders are not known to use non-fungal resources as either feeding or oviposition sites.

The mycophagous drosophilids in the eastern United States range from extreme host specialists to broad generalists. *Drosophila duncani* Sturtevant feeds on the more watery and fleshy species of bracket fungi and is found primarily on several closely related genera (*Grifolia, Tyromyces* and *Laetiporus,* family Polyporaceae). *Mycodrosophila claytonae* Wheeler and Takada feeds on a variety of polypore fungi, including many of the tougher and woodier forms (e.g., *Ganoderma*) that *D. duncani* does not utilize. Electrophoretic analyses have revealed *M. claytonae* to consist of two as yet morphologically indistinguishable species. The two species (labelled *M. claytonae A* and *M. claytonae B* throughout this paper) share no alleles at genetic loci coding for fumarase, malate dehydrogenase, malic enzyme, phosphoglucomutase and two glutamate-oxalate transaminase enzymes. The sibling species utilize the same mushroom hosts and have been reared simultaneously from the same specimens of *Polyporus squamosus*. *Drosophila ordinaria* Coquillett (=*D. magnafumosa* =*D. melanderi,* Lacy, 1981) feeds on polypores as well as some of the longer-lasting gilled fungi (e.g., *Russula* spp., Order Agaricales). The trophic resources of *D. testacea* von Roser and *D. putrida* Sturtevant include the hosts of *D. ordinaria* and also somewhat more ephemeral gilled fungi (e.g., *Amanita, Lactarius*) and boletes (e.g., *Boletus, Gyrodon,* family Boletaceae). The broadest generalists, *D. falleni* Wheeler, *D. recens* Wheeler and *D. tripunctata* Loew, include virtually all fleshy fungi (polypores, agarics and boletes) in their diets. With the exception of *Mycodrosophila dimidiata* Loew, which feeds on coral fungi (Clavariaceae) as well as polypores and some gilled fungi, the fungal trophic resources of these mycophagous drosophilids form a series of almost wholly included niches (see Lacy, in press, for extensive host lists).

The mycophagous drosophilid flies are coarse-grained with respect to their larval niches. Individuals are restricted to a single mushroom cap and its immediate vicinity until emergence as adults. Adult drosophilids have the capability for considerable switching between feeding sites, though it is not known to what extent they

do so. Initial mark-recapture experiments using fluorescent dusts (Lacy, unpubl.) suggest that adult mycophagous flies typically remain at a clump of mushrooms for several days.

Materials and Methods

Populations of the mycophagous drosophilid species described above were sampled in the Ithaca, New York area, and in the Great Smoky Mountains National Park in Tennessee. Collecting sites in both geographic regions were 60 m square, and were located in a variety of forest types. The six Ithaca sites were sampled from June to October in 1978, and in May, June, September and October in 1979, 1980 and 1981. They ranged from one to ten miles apart and included an uplands pine forest (predominantly *Pinus* and *Acer*), two mixed conifer-deciduous forests (*Tsuga, Pinus, Acer, Fagus, Betula* and *Fraxinus*), two deciduous forests (*Acer, Carya, Quercus, Tilia* and *Ulmus*), and an elm swamp (*Ulmus*). Nine sites in the Smokies were sampled in July and August of 1979, 1980 and 1981. These sites ranged over the 40 mi length of the park, and varied from lowland (1,500′) streambank forests (*Ostrya, Liquidambar, Liriodendron, Cornus* and *Tsuga*), through mid-elevation (3,000′) hardwood forests (*Acer, Betula, Quercus, Halesia, Liriodendron, Tilia, Tsuga* and *Rhododendron*), to high elevation (6,000′) spruce-fir stands (*Picea, Abies* and *Betula*). Detailed descriptions of all collecting sites are given in Lacy (1982). Adult flies were aspirated directly off any mushrooms encountered during periodic searches of the collecting sites; and mushrooms were brought back to the lab and placed in half-pint bottles over Instant *Drosophila* Medium (Carolina Biol. Supply) in order to rear flies from the eggs and larvae present in the mushrooms when picked. All flies aspirated as adults or reared from larval hosts were separated by species and sex, and stored at −80 C for later electrophoresis. The preferred oviposition sites, indicated by the relative abundances of flies reared from each species of mushroom, differed little from the adult feeding resources, and so larval and adult resources were pooled for calculations of niche breadth measures.

Within each collecting region (Ithaca, N.Y. and Smoky Mts., Tenn.) the niche breadth for each species of fly was expressed as the Shannon information measure (Shannon and Weaver, 1949),

$$H' = -\Sigma\, p_i \log_e p_i,$$

where p_i is the proportion of flies of that species which were aspirated or reared from mushroom species i, pooled across months, and across collecting sites (within the Smokies or within the Ithaca area). Mushrooms that I could not identify to species (about 15% of those collected) were classified to genus or family and the data pooled with all others identifiable only to that taxonomic level. While the Shannon statistic is not the one of choice for measurements of selectivity of host preferences, since it does not account for differences in the availabilities of resource states (Petraitis, 1979), it does seem appropriate for tests of the niche-variation hypothesis. Genetic systems would respond to the diversity in actual resource use as influenced by both availability and selectivity. Mushroom species probably do not represent equally distinct resources for mycophagous flies, however. Therefore, weighted Shannon statistics were calculated following the method of Colwell and Futuyma (1971), as modified by Clarke (1977). This method weights each resource state (mushroom species) to reflect its distinctness from other resource states with respect to the associated fly faunas. For each fly species, the weighting factors to be used in quantifying its niche breadth were calculated from the proportional distributions of the other fly species among their mushroom hosts (as described in Clarke, 1977). The Shannon diversity index is calculated on these weighted data and the exponent taken to scale the measure to a maximum value of 1. I denote this Colwell-Futuyma-Clarke niche breadth metric as C'. Niche breadths were also in-

TABLE 1. *Diversity of host species utilized by mycophagous drosophilids in Ithaca, N.Y., and the Great Smoky Mts., Tenn., as indexed by the unweighted Shannon statistic, H', a weighted Shannon statistic, C', or the number of host species used with a frequency >1%, S; and the numbers of flies collected in each region, N.*

	Ithaca populations				Smoky Mts. populations			
	H'	*C'*	*S*	*N*	*H'*	*C'*	*S*	*N*
D. falleni	1.905	.2231	10	15,193	3.158	.2299	22	2,955
D. recens	1.826	.1942	8	130	2.991	.2045	19	624
D. tripunctata	1.721	.1500	11	42	3.328	.2524	25	2,270
D. putrida	1.684	.1805	10	2,028	2.809	.1764	18	3,585
D. testacea	1.057	.1308	8	1,798	2.774	.2383	20	2,009
D. ordinaria	1.545	.1533	10	200	2.383	.1530	12	1,320
D. duncani	0.826	.1011	4	122	0.975	.1716	4	138
M. dimidiata	1.406	.1725	8	284	2.770	.1081	18	293
M. claytonae A	0.978	.1999	4	138	0.838	.1494	6	50
M. claytonae B	0.671	.1162	5	97	0.000	.0001	1	10

dexed by the numbers of host species exploited (those from which more than 1% of the flies were collected); denoted as *S*.

Genetic variation was assessed by horizontal starch gel electrophoresis, using apparatus similar to that of Selander et al. (1971). Eleven percent starch gels (47 g/400 ml buffer) were prepared initially with Electrostarch (Lot 307, Otto Hiller Co., Madison, Wisconsin), and later with a 2:1 mixture of Electrostarch (Lot 392) and Sigma starch (Sigma Chemical Co., St. Louis). Twenty-three enzyme systems were tested: acid phosphatase (ACP), alcohol dehydrogenase (ADH), aldehyde oxidase (AO), esterases (EST), fructose-1,6-diphosphatase (F16P), fumarase (FUM), glucose-6-phosphate dehydrogenase (G6PD), glutamate oxalate transaminase (GOT), glyceraldehyde-3-phosphate dehydrogenase (G3PD), alpha-glycerophosphate dehydrogenase (GPD), hexokinase (HK), isocitrate dehydrogenase (IDH), leucine amino peptidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), mannose-6-phosphate isomerase (MPI), octanol dehydrogenase (ODH), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI), 6-phosphogluconate dehydrogenase (6PGD), superoxide dismutase (SOD) and xanthine dehydrogenase (XDH). Esterase loci were distinguished by the colors of the bands of activity on the gels (*Est*-red, *Est*-blue, *Est*-black), which indicate different affinities for alpha and beta ester substrates. Otherwise, when more than one system with the same enzymatic function was scoreable, they were numbered from the least anodal (or most cathodal) to the fastest migrating anodal system (e.g., HK-1 through HK-4). Histochemical stains were modified from Shaw and Prasad (1970), Brewer (1970), Selander et al. (1971) and Harris and Hopkinson (1976): the exact recipes used are given in Lacy (1982). For the more abundant species I assayed any loci that could be reliably scored on a tris-citrate buffer (modified from Whitt, 1970), O'Brien and MacIntyre's (1969) tris buffer, or one of Selander's (Selander et al., 1971) buffer systems. A lack of sufficient samples prevented the complete survey of some of the fly species, and so the most consistently scoreable enzymes were surveyed first. The loci surveyed for each fly species are given in Tables 2 and 3. Interspecific homologies of the sampled loci were inferred from similarities in mobilities, shared electromorphs in closely related species, like modes of inheritance (sex-linked vs. autosomal) and expression (monomeric vs. dimeric enzymes), and, in the case of esterases, common substrate specificities. Some electromorphs undoubtedly represent more than a single genetic allele (e.g.,

TABLE 2. *Allozymic variation in samples of mycophagous drosophilids from Ithaca, N.Y., as indexed by the expected heterozygosities. Species are listed in order from the most to least allozymically variable, as indicated by pairwise comparisons across those loci scored in common to the species pair.*

Locus	*Drosophila recens*	*D. putrida*	*D. falleni*	*D. testacea*	*D. tripunctata*
Acp	.497 (48)*	.455 (702)	.382 (540)	.140 (214)	.095 (20)
Adh	.153 (12)	.046 (214)	.109 (280)	.032 (182)	.000 (20)
Ao		.344 (24)	.373 (38)	.000 (54)	
Est-blue	.590 (42)	.680 (120)	.762 (3,102)		
Est-red		.556 (96)		.631 (104)	
Est-black		.260 (82)		.411 (120)	
Fum	.000 (23)	.141 (171)	.019 (212)	.000 (84)	.000 (26)
F16p	.000 (12)	.011 (182)	.146 (130)	.099 (154)	
Got	.049 (40)	.519 (110)	.145 (182)	.070 (110)	.411 (26)
Gpd	.000 (40)	.000 (120)	.016 (382)	.000 (134)	.000 (26)
G3pd	.000 (48)	.000 (142)	.008 (266)	.000 (144)	.000 (26)
G6pd		.022 (92)	.040 (149)	.131 (115)	.463 (11)
Hk-1		.112 (170)	.242 (224)	.395 (88)	
Hk-2		.268 (72)	.000 (84)	.000 (96)	
Hk-3		.421 (92)	.491 (106)	.478 (96)	.515 (20)
Hk-4	.000 (40)	.064 (212)	.034 (174)	.000 (240)	.000 (20)
Idh	.000 (48)	.134 (142)	.029 (1,370)	.531 (206)	.000 (20)
Lap	.629 (42)	.257 (150)	.689 (206)	.168 (134)	.331 (26)
Mdh-1		.075 (154)	.024 (336)	.000 (192)	.000 (26)
Mdh-2	.631 (48)	.009 (214)	.023 (426)	.000 (248)	.074 (26)
Me	.000 (40)	.046 (212)	.012 (320)	.045 (86)	.000 (26)
Mpi	.153 (12)	.208 (44)	.206 (44)		.335 (20)
Odh-3		.189 (68)	.457 (96)	.023 (86)	.463 (11)
6Pgd	.292 (12)	.255 (163)	.100 (193)	.641 (127)	.000 (26)
Pgi	.408 (42)	.362 (858)	.028 (354)	.500 (144)	.000 (26)
Pgm	.386 (48)	.559 (832)	.585 (3,810)	.493 (214)	.338 (52)
Sod	.000 (74)	.000 (46)	.033 (416)	.033 (426)	.000 (46)
Xdh		.528 (46)	.711 (340)	.648 (26)	
Mean	.191 (18)**	.233 (28)	.218 (26)	.210 (26)	.151 (20)

Locus	*M. dimidiata*	*M. claytonae A*	*D. ordinaria*	*M. claytonae B*	*D. duncani*
Acp	.532 (72)	.027 (74)	.180 (10)	.000 (72)	.000 (28)
Adh	.000 (142)		.000 (28)		.000 (28)
Ao					
Est-blue	.718 (44)				
Est-red					.438 (18)
Est-black					
Fum	.000 (134)	.000 (50)		.000 (32)	.500 (12)
F16p	.038 (102)				
Got	.000 (50)	.000 (70)	.000 (10)	.000 (40)	.000 (14)
Gpd	.041 (96)	.069 (56)	.000 (10)	.000 (34)	.000 (28)
G3pd	.032 (62)	.000 (14)		.000 (30)	
G6pd	.000 (29)				
Hk-1	.239 (36)				
Hk-2					
Hk-3	.375 (48)				
Hk-4	.000 (138)	.000 (26)		.000 (22)	
Idh	.000 (120)	.278 (18)	.480 (40)	.000 (28)	.095 (20)
Lap	.659 (96)	.642 (24)	.180 (20)	.515 (20)	.000 (20)
Mdh-1	.000 (132)	.000 (40)		.000 (60)	.000 (28)
Mdh-2	.086 (112)	.000 (72)	.000 (10)	.033 (60)	.043 (46)
Me	.000 (82)	.000 (72)	.000 (10)	.000 (48)	.000 (28)
Mpi					
Odh-3	.080 (48)	.000 (84)		.101 (56)	
6Pgd	.589 (41)	.000 (27)		.337 (42)	.000 (28)

TABLE 2. *Continued.*

Locus	*M. dimidiata*	*M. claytonae A*	*D. ordinaria*	*M. claytonae B*	*D. duncani*
Pgi	.000 (96)	.000 (24)	.000 (38)	.000 (20)	.000 (28)
Pgm	.255 (92)	.574 (40)	.339 (40)	.500 (52)	.095 (20)
Sod	.024 (168)	.000 (60)	.000 (16)	.000 (34)	
Xdh	.375 (48)		.000 (28)		
Mean	.176 (23)	.099 (16)	.098 (12)	.093 (16)	.084 (14)

* Number of alleles scored.
** Number of loci.

Coyne, 1976; Singh et al., 1976); yet unless cryptic alleles are more common in specialist species than in generalists this lack of resolution would introduce a conservative bias to any test of correlations with genetic variation.

Electromorph variation at each locus was quantified (separately for the Ithaca and Smoky Mts. populations) by the heterozygosity expected under Hardy-Weinberg equilibrium, $h = 1 - \Sigma p_i^2$, where p_i is the frequency of the ith electromorph. Within each geographic region (New York and Tennessee) very little spatial or temporal heterogeneity was observed in electromorph frequencies. Between-site and between-year heterogeneities rarely accounted for more than 10% of the total variation at a locus. Therefore, heterozygosities were calculated from electromorph frequencies pooled across samples from various collecting sites (within the Smoky Mts., or within the Ithaca area), several years, and many different mushroom hosts. Since some loci tend to show consistently high or low electromorph variability, at least among related taxa (see Johnson, 1974; and Tables 2 and 3), it is essential that identical sets of loci be used in any comparison of genetic variability. Within this constraint, I obtained a relative ranking of the amounts of electromorph variation in the fly species as follows: for each pair of fly species, their comparative ordering was determined by averaging h values across only those loci which were scored in both species. These dichotomous orderings were then combined to create a single ranking for the set of all species.

A measure of the effective breeding population sizes was also desired. Since the abundances of fly species in my collections vary over more than two orders of magnitude, large differences in migration rates would be necessary for them to be unrepresentative of relative population sizes.

To test the niche-variation hypothesis, Spearman rank correlations between the niche breadth statistics and heterozygosities were calculated. Rank correlations were also used to assess the relationships between genetic diversity and abundance, and between niche breadth and abundance. Non-parametric statistics are required because of the procedure used to create rank relationships of genetic variation, and because there would be no basis for assuming the underlying normal distributions required for parametric statistics.

RESULTS

Abundance and the three measures of niche breadth (H', C', and S) calculated from the Ithaca and Smoky Mts. collection data are given for each fly species in Table 1. Expected heterozygosities of electromorphs are listed in Tables 2 and 3. For the Smoky Mountains data set the following overall species ranking of genetic variation was consistent with all pairwise comparisons of means of the 11 to 24 loci scored in both species: *D. recens* > *D. falleni* > *D. tripunctata* > *D. putrida* > *D. testacea* > *M. claytonae A* > *D. duncani* > *D. ordinaria* > *M. dimidiata* > *M. claytonae B*. For the Ithaca populations the ranking of species consistent with all pairwise comparisons at 10 to 26 loci was: *D. recens* > *D. putrida* > *D. fal-*

TABLE 3. *Allozymic variation in samples of mycophagous drosophilids from the Great Smoky Mts., Tenn., as indexed by the expected heterozygosities. Species are listed in order from the most to least allozymically variable, as indicated by pairwise comparisons across those loci scored in common to the species pair.*

Locus	*D. recens*	*D. falleni*	*D. tripunctata*	*D. putrida*	*D. testaceea*
Acp	.448 (42)*	.446 (1,870)	.422 (86)	.308 (918)	.076 (280)
Adh	.049 (40)	.047 (84)	.018 (220)	.000 (64)	.000 (122)
Ao		.522 (48)	.740 (44)		.000 (48)
Est-blue	.745 (136)	.756 (110)	.795 (38)		
Est-red			.728 (42)	.751 (188)	.673 (92)
Est-black				.358 (134)	.278 (186)
Fum	.000 (61)	.189 (617)	.020 (100)	.164 (525)	.000 (67)
F16p	.184 (40)	.065 (90)	.044 (44)	.346 (42)	.021 (94)
Got	.227 (94)	.042 (142)	.448 (312)	.482 (142)	.074 (286)
Gpd	.082 (94)	.017 (118)	.014 (144)	.000 (228)	.041 (238)
G3pd	.000 (116)	.052 (186)	.000 (160)	.000 (144)	.000 (108)
G6pd	.406 (75)	.145 (26)	.223 (56)	.073 (53)	.077 (50)
Hk-1	.219 (56)	.165 (112)		.054 (72)	.540 (46)
Hk-2	.000 (80)	.105 (128)		.180 (70)	.081 (48)
Hk-4	.000 (76)	.020 (194)	.026 (388)	.027 (144)	.000 (184)
Idh	.000 (138)	.035 (286)	.049 (1,074)	.083 (164)	.449 (1,530)
Lap	.372 (96)	.627 (118)	.207 (680)	.080 (72)	.209 (44)
Mdh-1	.029 (68)	.000 (96)	.000 (862)	.021 (96)	.000 (96)
Mdh-2	.297 (132)	.021 (192)	.127 (1,260)	.000 (192)	.021 (192)
Me	.101 (94)	.018 (226)	.000 (96)	.091 (190)	.000 (118)
Mpi		.718 (48)	.620 (72)	.648 (102)	.607 (114)
Odh-3	.288 (24)	.539 (76)	.381 (34)	.080 (48)	.017 (116)
6Pgd	.066 (59)	.052 (226)	.291 (76)	.259 (872)	.267 (96)
Pgi	.444 (96)	.052 (226)	.044 (90)	.325 (2,610)	.473 (1,584)
Pgm	.357 (90)	.674 (2,002)	.442 (1,480)	.543 (2,738)	.544 (1,606)
Sod	.019 (102)	.008 (238)	.026 (382)		.000 (202)
Xdh	.448 (24)	.674 (72)	.659 (68)	.319 (66)	
Mean	.208 (23)**	.240 (25)	.264 (24)	.216 (24)	.178 (25)
Locus	*M. claytonae A*	*D. duncani*	*D. ordinaria*	*M. dimidiata*	*M. claytonae B*
Acp	.000 (90)	.000 (112)	.390 (384)	.486 (94)	.095 (20)
Adh		.000 (126)	.043 (136)	.000 (18)	
Ao			.041 (48)		
Est-blue			.759 (104)	.000 (14)	
Est-red		.633 (58)			
Est-black		.648 (18)		.000 (12)	
Fum	.043 (46)	.487 (50)	.000 (80)	.000 (36)	.000 (8)
F16p		.463 (44)	.095 (40)	.000 (30)	
Got	.000 (12)	.044 (44)	.261 (92)	.027 (72)	
Gpd	.061 (64)	.000 (112)	.000 (184)	.000 (18)	.000 (8)
G3pd		.000 (24)	.061 (160)	.000 (46)	
G6pd			.117 (176)	.057 (103)	
Hk-1		.000 (30)	.000 (120)		
Hk-2		.430 (52)	.060 (196)		
Hk-4	.000 (24)	.000 (60)	.025 (236)	.000 (26)	
Idh	.500 (64)	.051 (38)	.416 (542)	.041 (48)	.000 (8)
Lap	.476 (26)	.051 (38)	.235 (132)		.000 (12)
Mdh-1	.000 (48)	.000 (112)	.006 (352)	.000 (48)	.000 (18)
Mdh-2	.000 (48)	.049 (160)	.041 (570)	.000 (48)	.000 (18)
Me	.000 (44)	.000 (112)	.000 (136)	.000 (18)	.000 (10)
Mpi		.420 (50)			
Odh-3	.198 (18)	.309 (38)	.153 (184)		
6Pgd	.000 (13)	.030 (65)	.040 (97)	.539 (57)	.245 (7)
Pgi	.000 (26)	.000 (90)	.000 (140)	.258 (92)	.000 (12)
Pgm	.688 (64)	.195 (38)	.333 (756)	.043 (92)	.180 (20)
Sod		.054 (36)	.013 (300)	.088 (108)	
Xdh	.180 (40)	.148 (38)	.034 (116)	.040 (98)	.000 (8)
Mean	.143 (24)	.167 (24)	.130 (24)	.079 (20)	.043 (12)

* Number of alleles scored.
** Number of loci.

leni > *D. testacea* > *D. tripunctata* > *Mycodrosophila dimidiata* > *M. claytonae A* > *D. ordinaria* > *M. claytonae B* > *D. duncani*.

In Ithaca populations, heterozygosity was significantly correlated with one of the measures of niche breadth (H'), but not with the others, nor with abundance (Table 4). In the Smoky Mts. data, heterozygosity was correlated with all measures of niche breadth (H', C', and S) and with abundance (Table 4). Unfortunately, no nonparametric methods exist for the separation of independent components of a multiple correlation. Although valid significance levels cannot be obtained from parametric analysis of ranked data, a partial correlation analysis was applied to indicate qualitatively whether either niche breadth or abundance could alone account for the differences in genetic diversity (Table 5). The correlation of h with H' in the Ithaca data is little affected by the removal of any possible confounding effect of abundance. The correlations of the niche breadth measures with heterozygosity in the Smoky Mts. data are all reduced slightly when the effect of abundance is removed, while the abundance-heterozygosity correlation is virtually eliminated if any of the niche breadth measures are first factored out.

TABLE 4. *Spearman rank correlations among abundance* (N), *three measures of niche breadth* (H', C', *and* S), *and heterozygosity* (h) *of 10 species of mycophagous drosophilids collected in the Great Smoky Mts., Tenn. (above the diagonal), and around Ithaca, N.Y. (below the diagonal). Levels of significance (2-tailed test):* P < .05 (*), P < .01 (**), P < .001 (***).

Smoky Mts. / Ithaca	*N*	*H'*	*C'*	*S*	*h*
N		.830**	.745*	.772*	.648*
H'	.370		.842**	.942***	.830**
C'	.539	.648*		.857**	.818**
S	.256	.773*	.243		.754*
h	.491	.794**	.624	.511	

DISCUSSION

The significant correlations between electrophoretically detectable variation and some (Ithaca) or all (Smoky Mts.) measures of the diversity of mushroom species exploited by mycophagous drosophilid flies is in accordance with the niche-variation hypothesis. In these species, the genetic variation uncovered by standard starch gel electrophoresis would seem, therefore, to be maintained at least in part because natural selection favors different alleles, at these or closely linked loci, in different environments. Yet genetic variation was observed to be correlated with estimates of relative population sizes in the Smoky Mts. data, suggesting an effect of genetic drift on allele frequencies. Although the niche breadth-genetic variation correlations are reduced when abundance is first eliminated as a possible confounding factor, it seems unlikely that the correlations of abundance with both niche breadth and genetic variation could fully account for the association between the latter two. I would conclude, therefore, that selection acting on populations that use diverse resources, and perhaps also random events acting in finite populations, have important influences on the amount of genetic variation in these species.

Multiple niche polymorphism can be maintained under complete panmixia (e.g., Levene, 1953), with no consequential development of genetic differentiation between microhabitats (except that which results from a single generation of selection). Yet if there are partial mating barriers between conspecific populations inhabiting different hosts, gene differences may develop (e.g., Bush, 1969). Jaenike and Selander (1979) failed to find such differentiation in their study of *D. falleni*. Likewise, preliminary genetic data on *D. falleni* (*Pgm* locus), *D. putrida* (*Pgm*), *D. testacea* (*Pgm, Pgi, Idh*), *D. tripunctata* (*Pgm, Lap, Mdh*) and *D. ordinaria* (*Pgm, Acp*) do not show significant differences in gene frequencies among host species within study sites (G-tests of heterogeneity all nonsignificant). Only at the *Pgi* locus of *D. putrida* did I find statistically significant ($P < .05$) heterogeneity: between-mushroom gene differences accounted for 5% of the variation at this locus, as measured by the Shannon information index

TABLE 5. *Partial rank correlations of abundance (N) and measures of niche breadth (H', C', and S) with heterozygosity, after removal of each other variable. Values on the diagonals are rank correlations with heterozygosity, with no factor removed.*

		Variable removed							
		Ithaca				Smoky Mts.			
		N	*H'*	*C'*	*S*	*N*	*H'*	*C'*	*S*
Variable correlated with heterozygosity	*N*	.491	.349	.235	.434	.648	−.132	.101	.158
	H'	.757	.794	.655	.732	.688	.830	.455	.543
	C'	.490	.237	.624	.599	.660	.396	.818	.508
	S	.458	−.267	.474	.511	.524	−.149	.179	.754

(method of partitioning as in Lewontin, 1972).

The time since speciation, or since other bottle-necking events, could determine the amount of genetic variation if populations have not yet reached the equilibrium levels expected from either selection or mutation-drift balance (Somero and Soulé, 1974; Babbel and Selander, 1975). The very recently evolved endemic Hawaiian *Drosophila,* however, are not depauperate in genetic variation (Ayala, 1975), suggesting that genetic variation in these species is not still increasing toward equilibrium levels from small founder gene pools. A recent divergence of the sibling species of *M. claytonae* may account for their lack of polymorphism, though the moderate genetic distance between them (Nei's $D = .359$, over 17 loci) indicates that there has been sufficient time for considerable genetic change since their divergence.

Frequencies of bottlenecks subsequent to the speciation process are difficult to infer. Specialized drosophilid species may be more vulnerable to population crashes if their few host species failed to fruit in a given season, yet the bracket fungi on which they feed (e.g., *Polyporus, Grifolia, Laetiporus, Ganoderma*) often fruit year after year on the same trees, remain for weeks, months or longer (*Ganoderma* is perennial), and are the only mushrooms easily found during prolonged dry weather (pers. observ.). Most of the hosts of the generalized mycophagous flies are much less predictable in abundance, both spatially and temporally, perhaps subjecting their associated fauna to more severe fluctuations in population sizes.

Trophic resource stability has been suggested as a determinant of genetic variation, especially in pelagic environments (Ayala et al., 1975; Ayala and Valentine, 1979). Stable environments may allow partitioning of the niche by individuals within species, maintaining many narrow-function alleles; while temporal variation in trophic resources may force species into a fine-grained generalist adaptive strategy that maintains only a few functionally flexible alleles (Levins, 1965; Levins and MacArthur, 1966). The trophic resource stability hypothesis is not in as direct opposition to the niche-variation hypothesis as is sometimes assumed (e.g., Nevo, 1978): both predict more genetic variation when resource exploitation is coarse-grained than when it is fine-grained. They differ in that Van Valen (1965) discusses coarse-grained resource use arising when a species occupied many varied habitats, while Ayala and Valentine see temporal stability permitting coarse-grained habitat specialization.

Among the mycophagous drosophilids, trophic resource stability does not seem to have permitted many narrow-function alleles, nor have temporally varying environments led to fixation of all-purpose genotypes. The specialist species feed on bracket fungi that last for one or more fly generations (Lacy, in press); yet they are among the least variable of the drosophilid species that have been surveyed (compare with Selander, 1976). The trophic resources of the generalist species are highly

variable over time, but coarse-grained use of resources is imposed by limited mobility during pre-adult stages of the life cycle. These species are more polymorphic than most *Drosophila* (see Selander, 1976). Thus the trophic resource stability hypothesis does not seem applicable when life cycles impose coarse-grained use of varied resources as Van Valen had postulated.

While patterns of genetic variation in mycophagous Drosophilidae accord with the predictions of the niche-variation hypothesis, and suggest that stochastic effects may be important as well, many more studies are needed before we can evaluate the generality of the results presented here. Surveys of genetic variation are needed for sets of populations showing both ecological and evolutionary affinities. Various ecological guilds should be examined to reveal the interacting effects of environmental grain, temporal versus spatial heterogeneity, and population size and structure on genetic variation.

Summary

Among the mycophagous Drosophilidae in the eastern U.S., electrophoretically detectable variation correlates positively with the diversity of host mushroom species, in accordance with the niche-variation hypothesis. A correlation of genetic variation with abundance indicates that stochastic forces may also be important, but drift cannot fully account for the association between niche breadth and genetic variation. Neither the frequency of bottlenecks nor trophic resource stability seem adequate to explain the levels of variation observed in these species. Only by concentrating future efforts on organisms whose ecology is (or can be) well known, can we test how the roles of selection and drift vary with environmental, demographic or other parameters.

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