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GENETIC DIFFERENTIATION AMONG HOST-ASSOCIATED POPULATIONS OF THE GALLMAKER *EUROSTA SOLIDAGINIS* (DIPTERA: TEPHRITIDAE)

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Abstract.—*Eurosta solidaginis*, a gallmaking tephritid (Diptera), infests at least two species of *Solidago* in the eastern United States. We used horizontal starch gel electrophoresis of enzymes to examine whether populations on the two principal host plant species, *Solidago altissima* and *S. gigantea*, have diverged genetically. At the D-β-hydroxybutyrate dehydrogenase (HBDH) locus, the predominant allele in all nine populations from *S. altissima* ($HBDH^{1.00}$) was absent or uncommon in all but 1 of the 12 populations from *S. gigantea*. At the phosphoglucomutase locus (PGM), the most common allele in all populations was $PGM^{1.00}$, but the frequency of this allele was, with one exception, higher in populations from *S. gigantea* than in populations from *S. altissima*. Genetic heterozygosity was usually greater in populations from *S. altissima* ($\bar{H} = 0.028$) than in populations from *S. gigantea* ($\bar{H} = 0.009$). A phylogenetic tree derived from a genetic distance matrix clustered gallmaker populations from the same host plant together.

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Although some phytophagous insect groups are composed of polyphagous species, others are represented by monophagous taxa composed of host races or host-associated sibling species, each utilizing different sets of host plants (e.g., Ross, 1962; Bush, 1969*a*, 1969*b*, 1975; Knerer and Atwood, 1973; Wood, 1980; Menken, 1981; Scriber, 1983; Tauber and Tauber, 1989). This observation has led some evolutionary biologists to hypothesize that many phytophagous insects speciate by shifting (allopatrically or sympatrically) and adapting to new host plants (Bush, 1974, 1975; Price and Willson, 1976; Wood, 1980; Wood and Guttman, 1983; Rice, 1987). According to Bush's (1974, 1975) model, there are two components to a successful host shift. The first is a genetic change in host recognition, and the second is a genetic change increasing survivorship on the new host. Diehl and Bush (1989) have shown that host-associated populations can, in theory, diverge rapidly when mating is confined within preferred habitats.

Recent work (Abrahamson et al., 1989) on the native North American gallmaker *Eurosta solidaginis* Fitch (Diptera: Tephritidae) found host-association patterns that suggested that this species exists either as host races or as a complex of sibling species. Over the entire geographic range of *E. solidaginis* (New Brunswick to Texas to British Columbia, Wasbauer, 1972), the host plants that support this gallmaker include *Solidago altissima* (*S. canadensis* var. *scabra*), the diploid taxon of *S. gigantea*, *S. canadensis* (var. *canadensis*), and very occasionally the diploid taxon of *S. rugosa* (Felt, 1917, 1940; Uhler, 1951; Miller, 1959; Wasbauer, 1972; Abrahamson, unpubl. data). However, in central Pennsylvania, *E. solidaginis* occurs only on *S. altissima* (W. G. Abrahamson, pers. obs.), whereas in Maine it occurs on *S. gigantea*, *S. canadensis*, and occasionally *S. rugosa* (K. D. McCrea, pers. comm.). *Eurosta solidaginis* occurs on both *S. altissima* and *S. gigantea* in Minnesota (Wasbauer, 1972; P. A. Morrow, pers. comm.), New Hampshire (K. D. McCrea, pers. comm.), and Illinois (Lichter et al., 1990). The primary host throughout most of the gallmaker's range is *S. altissima*. In no-choice experiments, *S. altissima*-attacking flies from Minnesota and Pennsylvania rarely attacked *S. gigantea* and Minnesota *S. gigantea*-attacking flies were unwilling to oviposit in *S. altissima* (Abrahamson et al., 1989; Craig et al., in prep.)

Adult *E. solidaginis* emerge in Pennsylvania in mid to late May. After mating on a host plant, females typically inject a single

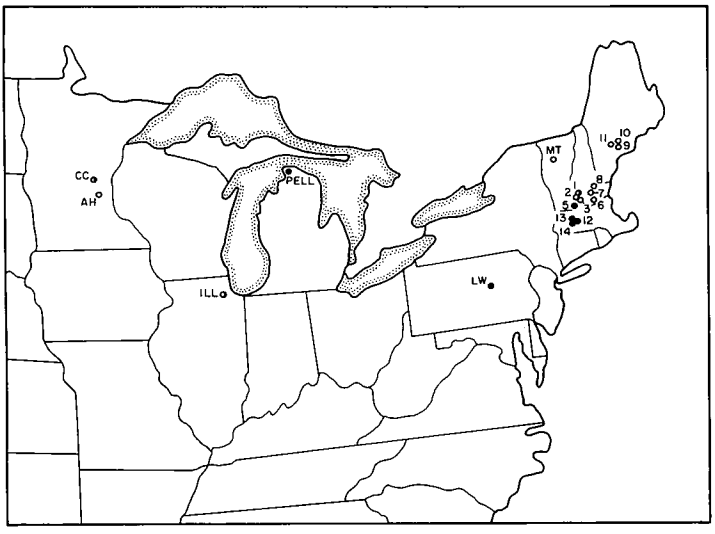

FIG. 1. Collection sites of *Eurosta solidaginis* in the eastern United States. Numbers are used for sites in New England (NE) except for Montpelier, VT. Half-filled circles represent collections from sympatric populations of *Solidago altissima* and *S. gigantea*: NE1, Keene, NH; ILL, DeKalb, IL; CC, Cedar Creek Natural Area, MN. Closed circles represent collections from isolated populations of *S. altissima*: LW, Lewisburg, PA; NE5, Winchester, NH; NE12, Athol, MA; NE13, Amherst, MA; NE14, Amherst, MA; PELL, Pellston, MI. Open circles represent collections from isolated populations of *S. gigantea*: NE3, Keene, NH; NE6, Hooksett, NH; NE7, Suncock, NH; NE8, Suncock, NH; NE9, Androscoggin, ME; NE10, Lewiston, ME; NE11, Durham, ME; MT, Montpelier, VT; AH, Arden Hills, MN.

egg into the unfolded leaves of a host plant's terminal bud (Abrahamson et al., 1989; Anderson et al., 1989). After hatching, the larva burrows through several millimeters of stem, settling just below the apical meristem (Beck, 1947). Larvae diapause within the gall during winter, then pupate in spring.

Solidago altissima and *S. gigantea,* both native to North America, have nearly identical eastern ranges; however, *S. gigantea* reportedly extends to the northwestern states and British Columbia while *S. altissima* extends only to the northcentral United States (Fernald, 1950; Croat, 1972; Semple et al., 1984). *Solidago altissima* is frequently found in old fields, remnant prairies, and roadsides, whereas *S. gigantea* is more frequent in damp areas (e.g., marsh or pond edges and ditches). In many areas, these two host plants occur sympatrically.

To determine whether genetic differentiation exists among host-associated populations of *E. solidaginis,* we used horizontal starch gel electrophoresis to analyze protein variation in 21 populations collected from *S. altissima* and *S. gigantea* in the eastern United States. The broad geographic area covered by these populations permitted the discrimination of resource-related variation versus geographic variation. Moreover, because ramets of *S. altissima* and *S. gigantea* clones often interdigitate, we were able to compare sympatric populations on alternative host plants.

MATERIALS AND METHODS

Eurosta solidaginis galls were collected from 9 *S. altissima* and 12 *S. gigantea* populations between October 1987 and April 1988 (Fig. 1). At three sites (NE1, ILL, and CC) the two host plants interdigitated or occurred immediately adjacent to one another in the same field and were considered to be sympatric. Third instar diapausing larvae or pupae were removed from galls in the laboratory and stored at −80°C until analyzed electrophoretically. Ming (1989) has recently recognized two subspecies of *E. solidaginis.* Based on Ming's (1989) key, all references to *E. solidaginis* in this study refer to the eastern subspecies *E. solidaginis* subsp. *solidaginis.*

From an initial survey, we obtained 21 enzymes that could be reliably scored: acid

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phosphatase (ACP), aconitase (ACON-1, -2), aldolase (ALD), diaphorase (DIA-1, -2), fumarase (FUM), glucose dehydrogenase (GDH), glyceraldehydephosphate dehydrogenase (GAP), glycerophosphate dehydrogenase (GPD), hexokinase (HK), D-β-hydroxybutyrate dehydrogenase (HDBH), indophenol oxidase (IPO), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), malic enzyme (ME), mannose phosphate isomerase (MPI-1, -2), phosphoglucomutase (PGM), and triosephosphate isomerase (TPI).

Allele designations were based on electrophoretic mobilities relative to the most common allele in the population from Lewisburg, PA, which was included as a standard on all gels. Genotype data were analyzed using the BIOSYS-1 program of Swofford and Selander (1981). We calculated mean heterozygosity per locus, percentage of polymorphic loci (0.99 criterion), and mean number of alleles per locus for each population. Conformance to Hardy–Weinberg equilibrium at each locus in each population was examined by calculating expected genotype frequencies using Levene's (1949) correction factor for small sample size and testing goodness-of-fit via chi-squared analyses. We assessed the genetic structure of *E. solidaginis* populations by using Wright's *F* statistics (Wright, 1965; Nei, 1973, 1977). The fixation index F_{ST} was directly tested for significance via the method of Workman and Niswander (1970). We also performed *G*-tests (Zar, 1984) to test for heterogeneity of allele frequencies among populations. Allele classes were pooled when necessary to minimize the number of cells with expected numbers less than five. We used the unweighted pair group method (Sokal and Sneath, 1963) to reconstruct the evolutionary relationship among the 21 *E. solidaginis* populations based on pairwise genetic distance measures calculated between populations from the allele frequency data. Nei's (1978) unbiased genetic distance (*D*) was used with UPGMA because this distance measure is proportional to the number of codon substitutions per gene and thus enhances the performance of UPGMA (Nei, 1987).

Results

Six of the 21 loci examined were polymorphic among *E. solidaginis* populations (Table 1). Average heterozygosity ($\bar{H}$) was higher for *E. solidaginis* populations from *S. altissima* ($\bar{H} = 0.028 \pm 0.016$ SD) than for *E. solidaginis* populations from *S. gigantea* ($\bar{H} = 0.009 \pm 0.010$). Variation at most loci in most populations conformed to Hardy–Weinberg expectations (122 of 126 χ^2 tests). Three *E. solidaginis* populations from sites where the alternate host plant occurred sympatrically were out of Hardy–Weinberg equilibrium at the HBDH locus (*S. gigantea* from CC had $P < 0.022$, *S. altissima* and *S. gigantea* from NE1 both had $P < 0.002$). These populations exhibited a lack of fit due to a small, but significantly higher than expected, number of homozygotes characteristic of populations on the alternative host plant. It is possible that the individuals homozygous for low frequency alleles represent the offspring of oviposition "mistakes" of females from the other host plant. Alternatively, the lack of fit to Hardy–Weinberg expectations may have been due to collection or scoring errors. The resolution of bands was poor in some of our early HBDH gels and it is possible that some heterozygotes were mistaken for homozygotes. The CC and NE1 populations were among the first populations analyzed in this study.

We found a high level of differentiation at the HBDH locus and statistically significant but lower levels of differentiation at four other loci (Table 2). The mean F_{ST} of 0.438 is among the highest intraspecific values reported for insects (Eanes and Koehn, 1978; Pashley et al., 1985*a*, 1985*b*; McCauley and Eanes, 1987; King, 1988). Significant heterogeneity among populations at TPI and GPD was attributable to differentiation in only two of the 21 populations (LW and CC). Heterogeneity at GAP was attributable to differentiation in one population (PELL).

Allele frequencies at HBDH and PGM exhibited statistically significant heterogeneity between populations of *E. solidaginis* from *S. altissima* and *S. gigantea* (Table 3). $HBDH^{1.00}$ was the most common allele in

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TABLE 1. Allele frequencies at six variable loci coding for enzymes in 21 populations of *Eurosta solidaginis*-attacking *Solidago altissima* and *S. gigantea*. *N* is the number of individuals sampled.

Solidago altissima

	Population								
Allele	LW	NE1	NE5	NE12	NE13	NE14	ILL	CC	PELL
GAP *N*	101	24	24	13	24	30	24	33	24
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.85
0.90	—	—	—	—	—	—	—	—	0.15
0.70	—	—	—	—	—	—	—	0.02	—
TPI *N*	101	24	24	13	24	30	24	33	24
1.00	0.80	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00
1.70	0.20	—	—	—	0.02	—	—	—	—
0.80	—	—	—	—	—	—	—	—	—
IDH *N*	101	24	24	13	24	30	24	33	24
1.00	0.99	1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00
1.15	0.01	—	—	—	0.02	—	—	—	—
0.80	—	—	—	—	0.02	—	—	—	—
HBD *N*	53	24	24	13	24	30	23	33	24
1.00	0.68	0.90	0.8	1.00	0.83	0.90	0.87	0.57	0.99
1.42	0.32	0.10	0.15	—	0.17	0.10	0.13	0.42	0.01
0.60	—	—	—	—	—	—	—	0.01	—
GPD *N*	99	24	24	13	24	30	24	33	24
1.00	0.82	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00
1.30	0.18	—	—	—	—	0.02	—	—	—
0.75	—	—	—	—	—	—	—	—	—
PGM *N*	100	24	24	13	24	30	24	33	24
1.00	0.74	0.81	0.71	1.00	0.60	0.77	0.75	0.82	0.80
1.20	0.22	0.17	0.25	—	0.34	0.20	0.25	0.10	0.12
0.78	0.04	0.02	0.04	—	0.06	0.03	—	0.08	0.08

Solidago gigantea

	Population											
Allele	NE1	NE3	NE6	NE7	NE8	NE9	NE10	NE11	MT	ILL	AH	CC
GAP *N*	18	20	14	24	20	24	24	24	24	24	17	25
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00
0.90	—	—	—	—	—	—	—	—	—	—	0.06	—
0.70	—	—	—	—	—	—	—	—	—	—	—	—
TPI *N*	18	20	14	24	19	24	24	24	24	24	17	25
1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.96	0.98	1.00	1.00	1.00	0.96
1.70	—	0.02	—	—	—	—	0.04	0.02	—	—	—	—
0.80	—	—	—	—	—	—	—	—	—	—	—	0.04
IDH *N*	18	20	14	24	20	24	24	24	24	24	17	25
1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.98	1.00	1.00
1.15	—	—	—	—	0.02	—	—	—	—	0.02	—	—
0.80	—	—	—	—	—	—	—	—	—	—	—	—
HBD *N*	17	20	14	24	19	24	24	24	24	24	17	25
1.00	0.19	0.02	—	0.02	—	—	0.02	—	0.61	0.29	0.40	
1.42	0.81	0.98	1.00	0.98	1.00	1.00	0.98	1.00	1.00	0.39	0.71	0.60
0.60	—	—	—	—	—	—	—	—	—	—	—	—
GPD *N*	18	20	14	24	19	24	24	24	24	24	17	25
1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.90	1.00	1.00	1.00	0.96
1.30	—	—	—	—	—	—	0.04	0.10	—	—	—	0.02
0.75	—	—	—	—	—	—	—	—	—	—	—	0.02
PGM *N*	17	20	14	24	19	24	24	24	24	24	17	25
1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.90	0.97	0.94
1.20	—	0.02	—	—	—	—	—	—	0.02	0.02	0.03	—
0.78	—	—	—	—	—	—	—	—	—	0.08	—	0.06

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TABLE 2. Wright's F_{ST} estimates and chi-square analysis (Workman and Niswander, 1970) of variable loci for all populations of *Eurosta solidaginis* (** $P < 0.005$).

Locus	F_{ST}	Approx. chi square	N
GAP-1	0.105	233.1**	555
TPI-1	0.114	126.3**	554
IDH-1	0.020	44.4	555
HBDH-1	0.623	1,308.3**	525
GPD-1	0.109	240.7**	552
PGM-1	0.139	306.9**	552
Mean	0.438	—	—

all *E. solidaginis* populations from *S. altissima* (Table 1). With one exception, the most common allele in populations from *S. gigantea* was HBDH$^{1.42}$. The single exception was the ILL population where HBDH$^{1.00}$ was the most common allele. PGM allele frequencies display a similar consistency. The most common allele (PGM$^{1.00}$) was the same in all populations, but the frequency of PGM$^{1.00}$ was, with one exception, higher in populations from *S. gigantea* than in populations from *S. altissima* (Table 1). The exceptional population was from NE12 where PGM$^{1.00}$ was fixed in *Eurosta* from *S. altissima.*

Populations on *S. altissima* were significantly heterogeneous at HBDH and PGM due to geographic variation (Tables 1, 3). Allele frequencies of New England populations were more similar to one another than to allele frequencies of other populations. When NE12, which was fixed for one allele at all loci, was removed from the analysis, the New England populations on *S. altissima* were genetically homogeneous (Table 3). Populations from *S. gigantea* also exhibited geographic variation. Excluding NE1, populations from New England were almost devoid of variation at HBDH and PGM. Northcentral populations were much more variable and displayed significant heterogeneity in HBDH allele frequencies (Tables 1, 3).

The three paired *S. altissima-S. gigantea* comparisons provided further evidence of allele frequency differences at HBDH and PGM between populations on different host plants. In each paired comparison the frequency of HBDH$^{1.00}$ was higher in the *S. altissima* sample than in the *S. gigantea* sample, although the difference was not significant at CC (Tables 1, 3). Similarly, in each paired comparison the frequency of PGM$^{1.00}$ was higher in the *S. gigantea* sample than in the *S. altissima* sample, although the difference was not significant at ILL (Tables 1, 3).

TABLE 3. Allele frequencies and *G*-tests of frequency heterogeneity at HBDH and PGM among *Eurosta solidaginis* populations on both host plants at all sites, within host plants, and on sympatric host plants (* $P < 0.05$, ** $P < 0.005$). Average frequencies are presented for all sites and among sites.

	HBDH$^{1.00}$	P	PGM$^{1.00}$	P
All sites				
S. altissima	84.3		77.8	
and		**		**
S. gigantea	13.0		98.1	
Among *S. altissima* sites				
All populations	84.3	**	77.8	**
New England	89.6	n.s.	77.8	**
New England w/o NE12	87.0	n.s.	72.2	n.s.
Northcentral	81.0	**	79.0	n.s.
Among *S. gigantea* sites				
All populations	13.0	**	98.1	*
New England	2.8	**	99.5	n.s.
New England w/o NE1	0.01	n.s.	99.4	n.s.
Northcentral	43.3	*	93.7	n.s.
Between *S. altissima* and *S. gigantea* at sympatric sites:				
NE1				
S. altissima	90.0		81.2	
and		**		*
S. gigantea	19.5		100.0	
CC				
S. altissima	57.0		82.0	
and		n.s.		*
S. gigantea	40.0		94.0	
ILL				
S. altissima	87.0		75.0	
and		**		n.s.
S. gigantea	61.0		89.8	

Two major groups were defined by UPGMA clustering of Nei's *D* (Fig. 2). One group contained all the populations from *S. altissima* plus the *S. gigantea* population from ILL. The other group consisted of populations from *S. gigantea.*

DISCUSSION

Populations of *E. solidaginis* associated with *S. altissima* exhibit clear allele frequency differences from *E. solidaginis* associated with *S. gigantea* (Table 1). The pat-

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tern is consistent over a wide geographic area and persists even when the host-plant populations interdigitate with one another in the same fields (see Results and Table 3). Thus the pattern is resource-related and not attributable to geographic variation.

Based on currently available evidence, the most likely explanation for the genetic differences between *S. altissima*- and *S. gigantea*-associated *E. solidaginis* is limited gene flow due, in part, to differences in host plant preference and phenology. In no-choice experiments, central Pennsylvania *E. solidaginis,* which occur only on *S. altissima,* strongly preferred to oviposit in *S. altissima* rather than in *S. gigantea, S. canadensis,* and *S. rugosa* (Abrahamson et al., 1989), three other species of *Solidago* that occur sympatrically with *S. altissima* in central Pennsylvania. Recent work (Craig, Itami, and Abrahamson, in prep.) has shown that Minnesota populations of *Eurosta* that attack *S. gigantea* emerge, on average, 10 days earlier than *Eurosta* that infest *S. altissima* and these sympatric taxa strongly prefer to mate on and oviposit in their respective host plant species.

Assuming that genetically controlled host preference differences explain the genetic differentiation between *E. solidaginis* populations on different host plants, the question remains as to the direction of the host shift, and how often and under what geographic circumstances it occurred. Patterns of genetic variation and host-plant association point to *S. altissima* as the ancestral host-plant species of *E. solidaginis. Solidago altissima* attacking *Eurosta* were considerably more variable than those associated with *S. gigantea.* Furthermore, *E. solidaginis* is associated with *S. altissima* throughout the majority of the plant's range (W. G. Abrahamson, pers. obs.). In some areas where both *S. altissima* and *S. gigantea* occur, such as central Pennsylvania, the sole host plant is *S. altissima.*

The estimates of phylogenetic trees (Fig. 2) cluster *E. solidaginis* from *S. altissima* and *E. solidaginis* from *S. gigantea* on separate branches. The only ambiguity was the placement of the *S. gigantea* population from ILL. These results suggest that the initial shift onto *S. gigantea* took place in a single geographic area and that the resulting

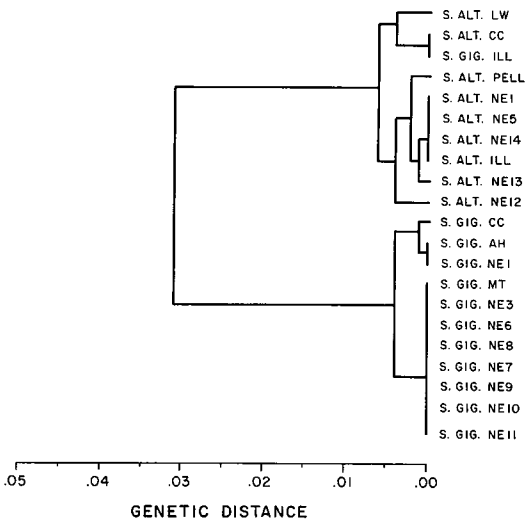

FIG. 2. Estimation of a phylogenetic tree for 21 populations of *Eurosta solidaginis* collected from *Solidago altissima* and *S. gigantea* based on UPGMA (Sneath and Sokal, 1973) clustering of the Nei's (1978) genetic distance matrix (matrix is available from authors by request).

population(s) was the progenitor for all current *S. gigantea*-associated populations. The alternative hypothesis, that shifts have occurred independently in different geographic regions, should lead to trees in which populations from the same geographic region cluster together, regardless of host-association. The absence of *E. solidaginis* infestations on *S. gigantea* in some regions where both the host plant and the fly are abundant provides further evidence that a successful host shift is a rare event and lends credence to the idea that the shift has occurred infrequently in the past, perhaps in a single geographic area.

The finding of host-specific differentiation in allozyme frequencies has been rare in studies of natural populations and the scarcity has been used to argue against the importance of sympatric speciation via host race formation (Mitter and Futuyma, 1983). Thus a positive result, such as that reported here, represents potentially important evidence for the role of host shifts in genetic differentiation and ultimately speciation (Bush and Howard, 1986), even though much work remains to be done to fully understand the conditions under which the host shift(s) occurred and the current level of in-

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terbreeding between the host-associated populations.

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