Ecology and Genetics of Ephemeral Plant Populations: *Eichhornia paniculata* (Pontederiaceae) in Northeast Brazil

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Organisms adapted to ephemeral habitats often display striking variation in population size owing to environmental stochasticity. Here we investigate the genetic consequences of demographic variation in *Eichhornia paniculata* (Pontederiaceae), an annual tristylous aquatic that inhabits ephemeral pools, ditches, and low-lying pastures in the seasonally arid caatinga region of northeast Brazil. Annual censuses of populations demonstrated striking temporal variation in census number. There was no association between population size and heterozygosity at allozyme loci, but a significant positive relation was evident with the harmonic mean of population size. Both population-size measures were positively associated with stylemorph diversity. Large populations were more likely to contain the three style morphs at similar frequencies than small. The amount of heterozygosity within populations was positively correlated with the local density of populations in a region, presumably reflecting greater opportunities for gene flow. Bottlenecks in population size were not severe enough to reduce genetic variation, and population persistence versus local extinction was unrelated to the amount of allozyme variation within populations. The demographic and genetic characteristics of ephemeral populations may be largely irrelevant to survival where catastrophic changes to local environments through drought, flooding, and human disturbance often occur.

Organisms of ephemeral or short-lived habitats usually possess distinctive ecological, demographic, and life-history characteristics. The distribution of populations across the landscape is often highly fragmented, with large spatial and temporal variation in population size and density. Periods of small population size commonly occur owing to frequent cycles of colonization and extinction and the finite size of many ephemeral habitats. When suitable conditions prevail, however, rapid population growth and large population sizes are often achieved. The unpredictable nature of many habitats occupied by ephemeral populations results in high environmental and demographic stochasticity (Hanski 1987). Plant adaptation in such environments often involves the evolution of the annual habit, well-developed phenotypic plasticity, high fecundity, and the capacity for uniparental reproduction usually through self-fertilization. These features of the ecology of ephemeral plants have important consequences for the genetics of populations, particularly the maintenance of genetic diversity (Baker 1974; Barrett 1992; Brown and Marshall 1981; Rice and Jain 1985).

Since stochastic forces play a dominant role during episodes of colonization, this should be reflected in the patterns of genetic variation within populations of plants adapted to ephemeral environments. The most elementary prediction is that small populations should contain less genetic diversity than large populations because of genetic drift. However, surveys of population genetic structure at allozyme loci have commonly revealed uniformly low levels of genetic diversity regardless of population size (reviewed in Barrett and Shore 1989; Warwick 1990). Many of the species examined are annual, predominantly selfing weeds and the extensive regional monomorphism observed likely results from historical bottlenecks associated with long-distance migration (reviewed in Barrett and Husband 1991). Because of genetic monomorphism these species have not been particularly informative for evaluating how population structure and spatial and temporal fluctuations in population size influence genetic diversity. In addition, few studies of plant

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populations have combined both demographic and genetic data to examine the association between genetic variation and population persistence or how bottlenecks directly influence genetic variation (but see Martins and Jain 1979; Polans and Allard 1989; Schwaegerle and Schaal 1979). Despite a well-developed theoretical framework for these issues (e.g., Hedrick et al. 1976; Lacy 1987; Nei et al. 1975; Watterson 1984), there is still a paucity of empirical studies, particularly for natural populations of plants.

Here we present the results of a study of the ecology and genetics of an ephemeral plant species with sufficient genetic diversity within populations that we can address issues concerned with the genetic consequencies of population-size fluctuations. *Eichhornia paniculata* (Spreng.) Solms-Laubach (Pontederiaceae) is an annual, emergent aquatic that inhabits ephemeral pools, ditches, and low-lying pastures in seasonally arid northeast Brazil (Barrett 1985). Atypically for most annuals, the species is largely tristylous and outbreeding in this part of its range. Hence populations maintain considerable polymorphism at allozyme loci as well as at genes controlling mating type. We have used this variation to ask several questions not addressed before in genetic studies of ephemeral plant populations: (1) What is the relation between measures of population size and genetic variation and, more specifically, how useful is a single census of population size for predicting levels of genetic variation? (2) Is the level of genetic diversity within a population influenced by the density of populations within an area? To what extent should we take account of the regional distribution of populations when considering levels of variation within local populations of a species? (3) What evidence exists that population bottlenecks reduce genetic variation? Theory predicts that bottlenecks result in the loss of genetic variation, particularly following long-distance migration; however, it is unclear how often this occurs in situ via fluctuations in population size. (4) Is population persistence versus extinction associated with levels of genetic variation? In particular, how important is the amount of variation within a population in the face of environmental stochasticity? Before addressing these questions we begin by giving a brief overview of the natural history of *E. paniculata* in northeast Brazil and provide evidence of the striking changes in population size that the species displays in this region.

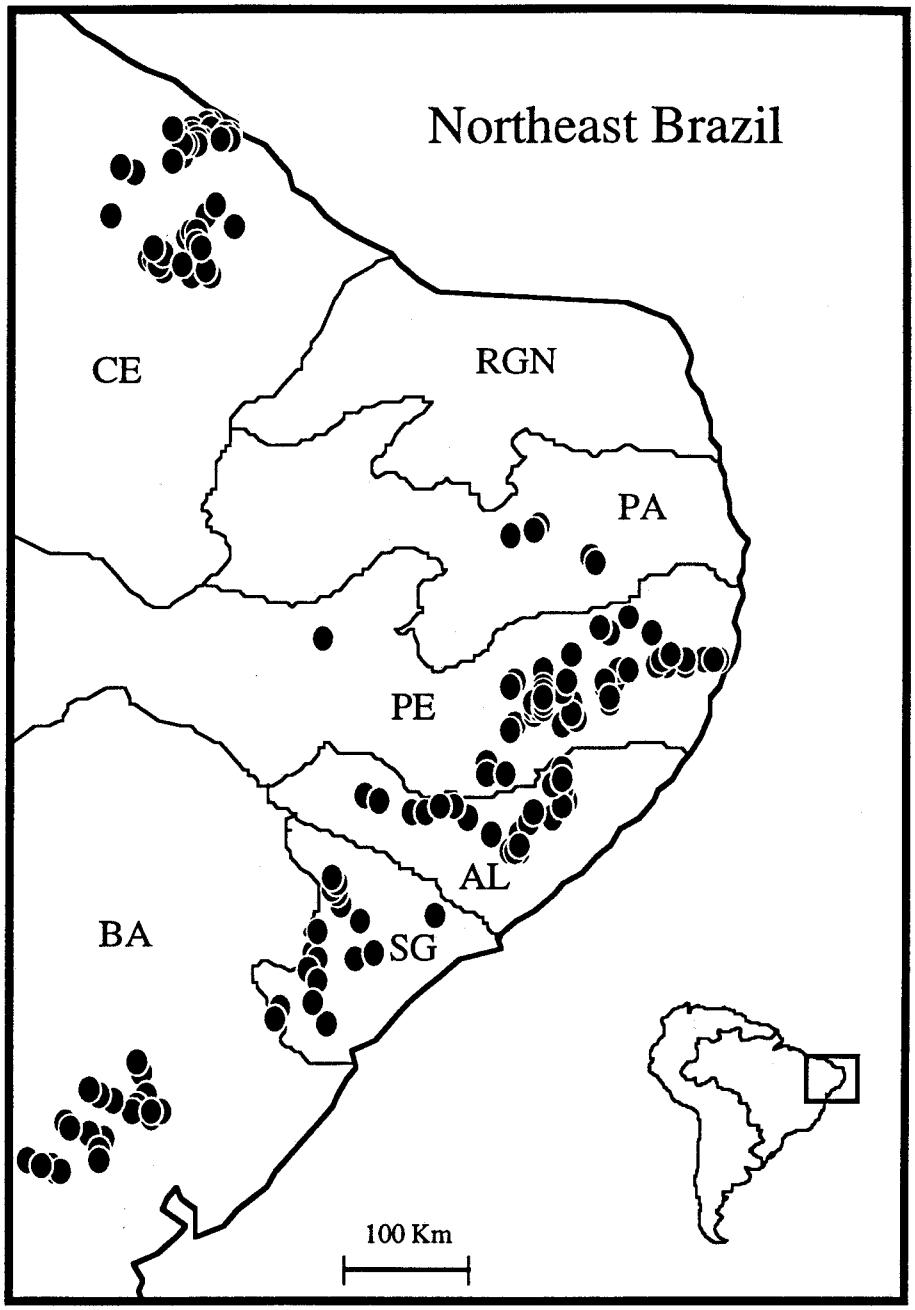

Figure 1. The distribution in northeast Brazil of *E. paniculata* populations sampled in this study. The states of northeast Brazil are indicated: CE—Ceará, RGN—Rio Grande de Norte, PA—Paraíba, PE—Pernambuco, AL—Alagoas, SG—Sergipe, BA—Bahia. Populations were sampled over the entire geographical range of the species in northeast Brazil.

Natural History

E. paniculata occurs commonly in seasonal aquatic habitats throughout much of northeast Brazil (Figure 1). The region is extremely arid and mostly covered by thorn scrub (caatinga) with agriculture and human settlement resulting in considerable disturbance. Rainfall is highly unpredictable and unevenly distributed in space and time, giving it one of the highest coefficients of variation of annual rainfall in the world (Nimer 1972). The seasonal pools and ditches suitable for *E. paniculata* are usually dry for most of the year, but with precipitation (usually between March–May) standing water occurs enabling population establishment. Habitats of *E. paniculata* are usually discrete and represent small islands in space and time in a seasonally arid landscape.

Due to the sparse distribution of sites suitable for *E. paniculata* and their ephemeral nature, only a narrow window of time is available for germination, growth, repro-

duction, and dispersal. Populations behave primarily as annuals and, depending on water depth, occur in monospecific stands around the periphery of ponds, or if shallow, throughout the entire site. Most plants flower synchronously and continue flowering until site conditions deteriorate through desiccation. While most ponds and ditches colonized by *E. paniculata* are ephemeral, they may reappear for several consecutive generations. Alternatively they may be temporarily unsuitable for germination because of limited rainfall or become destroyed by flooding, erosion, or through human activities. As a result of the ecological instability of habitats occupied by *E. paniculata* the species displays dramatic year-to-year fluctuations in population size (Figure 2).

Studies over the past decade on the population biology of *E. paniculata* in northeast Brazil provide useful background information for the current investigation. These can be briefly summarized as follows (for further details see Barrett et al. 1989; Husband and Barrett 1992a,b, 1993, unpubished data). Annual censuses and surveys of suitable aquatic habitats throughout northeast Brazil indicate that, on average, 22% of sites present are occupied. Patch occupancy varies widely and is positively correlated with the density of available habitats. The annual extinction rate of populations is 34%, owing to drought, disturbance, and severe flooding. The local extirpation of populations is independent of population size or age, undoubtedly reflecting the importance of environmental stochasticity in determining the persistence of populations. Population sizes range from a few plants to several thousand, with approximately half of all populations containing less than 100 individuals.

The role of the seed bank in maintaining populations of *E. paniculata* from year to year is problematic. The majority of populations that are absent from a given site the year after a census do not reappear in subsequent years. Experimental studies indicate that populations possess relatively weak seed dormancy, with 70% or more of seeds germinating within a month of harvest from the plant (Barrett SCH and Husband BC, unpublished data). Nevertheless, a few cases have been observed where populations reappear, following a year from which they were absent from a site, indicating the presence of some seed bank. For the purposes of this study we assumed that populations that did not reappear at a site after 2 years were locally extirpated.

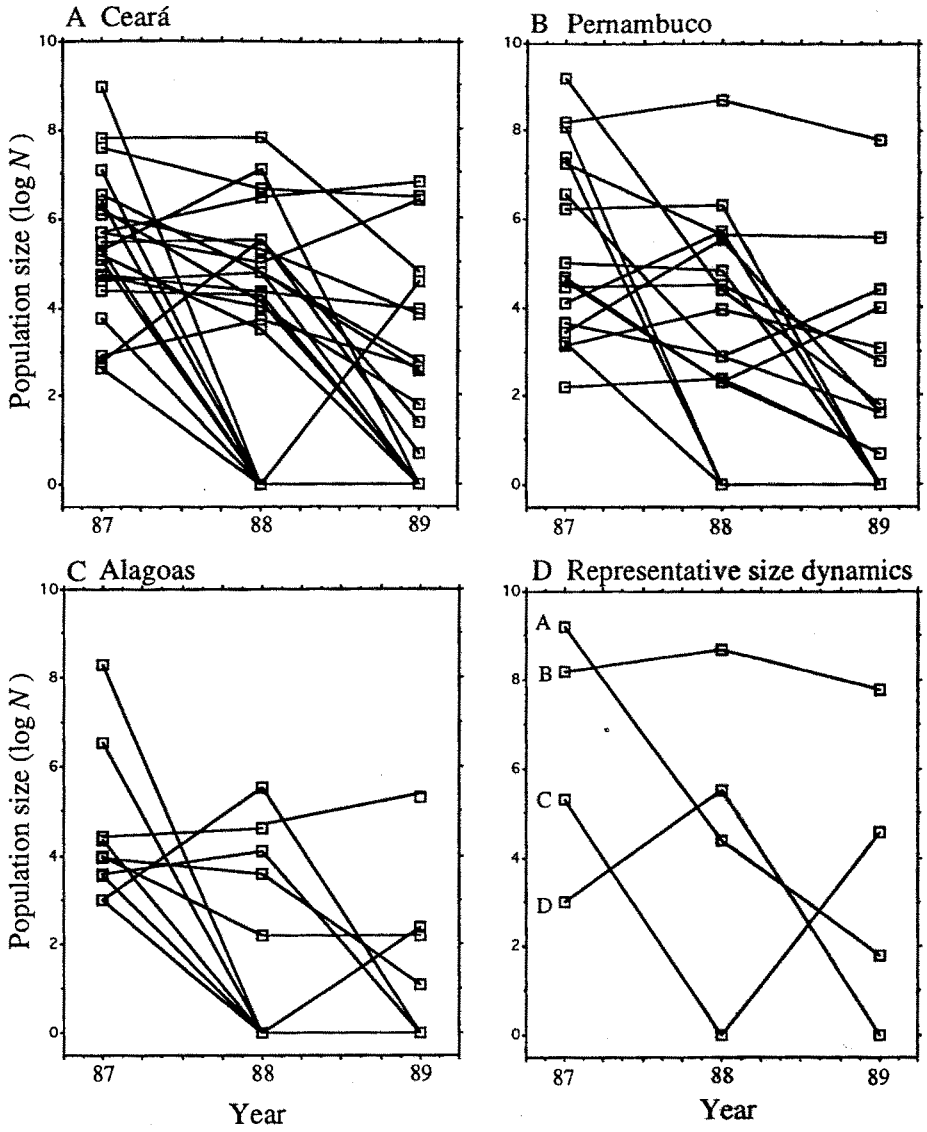

Figure 2. Changes in the size of *E. paniculata* populations over a 3-year period (1987–1989) in the states of (A Ceará, (B) Pernambuco, and (C) Alagoas. Panel (D) illustrates four representative populations showing differen size dynamics: A—a steadily declining population, B—a stable population, C and D—populations with large fluc tuations in size. Note the large number of populations experiencing population crashes; in many cases these resul in the local extirpation of populations.

Genetic measures of effective population size (N_e) were estimated in 10 populations based on temporal variation in allele frequency at allozyme loci (see Waples 1989 for method). Values ranged from 3.4 to 70.6 with a mean of 15.8, which is approximately 10% of the census number (Husband and Barrett 1992a, 1995; but see Nunney 1995). Estimates of gene flow inferred from genetic differentiation at 24 isozyme loci among 44 populations were low and strongly influenced by range substructure within northeast Brazil (Husband and Barrett 1993). Population differentiation decreased and gene flow increased with successive reductions in the spatial scale of populations sampled (e.g. from a rangewide estimate of $Nm = 0.3$ to $Nm = 0.58$ for neighboring populatio pairs within local areas). The small effec tive population sizes and low levels o gene flow imply that genetic drift plays a important role in the genetics of *E. pan culata* populations. Studies of mating-sys tem variation and the maintenance of tr styly support this view.

Populations of *E. paniculata* in northeas Brazil are primarily bee pollinated and ex hibit a wide range of mating systems fror predominant outcrossing to high levels c selfing (mean $s = 0.26$, range 0–0.81, $N =$ 44; Barrett and Husband 1990; Barrett e al. 1993). Increased selfing in population is associated with the loss of styl

morphs, particularly the short-styled morph, and the spread of self-pollinating mid-styled variants (Barrett et al. 1989). Surveys of style morph frequencies in 167 populations indicate that 29.3% of populations are missing at least one style morph. Genetic drift is implicated in the loss of morphs from populations (Husband and Barrett 1992a,b). Populations missing morphs are significantly smaller than those that are tristylous and the observed pattern of morph loss is that predicted by stochastic models of the influence of finite population size on the two-locus genetic system governing tristyly (reviewed in Barrett 1993).

Methods

Population-size data presented in this study were obtained from surveys of *E. paniculata* populations in northeast Brazil in 1982, 1987, 1988, and 1989 in the states of Ceará, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia. We sampled the vast majority of populations encountered in each survey and recorded their locations so as to enable relocation in future surveys. Virtually all (96%) of the previously sampled sites were relocated each year for study; however, because of the ephemeral nature of the habitats, populations were often absent from the site. Of the 167 populations sampled over the four surveys, 112 were sampled once, 28 were sampled twice, 24 were sampled three times, and 3 were sampled in all four surveys. Population size (N) was estimated each time a population was sampled, based on at least two independent estimates of the number of reproductive individuals. If a population contained less than 250 individuals, the entire population was censused. Since *E. paniculata* does not exhibit clonal propagation individual genets are easily distinguished. Since most populations comprise a single cohort of plants that germinate and flower synchronously, a single visit was sufficient to estimate population size.

Two classes of genetic variation (style morph and allozyme diversity) were measured in populations censused for size. In all populations the frequencies of style morphs were obtained following methods described in detail in Barrett et al. (1989). Morph frequencies within populations in a given year were summarized as a single measure of diversity or evenness (O) described by the position of a population on a triangular plot. Each side of the triangle represents a different style morph and the distance a population is plotted from a given side is in direct proportion to the frequency of the morph within the population. The Euclidean distance between a given population and the point of equal frequency (isoplethy) was normalized by the maximum possible distance (0.6667) such that evenness measures ranged from 0 for monomorphic populations to 1 for tristylous populations with equal frequencies of the three morphs (see Husband and Barrett 1992b for further details).

Genetic variation at allozyme loci was investigated for a subset of the populations discussed above. A sample of open-pollinated progeny were obtained from 49 populations distributed among the six states. In each population an average of 26 seed families (range 4–59) and 6 plants per family (range 1–20) were sampled. Polymorphisms at 24 allozyme loci were later assayed using starch-gel electrophoresis. Further details of sampling, sample sizes, and electrophoretic methods are given in detail in Barrett and Husband (1990) and Husband and Barrett (1993). Standard population genetic parameters were obtained for each population (see earlier articles). For the purpose of this study we present data on the observed frequency of heterozygotes (H_o) averaged over all loci sampled, the mean number of alleles per locus (A), and the percentage of loci that were polymorphic (P). We chose to examine H_o rather than H_e because this measure incorporates both changes in allele frequency and the effects of inbreeding.

Results

Relation Between Population Size and Genetic Variation

There was no significant relation between the log of the number of reproductive individuals in a population (N) and the observed heterozygosity (H_o) at allozyme loci (Figure 3A). A similar pattern was also observed with respect to the percent of loci that were polymorphic ($P - r_s = 0.19$, $P > .1$, $n = 49$) and the mean number of alleles per locus ($A - r_s = 0.21$, $P > .1$, $n = 49$). For populations sampled on more than one occasion it was possible to calculate the harmonic mean of population size. A significant positive relation was revealed between the log of the harmonic mean of population size and observed heterozygosity (Figure 3B). While the relations between the log of the harmonic mean of population size and P and A were nonsignificant ($P - r_s = 0.31$, $P > .05$, $n = 33$; $A - r_s = 0.34$, $P > .05$, $n = 33$), in each

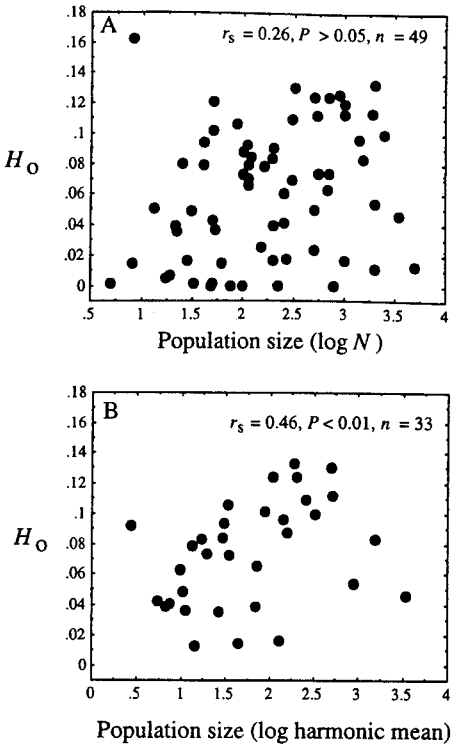

Figure 3. The relation between observed heterozygosity (H_o) at 24 allozyme loci and **(A)** log population size (N), and **(B)** log harmonic mean of population size in *E. paniculata* from northeast Brazil; n = the number of populations sampled. The statistical association presented is Spearman's rank correlation.

case the correlation was stronger than was observed with N. Both measures of population size were positively correlated with (O), a measure of style-morph evenness (Figure 4A,B). Larger populations were more likely than small to contain the three style morphs at similar frequencies. Despite the substantially smaller sample of populations for which the harmonic mean could be calculated compared to the total sample (N = 167 versus 55), a stronger positive relation with observed heterozygosity was evident.

Influence of Local Density of Populations on Genetic Variation

To investigate the influence of the local density of populations on genetic variation within populations, the total sample of 49 populations from which allozyme variation was assayed were grouped into 19 separate regions. These were determined based on road transects through areas chosen for uniformity in landscape patterns. The average transect length was 113 km. We examined the relation between population density and heterozygosity, while controlling for variation in population size using a partial correlation analysis. A linear regression between mean pop-

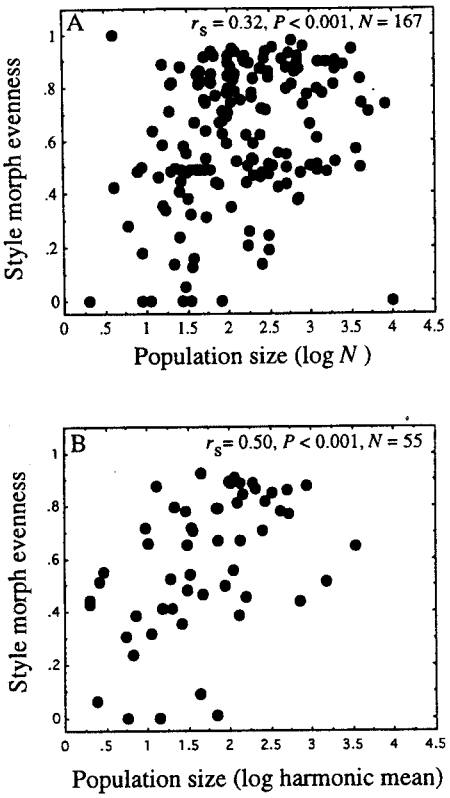

Figure 4. The relation between style-morph evenness (O) and **(A)** log population size (N), and **(B)** log harmonic mean of population size in *E. paniculata* from northeast Brazil; n = the number of populations sampled. See text for details concerning the measure of style-morph evenness. The statistical association presented is Spearman's rank correlation.

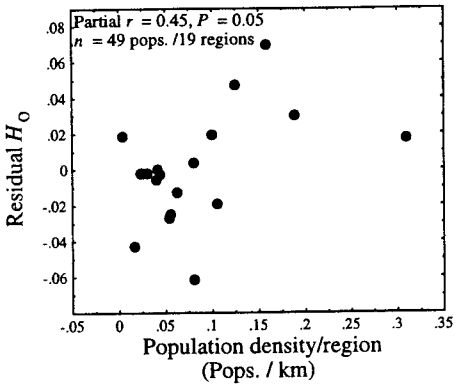

Figure 5. The relation between observed heterozygosity (H_o) within populations and the density of populations within a region in *E. paniculata* from northeast Brazil. Allozyme variation was assayed at 24 loci in 49 populations. The populations were grouped into 19 regions within northeast Brazil differing in density. Population density was estimated by the number of populations per kilometer from road transects, see text for further details. The statistical association presented is Spearman's rank correlation.

ulation size and observed heterozygosity per region for the 19 regions was conducted. The residual heterozygosity from this analysis was then regressed in a second analysis against population density per region. There was a significant positive correlation between observed heterozygosity and population density within a region (Figure 5). Populations occurring along transects with high population densities maintained more heterozygosity than those along low-density transects, after controlling for the effects of population size. This analysis was also conducted for P and A; however, no significant correlation was observed between these measures and the density of populations within a region ($P - r_s = 0.31, P > .1, n = 19$; $A - r_s = 0.34, P > .1, n = 19$).

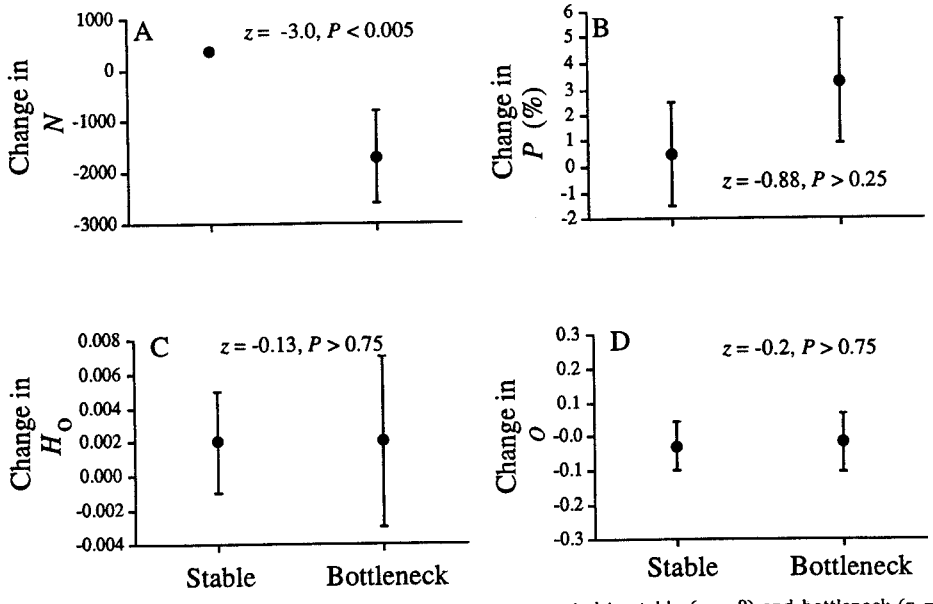

Figure 6. Comparisons of genetic variation over a two-year period in stable (n = 9) and bottleneck (n = 5) populations of *E. paniculata* in northeast Brazil. Parameters compared in the two groups of populations are mean changes from year 1 to year 2 for **(A)** population size (N), **(B)** percent of allozyme loci polymorphic (P), **(C)** observed heterozygosity (H_o) and **(D)** style-morph evenness (O). Bars are two standard errors. The apparent absence of variation in the size of stable populations in **(A)** results from the scale used for changes in N. All statistical comparisons involved nonparametric Mann-Whitney U tests.

Effects of Population Bottlenecks on Genetic Variation

To investigate whether a sharp reduction in population size reduces genetic variation in *E. paniculata* we compared populations that remained stable in size over a 2-year period with those that experienced a bottleneck in the second year. We classified populations as stable if their population sizes changed by 10% or less over the 2 years and as experiencing a bottleneck if population size in year 2 was reduced to 10% or less of the census number in year 1. There were no significant differences in mean percent polymorphic loci (P), observed heterozygosity (H_o), or style-morph evenness (O) in stable and bottleneck populations (Figure 6). A similar result was obtained (data not shown) for the mean number of alleles per locus (A-stable populations; mean change in A = 0.02, SE = 0.08; bottleneck populations: mean change in A = 0.08, SE = 0.06, $z = -0.61, P > .50$).

Genetic Variation and Population Persistence

To examine whether populations that are locally extirpated from a site differ genetically from those that persist we examined variation in a group of 33 populations of which 11 were absent the following year and 22 remained. Figure 7 compares mean population sizes, measures of allozyme variation (P, H_o), and the percentage of populations that were trimorphic for the two groups in year 1. There were no significant differences in the size of populations or in the amounts of allozyme variability maintained in the two types of populations. Data for A are not presented in Figure 7 but also exhibited no relation to population persistence (A for populations present: mean in year 1 = 1.32, SE = 0.02; populations absent: mean in year 1 = 1.29, SE = 0.04, $z = -0.54, p > .50$). A significant effect of style-morph structure on the likelihood of local extirpation was evident; tristylous populations were more likely to persist than those missing one or two style morphs.

Discussion

The relation between population size and genetic variation at allozyme loci has been

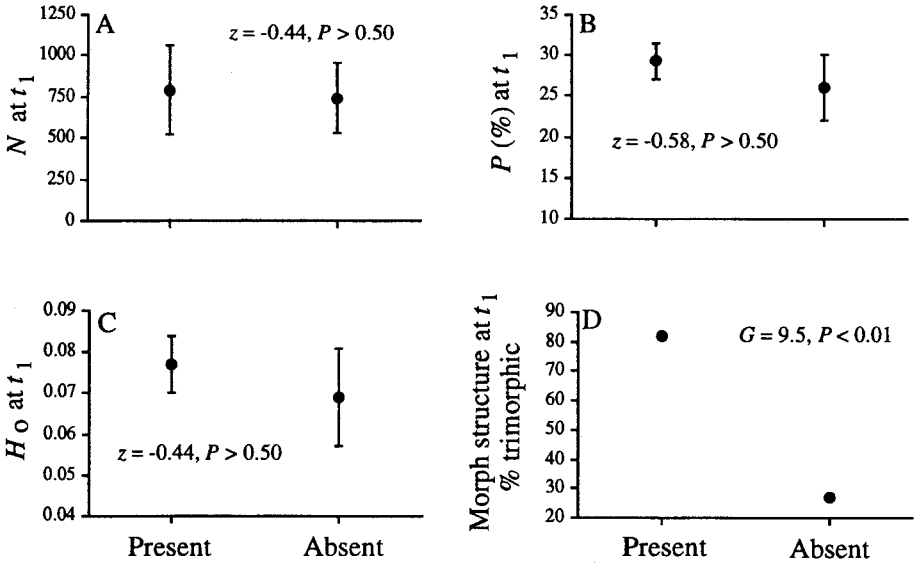

Figure 7. Comparisons of genetic variation in populations of *E. paniculata* in northeast Brazil that persisted over a 2-year period (n = 22) with those that were locally extirpated (n = 11). Parameters compared in the two groups of populations are the mean values in year 1 for **(A)** population size (N), **(B)** percent of allozyme loci polymorphic (P), **(C)** observed heterozygosity (H_o), and **(D)** percent of populations that were trimorphic. Statistical comparisons of **(A)**–**(C)** used nonparametric Mann-Whitney U tests, **(D)** involved a G test.

investigated in a variety of different organisms (reviewed in Nei and Graur 1984; Soulé 1976; Frankham R, unpublished manuscript). Most work on plants has involved rare and endangered species and trees (reviewed in Barrett and Kohn 1991; Ellstrand and Elam 1993). In most cases the data are consistent with theoretical predictions. Large populations maintain more genetic variation owing to the greater likelihood of genetic erosion in small populations due to drift (Bijlsma et al. 1994). Reports of a lack of association between population size and measures of genetic diversity in individual studies often result from low power due to the small number of populations examined. Because of the many ecological and historical factors influencing genetic variation within populations (see Hamrick and Godt 1990; Loveless and Hamrick 1984) a large sample of populations should ideally be examined.

We failed to detect a relation between population size and heterozygosity in *E. paniculata* from northeast Brazil. This is unlikely to be the result of a small sample size. Indeed our sample involving 49 populations and 24 allozyme loci represents one of the more extensive surveys of allozyme variability conducted in a plant species to date. The lack of association more likely results from ecological factors related to population size. The ephemeral nature of aquatic habitats occupied by *E. paniculata* in northeast Brazil results in considerable spatial and temporal variation in population size. Because of fluctuations in the size of populations from year-to-year a single census is of less value in reflecting effective population size. Years in which population sizes are low are considerably more important in determining future levels of variability and a single census is unlikely to capture this information. When we analyzed our data using the harmonic mean of population size, in which low census numbers are weighted more than high, a significant relation with heterozygosity was revealed. This is undoubtedly because this measure is a better predictor of effective population size than a point estimate of census number.

The two classes of genetic variation investigated in this study differ with respect to how selection operates on them. We assume that the polymorphisms at allozyme loci are either selectively neutral or are at most under weak selection (Lewontin 1974). In contrast, polymorphisms at the mating-type loci governing tristyly are under strong frequency-dependent selection (Barrett 1993). It is of interest to compare how these different classes of variation are affected by demographic factors. Because of the ease with which plants can be scored for mating type it was possible to survey all populations from which population-size data were obtained. While strictly speaking these surveys involve estimates of phenotypic as opposed to genotypic diversity, this should not affect comparisons because the relation between the phenotype and genotype in tristylous species is well known (Heuch and Lie 1985).

Both the census number in one year and the harmonic mean of population size were significantly correlated with stylemorph diversity. Large populations were more likely than small to be trimorphic and to contain floral morphs at similar frequencies. As with allozyme variation, the harmonic mean provided a more biologically useful measure of population size as judged by the smaller sample required to detect a significant relation. Theoretical studies on the maintenance of tristyly indicate that effective population sizes below 30 to 40 are required for genetic drift to overcome the frequency-dependent selection that maintains the mating polymorphism (Heuch 1980; Husband and Barrett 1992a,b). However, because N_e:N ratios in *E. paniculata* average approximately 0.10 (Husband and Barrett 1992a), many populations with census numbers above 40 are also likely to be influenced by genetic drift. This most probably accounts for the striking scatter of points in Figure 4a.

Notwithstanding the recent growth in metapopulation studies (reviewed in Gilpin and Hanski 1991; Hanski and Gilpin 1996; Hastings and Harrison 1994; Husband and Barrett 1996; McCauley 1993), little empirical work on plant populations has considered the distribution of populations across the landscape in accounting for the levels of genetic variation within local populations. After controlling for population-size effects we found a positive association between population density in a region and observed heterozygosity within a population. Populations occurring in areas of northeast Brazil with few other populations were significantly less heterozygous than those from regions with high population density. This result probably reflects differences in the intensity of gene flow among regions with contrasting population densities. Although measures of gene flow in *E. paniculata* are relatively low (see above), it would seem reasonable to assume that isolated populations would be more susceptible to genetic erosion through drift and inbreeding. Interestingly, regions of high population density also had a higher proportion of trimorphic populations compared to those with a low density of populations, suggesting the importance of gene flow in maintaining the tristylous polymorphism. A similar pattern has also been reported in native and introduced populations of tristylous *Lythrum salicaria* by Eckert et al.

(1996). Unlike H_o and style-morph diversity, P and A were not associated with the density of populations in a region. This result is not consistent with the expected role of drift in isolated populations and raises the possibility that inbreeding may be a more important factor influencing allozyme variation in isolated populations.

Comparisons between stable and bottleneck populations of *E. paniculata* failed to detect any influence of population-size reductions on genetic variation. Mean values for allozyme and style-morph polymorphisms were remarkably similar between the two classes of population. This result at first seems surprising but is interpretable when the data are considered in the light of theoretical expectations. While from an ecological viewpoint the bottleneck populations certainly experienced a sharp reduction in numbers (90% or more), from a genetic perspective the critical issue is what the minimum absolute size of the populations were after the bottleneck. In no case did the bottleneck populations crash to small enough numbers that a significant loss of variation would have occurred. Mean population size before and after the bottleneck in the five populations examined was 1,808 and 99.6, respectively. The minimum sizes were therefore more than sufficient to maintain most of the variation present before the bottleneck.

The genetic and evolutionary significance of population bottlenecks remains quite controversial. Some workers see them as playing a creative role in generating new sources of variation and stimulating evolutionary diversification, while others doubt that this occurs very often (Barton and Charlesworth 1984; Bryant et al. 1986; Bryant and Meffert 1995; Carson and Templeton 1984; Goodnight 1987, 1988; Willis and Orr 1993). Unfortunately most work on bottlenecks has involved theoretical studies or investigations on laboratory animals and few, if any, studies have documented the patterns of genetic variation before and after bottlenecks in natural plant populations. Most of the data for plants infers the occurrence of past bottlenecks based on low variation without historical information of the ecology or demography of populations (reviewed in Barrett and Kohn 1991).

Our results raise several issues concerning the ecology of population bottlenecks. Despite sharp reductions in population size in *E. paniculata* the minimum census number was not low enough to affect genetic diversity. In fact, relatively few of the sites in our entire sample were occupied by populations that had crashed to small enough numbers that significant losses in genetic variation would be likely. It is possible that in *E. paniculata* genetic bottlenecks more commonly arise by local dispersal and the founding of populations at new sites rather than through in situ population crashes. Certainly genetic bottlenecks associated with long-distance dispersal in the species are well documented (Glover and Barrett 1987; Husband and Barrett 1991). When catastrophic changes to local site conditions in northeast Brazil occur, their effect is most commonly the loss of entire populations rather than the limited survival of a few plants. It would be of interest to know the relative importance of catastrophic population crashes versus dispersal as causes of genetic bottlenecks for other plant species.

The censuses of population size in this study took no account of the potential occurrence of a seed bank in *E. paniculata*. This possibility could influence the interpretation of several of our results. For example, populations described as locally extirpated may in fact be capable of persisting through unfavorable conditions. Similarly, our estimates of bottleneck size would be underestimated if a significant seed bank were present in the populations we sampled. Our investigations to date suggest that seed dormancy in *E. paniculata* is not well developed (see above), however, we cannot discount the role of induced dormancy resulting from ecological factors in causing some seeds to persist in the soil over several growing seasons. While the presence of a significant seed bank increases population size, it is unclear to what extent this will influence effective population size. To our knowledge there has been little theoretical analysis of this problem for plant populations. In animals with overlapping generations where individuals only breed once, the effective population size increases in proportion to the average age at reproduction and the number of breeding individuals per season (Waples 1990). If one extends this result to plant populations it would imply that the difference between the census number and effective population size will depend on the persistence time of the average seed in the seed bank and the number of flowering plants observed. To what extent these considerations influence how demographic factors govern patterns of genetic diversity in *E. paniculata* awaits further investigation of the seed biology of the species.

The final problem we addressed concerned the general problem of the adaptive significance of genetic variation. Previous studies of *E. paniculata* in northeast Brazil have demonstrated that the local extirpation of populations is independent of their size or age (Husband and Barrett 1996, unpublished data). Given this finding, the present result, indicating that populations that persist from year to year contain similar levels of allozyme variation to those that are lost from a site, is not altogether unexpected. The demographic and genetic characteristics of ephemeral plant populations are likely to be largely irrelevant when catastrophic changes through flooding and human disturbance frequently occur. However, one pattern that did emerge from our analysis was the finding that tristylous populations were more likely to survive than those that were missing style morphs. This result suggests that the ecological conditions under which trimorphic and nontrimorphic populations occur may be different (and see Husband and Barrett 1993). Nontrimorphic populations contain selfing variants and it is possible that the environments colonized by these types of populations are less suitable for the persistence of the species. The association between selfing and ecological marginality has frequently been invoked to account for the evolution of self-fertilization in plants (Jain 1976; Lloyd 1980).

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