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Demography versus habitat fragmentation as determinants of genetic variation in wild populations

James P. Gibbs

State University of New York, College of Environmental Science and Forestry, 350 Illick Hall, Syracuse, NY 13210, USA

Abstract

A critical question in conservation biology concerns how loss of natural habitat affects the persistence of plant and animal populations and the distribution of genetic variation within them. In this study a simulation model was used to examine how primary demographic and habitat factors affect secondary population processes and thereby influence population genetic structure. The model revealed that both genetic diversity and divergence were most affected by the proportion of patches in a landscape that remain occupied, which in turn was affected primarily by patch disturbance frequency. Patch carrying capacity also controlled the density of individuals within patches and thereby influenced levels of diversity within populations. Habitat availability influenced dispersal success and thereby secondarily influenced genetic divergence among populations. This study emphasizes that conservation of genetic diversity in wild populations should be based on both habitat and population management and can best be achieved by maintaining healthy sized, local populations well-distributed among a network of infrequently disturbed habitats. © 2001 Published by Elsevier Science Ltd.

Keywords: Habitat fragmentation; Demography; Genetic diversity; Heterozygosity; Population subdivision

1. Introduction

Human activities increasingly fragment natural habitats and greatly alter the size, shape, and spatial arrangement of habitats for wild species (e.g. McLellan et al., 1986; Sader and Joyce, 1988; Dodson and Gentry, 1991). These properties of habitats affect extinction rates and sizes of local populations as well as dispersal patterns of individuals among local populations (Fahrig and Merriam, 1994). From a population genetics perspective, such changes can promote genetic drift in local populations if sizes of local populations are small enough to effectuate drift yet remain large enough to buffer populations against chance extinction (Lande, 1988). Such changes can also promote genetic divergence among local populations if habitat fragmentation substantially reduces gene flow among them (Whitlock and Barton, 1997). These outcomes are significant because prolonged drift can reduce heterozygosity and thereby lower population viability, via depression in a variety of fitness components (e.g. Lacy, 1993) and because reduced allelic diversity may constrain future adaptive evolution (e.g. Franklin, 1980).

For any given landscape and species, the effects of habitat fragmentation on patterns of genetic diversity in populations are difficult to predict because a complex suite of factors contribute directly and interact indirectly to influence the microevolutionary processes in local populations that ultimately generate the genetic structure of metapopulations. These factors relate broadly to a species' demography (e.g. density, sensitivity of demographic parameters to environmental variation, and dispersal ability) as well as to the structure of the landscape in which the species resides (e.g. the amount of habitat present, its configuration, and its temporal stability).

Many researchers have examined through field studies the effects that habitat structure can exert on genetic diversity in populations of many plant and animal taxa. Whereas a few studies have detected clear associations between population genetic structure and contemporary landscape structures (Hall et al., 1996; Hitchings and Beebee, 1998; Van Dongen et al., 1998), many others have not (Fore et al., 1992; Young et al., 1993, 1999; Ballal et al., 1994; Prober and Brown, 1994; Spencer et al., 1995; Fore and Guttman, 1996; Johannesen et al., 1997; Peacock and Smith, 1997; Cunningham and Moritz, 1998; Gibbs, 1998; Pope, 1998; Prober et al., 1998; Soejima et al., 1998; Von Segesser et al, 1999).

E-mail address: jpgibbs@syr.edu

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Thus, it is not clear the extent to which anthropogenic fragmentation of natural habitats can substantially alter the genetic structure of populations over the brief evolutionary time frames of a century or less that typically preoccupy land managers and conservation biologists. Furthermore, it is not clear whether a focus by managers on habitat management versus population management is of greater consequence for conservation of genetic diversity in wild populations.

In this study, I developed a spatially-explicit, individual-based model that incorporated essential components of species demography and landscape structure. The model examined how fundamental demographic and habitat factors (spatial autocorrelation of population processes, carrying capacity of habitat patches, dispersal ability of individuals, annual variation in population growth rates, habitat availability, and habitat disturbance frequency) affect secondary population processes (the fraction of patches occupied, density of individuals per patch, dispersal success, and dispersal probability) and thereby influence population genetic structure (heterozygosity and degree of genetic subdivision). My intent was to provide a comprehensive evaluation of the relative contributions that landscape structure makes in conjunction with demographic parameters toward structuring wild populations genetically over the short evolutionary time frames that preoccupy land managers.

2. Methods

Realistic models of population dynamics in complex landscapes should incorporate four components (Pulliam et al., 1992): (1) the extent of habitats within a landscape, (2) the temporal dynamics of habitat patches, (3) demographic processes within suitable habitat patches, and (4) dispersal processes among habitat patches. To this end, a spatially explicit grid model (cf., Fahrig, 1991) was developed in which the fates of individuals located in a gridwork of habitat patches were followed over time. Individuals possessed genotypes and were aggregated into 'local populations' within suitable grid cells or habitat patches. Individuals bred with other members of their local population and migrated if densities exceeded local carrying capacities. Landscapes were composed of varying amounts of suitable habitat disturbed at varying frequencies. Each demographic or landscape-related parameter was varied over a realistic range (Table 1) in an attempt to evaluate the genetic outcomes of changes in demographic processes within landscapes fragmented to varying extent.

In terms of model details, simulations were performed within a landscape subdivided into 10,000 units, with each unit consisting of either suitable habitat, which could support local populations, or unsuitable habitat, which could not. A random configuration of suitable habitats was assumed, with individual grid cells assigned as suitable or unsuitable based on whether a uniform random number drawn was less than the overall fraction of habitat sought for the landscape. Habitat turnover was simulated based on an annual probability that any individual habitat patch would transition from being suitable to unsuitable, or vice versa. Such transitions occurred if a uniform random number generated in any given year for a particular habitat patch was less than a given transition probability (Table 1).

All local populations (N) in each habitat patch were initially established at the same densities (at half carrying capacity) to mimic relative densities of rare versus common species (Table 1). Genotypes of individuals were based on a one-locus/two-allele system with simple Mendelian inheritance, with allele identities and sex initially assigned to individuals at random, based on a 1:1 allele and 1:1 sex ratio in local populations. Local populations were subsequently projected over 100 one-year (t) time intervals based on the relationship

$$N(t+1) = R(t)\cdot N(t),$$

where $R(t)$ = the population growth rate at time t. Lognormal distributions typically describe adequately the temporal variation that occurs in population growth rates (R) of populations (Burgman et al., 1993). Therefore environmental influences on population dynamics were modeled by annually drawing random values of $R(t)$ from a lognormal distribution defined by a mean = 1 with selected annual coefficients of variation (Table 1). Population increments were composed of offspring with genotypes drawn from random pairings of individuals within the local population (only if both sexes were present, otherwise no reproduction occurred), whereas population decrements were composed of dying individuals randomly drawn from the local population. Vacant local populations were recolonized if at least one male and one female disperser arrived and survived to breed. Spatial autocorrelation in population processes (Table 1) was modeled by applying the same random variate to population growth in all habitat patches at any given time step (perfect, positive spatial autocorrelation in demographic processes among local populations) or applying an independent variate for each patch at each interval (no spatial autocorrelation).

Carrying capacity (K) for each patch was set at a ceiling of 2× initial local population size (Table 1). Dispersal mimicked a density dependent process in which migrants each year were composed of individuals produced in excess of local carrying capacity of each local population. Each such individual migrated a randomly determined distance d based on a negative exponential dispersal function

$$m = \mathrm{e}^{-d/b}$$

Table 1
Primary demographic and habitat factors used in an assessment of their relative contributions to secondary demographic parameters (individual densities, population distributions, and migration) that are important determinants of population genetic structure

Demographic parameters	Levels
Carrying capacity of patches	Individuals per local population = 20 or 200
Annual variation in growth rate of local populations	Annual coefficient of variation in growth rate of local populations = 0.1 or 1.0
Dispersal ability of individuals	Average dispersal distance of individuals on migratory forays following random walks = 1, 10, or 100 patches
Spatial autocorrelation in annual variation in population growth rates	Local population dynamics across landscape completely synchronous or asynchronous
Habitat parameters	**Levels**
Extent of suitable habitat within landscape	Fraction of landscape composed of suitable habitat = 0.1, 0.2, 0.3, . . ., 1.0
Frequency of disturbance to habitats supporting local populations	Annual probability of habitat patch turnover 1/10 or 1/100 years

where b = average dispersal distance and m = the probability that the individual would travel as far as distance d (Wolfenbarger, 1946). Individuals moved on a random walk to adjacent or diagonal habitat patches over different average distances, b (Table 1). Individuals died that ended their migration foray in an unsuitable patch or in a suitable patch where $N \geqslant K$. Those ending in a suitable patch where $N < K$ were incorporated into the local population. Individuals encountering a grid edge changed directions to avoid leaving the grid (Fahrig, 1991).

Four demographic statistics were calculated each year and then averaged across each projection to characterize how the primary habitat and demographic factors influenced secondary population processes: the proportion of suitable patches that were occupied, the average density of individuals in occupied patches, the proportion of individuals that migrated, and the proportion of migrating individuals that successfully moved to a new patch. Two genetic statistics were also calculated at the end of the projection interval to describe levels of genetic diversity and divergence within the entire set of local populations remaining within the landscape. Levels of within-subpopulation diversity were indexed by observed heterozygosity, H_{SUB}, calculated as the proportion of individuals within each local population that possessed two dissimilar alleles, averaged over all extant local populations. Genetic divergence within the metapopulation was determined using Wright's (1965) "fixation index," or F_{ST}, which indexes the proportional reduction in local expected heterozygosity relative to global expected heterozygosity owing to variation in allele frequencies among populations.

All programming was done in Turbo Pascal 7.0 (Borland International, Scotts Valley, CA) with algorithms from Press et al. (1990). A single projection ($n = 1$) was made for each combination of levels of main effects (Table 1), with resulting values of patch occupancy, local density, migration probability and migration success subjected to a fixed-effects analysis of variance (Zar, 1984) to determine the contribution of each main effect to levels of each demographic variable. Relative contributions were measured by the fraction of the total mean square error in the final model accounted for by each main effect. Values of H_{sub} and F_{st} from each projection were subsequently regressed, using stepwise regression (Zar 1984, with the RSQUARE option of PROC REG in SAS, SAS Institute 1989), against values of the four demographic variables (patch occupancy, local density, migration probability and migration success) to examine the relative contribution of secondary demographic parameter to variation in H_{sub} and F_{st}. With this two-stage analysis I sought to integrate information across three levels, that is, to evaluate how basic habitat and demographic properties (the first level) influence those intermediate demographic processes (the second level) that in turn determine population genetic structure (the third level).

3. Results and discussion

This study attempted to identify the key interactions between landscape change, demographic processes, and population genetic structure. Notably, the analysis of variance (Table 2) indicated that each secondary demographic parameter was affected by distinctly different primary demographic and habitat factors. Patch occupancy was influenced primarily by patch disturbance frequency. More frequent patch turnover resulted in local extinctions of patches that often remained uncolonized because of limitations on dispersal within the metapopulation. Patch occupancy also was affected by patch carrying capacity, higher levels of which permitted increased densities of individuals within patches and buffered local populations from chance extinction. A third influence on patch occupancy was spatial autocorrelation of population processes. Years of low population growth that were synchronized spatially and temporally caused widespread local extinctions, depressed

Table 2
Relative contributions (% total mean square error explained, see Section 2) by primary demographic and habitat factors to variation in secondary demographic parameters of importance to population genetic structure

	Secondary demographic parameter			
Primary population or habitat factor	Occupancy	Density	Migration probability	Migration success
Spatial autocorrelation	12.4	3.3	18.6	3.6
Carrying capacity	16.1	91.2	0.3	0.0
Dispersal ability of individuals	2.0	0.0	0.0	1.9
Variation in population growth	0.0	0.0	78.0	40.2
Habitat availability	7.6	1.1	2.9	54.4
Habitat disturbance frequency	61.8	4.4	0.1	45.5

population sizes, and curtailed opportunity for recolonization in subsequent years of higher population growth.

In contrast, migration probability was primarily influenced by annual variation in population growth rates, such that "boom" years created excess individuals whereas "drought" years produced none to became migrants under the density-dependent migration scenario implemented, an effect that became pronounced when all patches were synchronized through spatial autocorrelation. Under more constant growth conditions mortality generally balanced recruitment within patches, yielding few migrants. The dispersal success of these migrants was most affected by habitat availability because abundant habitat provided an increased number of destinations for randomly orienteering migrants. Similarly, habitat disturbance and highly variable population growth rates created many vacant patches that could be colonized by dispersers, thereby increasing dispersal success independent of the number of dispersers present in the landscape. Density was almost entirely a function of patch carrying capacity, suggesting a relatively limited role for migration in sustaining population numbers independent of patch carrying capacity.

The model results suggest a major role for maintaining populations well-distributed throughout the landscape to minimize local homozygosity and the fitness reductions sometimes associated with it. H_{sub} and F_{st} were negatively correlated ($r = -0.51$), implying that high levels of subdivision do not serve, as has been suggested, to protect genetic variation within local populations but rather are associated more with processes that erode genetic diversity in local populations. The stepwise regression procedure indicated that the primary demographic determinant of levels of heterozygosity in local populations, explaining 44% of overall variation, was the fraction of patches occupied over time. A smaller, additional contribution to variation in heterozygosity was made by the density of individuals within patches (10%), whereas the two migration parameters accounted for little (<1%) additional variation in heterozygosity within patches. Degree of genetic subdivision was explained also primarily (36% of overall variation) by the degree of patch occupancy maintained over time. Smaller, additional contributions were made by dispersal success (9%), migration probability (4%), and average densities of individuals within patches (1%).

Together these simulations suggest the following primary interactions occur between demography, habitat fragmentation, and genetic variation in wild populations. Both H_{sub} and F_{st} were most affected by the proportion of patches in a landscape that remain occupied, which in turn was affected primarily by patch disturbance frequency. Patch carrying capacity also controlled the density of individuals within patches and thereby influenced levels of H_{sub}. Habitat availability influenced dispersal success and thereby secondarily influenced F_{st}. These results reemphasize the importance drift and gene flow processes associated with patch extinction-recolonization dynamics (e.g. McCauley, 1991; Lacy and Lindenmayer, 1995; Whitlock and Barton, 1997) as determinants of patterns of genetic diversity and divergence within wild populations.

The parameter space explored was independent of any specific spatial scale and therefore the results have implications for a variety of organisms and types of landscapes. The modeling approach used in this study was not, however, without limitations. First, the focus was explicitly on genetic diversity at the level of local populations, not allelic diversity at the metapopulation level, although the positive relationship that occurs between average levels of heterozygosity local populations and polymorphism in metapopulations (Gilpin, 1991) suggests that the study has implications for conservation of allelic richness in regional populations. Second, the levels of each parameter invoked in simulations were intended to reflect biologically reasonable ranges of variation for each. The final partitioning of variation among parameters is highly sensitive, however, to the specific levels of each parameter examined. Ranges of certain parameters may have represented extremes (e.g. spatial autocorrelation in population processes ranging from 0 to 1) whereas those of others might have been overly restrictive (e.g. carrying capacity could have well been increased to 1000/habitat patch and degree of variation in population growth rates could well have exceeded a coefficient of variation of 100% to be more representative of the demography of certain taxa, for example, insects). Nevertheless, the parameters were varied over biologically reasonable ranges and it is unlikely that changes in parameter values would have altered substantially the general conclusions from the analysis although the ranks of major contributing factors might well have changed. A third limitation of the modeling approach used was that no explicit mechanism for a feedback between population growth rate and genetic diversity within a local population was incorporated. The synergism between these factors is an important aspect of the 'extinction vortex' (Gilpin and Soulé, 1986) and, if included, likely would have exerted an effect on the partitioning of variance, most likely by enhancing the contribution of population density owing to its close association with inbreeding and genetic drift. Similarly, no explicit "edge effects" (cf. Esseen and Renhorn, 1998) on population viability were included in the model, which would likely enhance the influence of habitat availability on local population size and hence of drift processes that would affect population genetic structure. Habitat configuration also was not considered although it is unclear what effect, if any (see Fahrig, 1997), it might have exerted on the results. A final caveat is that the results presented are relevant only within the time frame evaluated, i.e. 100 years or the upper-limit of the time horizon typically governing decision-making by conservation agencies. Over longer time frames, the importance of habitat extent as a determinant of population genetic structure might well manifest itself increasingly once demographic influences on genetic processes had equilibrated.

I conclude that, over the short evolutionary time scales that preoccupy land managers and conservation biologists, genetic diversity in wild populations can best be conserved by maintaining healthy local populations well-distributed among a network of infrequently disturbed habitats. It is important to emphasize that certain habitat and demographic factors that are often under the control of land managers and conservation biologists do exert substantial influences on genetic diversity in populations and do so over very short evolutionary time periods. Thus, from the strict perspective of retaining genetic diversity in local populations, a practical focus on maintaining healthy patterns of abundance and distribution of individuals in the landscape (e.g. by preventing severe and widespread declines in local abundance and occurrence through overharvest) and reducing the frequency of human disturbance to local populations (e.g. by lengthening disturbance rotations of habitat patches and ensuring the stability of habitat remnants) may well be, in the short-term, as important as simply retaining large amounts of habitat distributed within landscapes. Clearly a focus on both habitat preservation and population management is needed to conserve genetic variation in wild populations.

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